SEASONAL CHARACTERISTICS OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN SOUTHEASTERN ALASKA

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SEASONAL CHARACTERISTICS OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN SOUTHEASTERN ALASKA

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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 breeding grounds was 39 days, indicating that the stay on the feeding grounds may be longer than previously thought. Generally, reproductive rates did not vary from a breeding cycle of one calf every two or three years; individual variation in birth intervals 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.

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INTRODUCTION

Five species of mysticete or baleen whales have frequented the waters of southeastern Alaska within historic times. The rorquals, family Balaenopteridae, were the most numerous. These were the humpback whale, *Megaptera novaeangliae*, fin whale, *Balaenoptera physalus*, and minke whale, *Balaenoptera acutorostrata* (Davidson, 1869; Andrews, 1909). The northern right whale, *Eubalaena glacialis*, (family Balaenidae) was also present throughout the summer (Davidson, 1869; Townsend, 1935; Berzin and Doroshenko, 1981; Scarff, 1986), and the gray whale, *Eschrichtius robustus*, (family Eschrichtiidae) was present in the spring and fall, during its northward and southward migrations (Pike, 1962; Braham, 1984).

Humpback whales are present throughout the oceans of the world. They are thought to be fourth in rank of the most numerically depleted large whales in the world today, just behind the northern right whale, blue whale (*Balaenoptera musculus*), and bowhead whale (*Balaena mysticetus*). The current worldwide population is about 10% of the initial pre-whaling population, which has been estimated at more than 125,000 individuals (NMFS, 1991). In 1973, the United States Congress passed the Endangered Species Act and classified the humpback whale as an endangered species. The North Pacific population is thought to be increasing, but its recovery is slower than predicted (Johnson and Wolman, 1984).

The pre-exploitation number for North Pacific humpback whales was estimated by Rice (1978) as about 15,000, which was approximately 12% of the estimated worldwide pre-whaling population. Some 28,000 North Pacific humpback whales were taken between 1905-1965. They have been protected from worldwide commercial whaling by the International Whaling Commission since 1966. The current population is thought to number around 1,200 (Berzin and Yablokov, 1978; U.K., 1979; Rice and Wolman, 1982). Approximately 500-600 humpbacks are thought to be present on their historical feeding grounds in southeastern Alaska today (Baker *et al.*, 1992).

In this thesis, I describe the seasonal distribution, numbers, movements, and productivity of humpback whales in one of the three described feeding areas of the North Pacific. The goal of this analysis is to further the understanding of the North Pacific humpback whale, as an aid to management of the recovery of this species.

Natural History of North Pacific Humpback Whales

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, and the Russian Far East (NMFS, 1991). 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.

North Pacific humpback whales breed in the warmer, lower latitude waters of western Mexico, Hawaii, and the Ryukyu and Ogasawara islands (Herman and Antinoja, 1977; Rice and Wolman, 1978; Urban and Aguayo, 1987; Darling, 1991). Other possible Asian breeding grounds are the waters southwest of Okinawa, southeast of Taiwan, and southeast of the Ogasawara Islands to the Mariana Islands, which were areas used by humpback whales in the past (Tomilin, 1957; Nishiwaki, 1959, 1960, 1962).

Prior to the prohibition of humpback whaling in 1966, information about the biology and physiology of this species was acquired through the efforts of biologists on whaling ships and at shore-stations. Since then, significant gains in the understanding of the natural history and biology of the humpback whale have been made through longitudinal observational studies by independent biologists. Nonetheless, much remains to be learned about many basic biological questions.

The humpback whales that feed in the eastern North Pacific constitute feeding aggregations that are essentially discrete and geographically isolated. For example, there is no known exchange of individuals between the feeding area that extends from California to Washington and the feeding areas in Alaska (Baker *et al.*, 1986; Calambokidis *et al.*, 1989, 1993, in preparation; Perry *et al.*, 1990). One whale was observed in British Columbia and southeastern Alaska in different years (Darling and McSweeney, 1985). Intensive studies of humpback whales in northern British Columbian waters were begun in 1992 by the Pacific Biological Station, Nanaimo, BC, Canada (G. Ellis, personal communication). Since then, three individual whales have been matched between northern British Columbia and southeastern Alaska (G. Ellis and J. Straley, unpublished data). Within Alaska very little exchange has been documented between Prince William Sound and southeastern Alaska (Baker *et al.*, 1986; von Ziegesar and Matkin, 1989; Perry *et al.*, 1990; J. Straley, unpublished data).

The whales that feed in Prince William Sound and southeastern Alaska intermingle while on the breeding grounds in Hawaii. These are the primary breeding grounds for Alaskan humpback whales, but a few (seven) Alaskan whales have been observed in the waters of Mexico (Darling, 1983; Darling and Jurasz, 1983; Baker *et al.*, 1985, 1986; Darling and McSweeney, 1985; J. Urban, personal communication). The California, Oregon, and Washington feeding aggregation primarily migrates to Mexican waters for breeding purposes, with an occasional individual south to Costa Rica or west to Hawaii (Calambokidis *et al.*, 1989, 1993; Perry *et al.*, 1990; Steiger *et al.*

1991). The whales inhabiting the feeding area in the Bering Sea, near the eastern Aleutian Islands, have been linked with the Asian breeding ground near Japan, as indicated by observations by Soviet scientists and Japanese whale marking studies (Berzin and Rovnin, 1966; Nishiwaki, 1966; Ivashin and Rovnin, 1967; Ohsumi and Masaki, 1975). The migratory destinations of humpbacks feeding in the western Gulf of Alaska are not yet fully understood.

Exchange between the breeding grounds in Mexico and Hawaii, and between Hawaii and Japan, has been confirmed by observations of the same individual whales seen in these different areas. There have been eight whales resighted in both Mexican and Hawaiian waters. Seven of these were seen in different years in either Hawaii or Mexico (Darling, 1983; Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.*, 1986; Perry *et al.*, 1988; J. Urban, personal communication); one individual appeared first in Mexican waters and then, seven weeks later, in Hawaii (J. Urban, personal communication; Pacific Whale Foundation, unpublished data). One whale sighted near the Ogasawara Islands of Japan was resighted the following year in Hawaii (Darling and Cerchio, 1993). Research on the Asian breeding grounds has been underway only since 1987, and researchers in different regions have just begun to compare their findings.

Traditionally, humpback whales have been considered to exist as separate geographical stocks. The definition of a stock or population has been a confusing term for years, however, mostly due to the lack of knowledge concerning migratory destinations of specific groups of humpback whales. For example, Kellogg (1929) and, later, Tomilin (1957) and Berzin and Rovnin (1966) designated two stocks for the North Pacific, American and Asian, based on eastern and western North Pacific breeding areas. Apparently, the Hawaiian mid-Pacific breeding area was either unknown or unidentified at that time. Slowly, a clearer picture defining these stocks is emerging from longitudinal resighting studies. It is likely that one stock exists for the North Pacific, as proposed by Baker (1985) and Darling and McSweeney (1985), with intermingling and genetic exchange occurring among the three main breeding grounds.

Southeastern Alaska Feeding Aggregation

The largest known humpback whale feeding aggregation in Alaskan waters is in the southeastern part of the state. Humpback whales have been seen there in all months of the year (Straley, 1990a); peak numbers occur during late summer (Baker *et al.*, 1985). Seasonal shifts in the distribution of these whales also have been observed. Whales have been documented to arrive during the spring and early summer in the Icy Strait and Glacier Bay area, where they feed on schooling fishes. They then travel southward to Frederick Sound and Stephens Passage in late summer and feed on euphausiids (Andrews, 1909; Wing and Krieger, 1983; Krieger and Wing, 1984, 1986; Perry *et al.*, 1985; Dolphin, 1987a, 1987b; Baker *et al.*, 1992). They continue to feed in this area throughout the fall and early winter (Baker *et al.*, 1985, 1992; Straley, 1990a). A few whales have been observed in reverse transit in late summer, from Frederick Sound and Stephens Passage to Icy Strait and Glacier Bay (Baker *et al.*, 1992).

Individual humpback whales have been documented to remain in southeastern Alaskan waters for more than 6 months. The longest known stay was 192 days (Baker *et al.*, 1992). Whales remaining during the fall and early winter, just prior to the southward migration, were not segregated by age or sex (Straley, 1990a). This lack of segregation differs from findings of researchers studying migrating South Pacific and Indian Ocean humpback whales (Chittleborough, 1958; Dawbin, 1966) and western North Pacific humpback whales (Nishiwaki, 1959, 1960, 1962, 1966).

Group size and composition of adult humpback whales present in southeastern Alaska during 1981 and 1982 were analyzed by Baker (1985). Group size was found to vary from 1 to 10 whales and was not random, for singles and large groups were seen more frequently than expected. Group size often was associated with prey type; zooplankton attracted single whales, and the larger groups were feeding on schooling fishes. When a calf was present, the predominant group size was two, the mother and calf. These groups seldom and only briefly associated with other groups containing a calf. Most associations between members of a group were transitory, but repeated affiliations between whales occurred across seasons and years for some individuals (Baker, 1985).

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 reproductive rate of 0.36 calves/year (a birth interval of 2.8 years) was calculated for females in southeastern Alaska, during the years 1981-86 (Baker *et al.*, 1992). Historical pregnancy rates derived from anatomical whaling data, range from 0.37-0.47 calves/year (Omura, 1953; Nishiwaki, 1959; Rice, 1963; Chittleborough, 1965). These historical data reflect pregnancy rates because the females examined were killed during the migration just prior to parturition. This differs from longitudinal observations where data are gathered from sightings of females with calves, and the reproductive rate reflects the number of successful births, not how many females were pregnant. After the mid-1930s, capture of females with calves was prohibited; therefore, the historical data excluded observations of annual reproduction, because it would have been the postpartum females that successfully ovulated and conceived to have annual reproduction. Humpback whales studied in the North Atlantic from 1979-87 yielded a mean reproductive rate of 0.41 calves/year (Clapham and Mayo, 1990). These longitudinal studies in the North Pacific and North Atlantic have shown that there is considerable individual variability in the birth interval of female humpback whales, ranging from one to four years. Analyses of pregnancy rates in southern baleen whales also showed a high degree of variability from year to year (Mizroch, 1983). Mizroch suggested that the reproductive rate is directly linked to availability of food rather than being a reflection of density-dependence. Baker *et al.* (1987) argued that the apparently lower reproductive rate of 0.37 calves/year for southeastern Alaskan female humpback whales during 1980-85, although not statistically tested, demonstrated that these females are not currently reaching their reproductive potential. Reproductive rates and birth intervals will give some indication as to the recovery of this population, but calf survival and eventual recruitment of these offspring into the population will ultimately determine the recovery status of humpback whales in the North Pacific.

Age at first birth was eight years for one humpback whale in the North Pacific (Gabriele, 1992a). Additional observations of known-age whales, first seen as calves and later with their own calves, will be necessary to determine a more precise age at first birth for the North Pacific.

North Atlantic, South Pacific, and Indian Ocean humpback whale data have shown five years to be the average age at sexual maturity there (Chittleborough, 1958, 1959; Robins, 1960; Clapham and Mayo, 1987a; Clapham, 1992).

Feeding behavior has been categorized as subsurface and surface. Subsurface feeding is that in which whales dive and presumably feed on a prey layer at depth. Surface feeding includes flick, echelon, vertical, and horizontal lunge-feeding (Jurasz and Jurasz, 1979; Baker and Herman, 1984; Baker, 1985; Straley, 1990a), each of which involves some process to assist in bringing prey to the surface or in corralling them near the surface prior to ingestion. Lunge-feeding often is preceded by creation of a clockwise bubble-net, which is a series of bubbles blown at depth to assist in herding the prey to the surface. Flick and echelon feeding utilize body motion and positioning to aid in corralling surface-swarming prey. The principal kinds of prey for humpback whales in southeastern Alaska have been identified as euphausiids (primarily *Thysanoessa raschii*, with lesser amounts of *Euphausia pacifica*, *Thysanoessa longipes* and *Thysanoessa spinifera*), capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), and Pacific herring (*Clupea harengus pallasi*) (Andrews, 1909; Bryant *et al.*, 1981; Wing and Krieger, 1983; Krieger and Wing, 1986; Dolphin, 1987a, 1987b; Straley, 1990a).

Previous studies on humpback whales in southeastern Alaska focused primarily on two areas, the Glacier Bay-Icy Strait and the Frederick Sound areas, during the years 1974 to 1986 (Jurasz *et al.*, 1981; Jurasz and Palmer, 1981; Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.* 1985, 1990, 1992; Dolphin, 1987a; 1987b; Glacier Bay National Park, unpublished data, 1981-86). These studies made important contributions to the knowledge of this species, but humpback whales are present in large numbers in other areas. This fact complicates the present understanding of the biology and natural history of the humpback whale in southeastern Alaska. The objectives of this research on humpback whales 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, reproductive rates, calf survival, and recruitment. This thesis will expand on the current knowledge of humpback whales and assesses the distribution and population characteristics of humpback whales across seasons and years for seven study areas of southeastern Alaska, primarily from 1985-1993 and including data from earlier years (1976 to 1984).

METHODS

Study Areas

The study was conducted in southeastern Alaska, which is an extensive archipelago with a complex network of 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-Salisbury Sound. Other areas, including Lisianski Inlet, Chatham Strait, Peril Strait, and Ulloa Channel near Bucareli Bay, were used occasionally.

Glacier Bay is a large, recently deglaciated fjord system entering the northern edge of Icy Strait. Icy Strait is the northernmost entrance to the inside waters of southeastern Alaska. Frederick Sound is centrally located within the archipelago and is a confluence of two major waterways, Stephens Passage, and Chatham Strait. Seymour Canal is a long, narrow fjord along the eastern side of Admiralty Island, connecting with Stephens Passage to the south. Sitka Sound and Salisbury Sound are two principle entrances to the inside waters of southeastern Alaska and are bounded by Baranof, Kruzof, and Chichagof islands. Lisianski Inlet is a narrow inlet, just south of Glacier Bay, in the northwestern corner of Chichagof Island. Ulloa Channel, the southernmost study area in southeastern Alaska, is bounded by

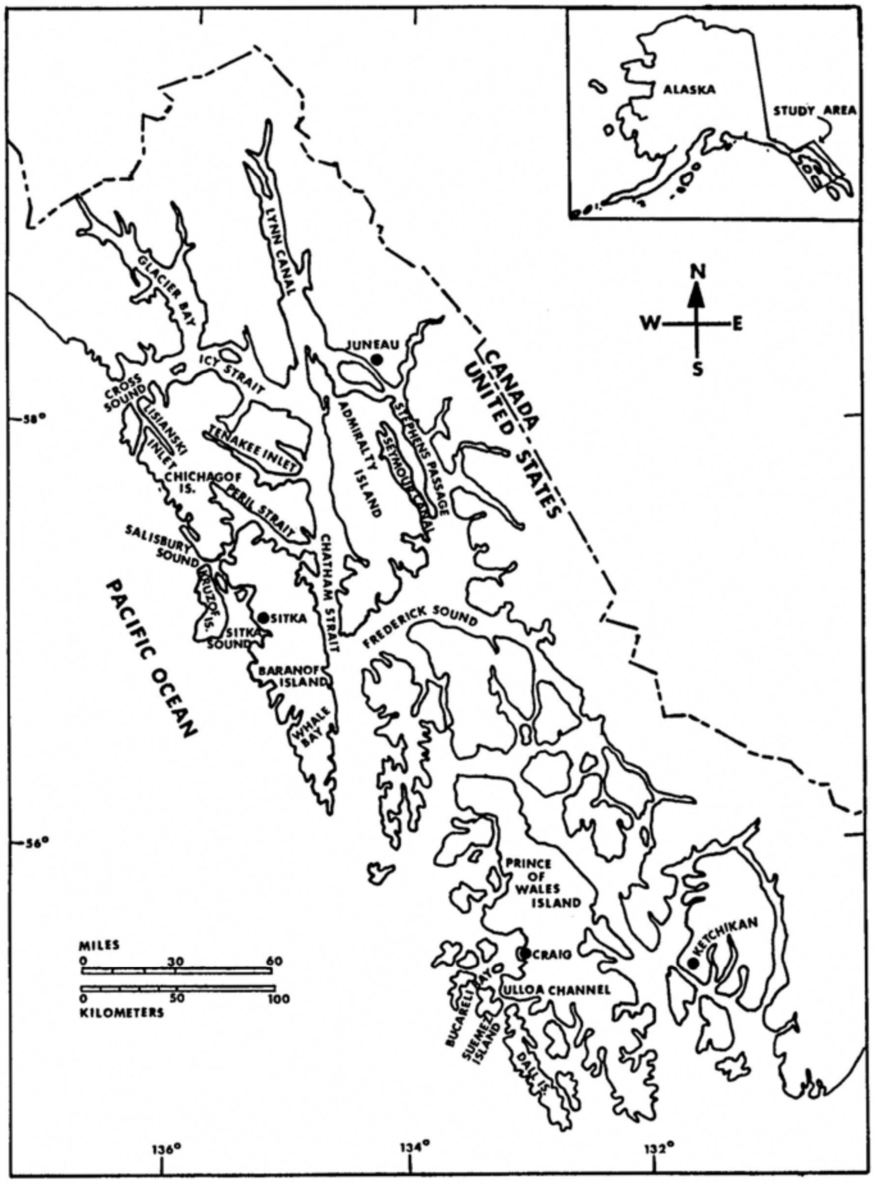

Figure 1. Map of southeastern Alaskan study areas.

Prince of Wales, Suemez, and Dall islands. Icy Strait, Lisianski Inlet, Salisbury Sound, Sitka Sound, and Ulloa Channel are transition zones between the waters of the archipelago and the Gulf of Alaska. As such, these areas are exposed to rougher seas and more severe weather than the inside waters of Glacier Bay, Peril Strait, Chatham Strait, Frederick Sound, Seymour Canal, and lower Stephens Passage.

Vessel Surveys and Dates

This study was conducted from November 1979 to January 1993 (Table 1) with some additional 1976 to 1984 data obtained from unpublished documents (Table 2) and published reports (Baker *et al.*, 1987).

Glacier Bay-Icy Strait

The data collected from this area were obtained in the course of monitoring humpback whale distribution and numbers for the National Park Service (NPS), Glacier Bay National Park and Preserve (GBNP&P), during the years 1985 to 1992 (Vequist and Baker, 1987; Baker and Straley, 1988; Straley, 1989, 1990b; Gabriele, 1991, 1992a).

The whales were observed and photographed from a 5.1m fiberglass skiff, powered by a 50hp or 60hp outboard engine. Surveys were conducted during one to three days per week from May or June to September and in either October or November each year (Table 1).

Table 1. Humpback whale study periods and study areas in southeastern Alaska.

YEAR	GLACIER BAY/ICY STRAIT	FREDERICK SOUND/SEYMOUR CANAL	SITKA SOUND	SALISBURY SOUND	CHATHAM STRAIT	LISIANSKI INLET	ULLOA CHANNEL	PERIL STRAIT
1979		18 NOV- 07 MAR 80						
1980		18 NOV- 07 JAN 81	08 OCT- 16 NOV					
1981		18 NOV- 04 DEC	14 DEC- 19 DEC					
1982		23 NOV- 10 DEC	30 JUL- 23 JAN 83					
1983		08 NOV[1]	06 NOV- 06 FEB 84				03 JAN- 05 JAN 84	
1984			18 JUN- 20 DEC					
1985	04 JUN- 04 SEP	29 AUG- 09 DEC	15 JUN- 21 NOV		20 JUN 29 JUL			07 SEP
1986	22 MAY- 01 SEP	31 JUL- 10 DEC	04 APR- 22 DEC		29 NOV			
1987	09 MAY- 28 SEP	21 AUG- 10 SEP	30 MAR- 08 JAN 88		22 JUN- 23 JUN			
1988	01 JUN- 25 SEP	02 AUG- 05 AUG	28 MAR- 05 FEB 89		01 AUG- 06 AUG			
1989	17 MAY- 25 NOV	27 NOV- 06 DEC	12 APR- 22 FEB 90					
1990	19 MAY- 16 OCT	09 JUL- 25 JUL	08 MAY- 03 JAN 91		15 JUN- 26 JUL			
1991	21 MAY- 15 SEP	11 AUG- 13 AUG	19 JUN- 06 FEB 92	07 AUG- 07 DEC	08 AUG- 11 AUG	26 DEC		04 AUG 08 AUG
1992	20 MAY- 02 SEP	03 AUG- 01 SEP	06 APR- 27 JAN 93	30 JUN- 12 NOV	01 AUG- 01 SEP			01 AUG- 01 SEP

[1]Aerial survey only

The daily survey routes in Glacier Bay were determined on the basis of whale sightings reported that day to the NPS' Bartlett Cove Visitor Information Station. If whales were not reported on that day but were reported on the previous day in an area not surveyed for two or more days, then the latter area was surveyed. If whales were not reported, and none had been reported the previous day, a semi-systematic route was followed in the lower bay, mid-bay, or upper bay. Surveys were not conducted in the same area on consecutive days, unless the whales that were present had not been photographed during the previous day's survey.

In 1976 to 1982 and in 1984, data were collected with NPS funding and under the direction of two other research groups: SeaSearch, Juneau, AK (1976 to 1980) and University of Hawaii, Honolulu, HI (1981, 1982, and 1984). NPS collected data during 1983. The study periods in 1976 to 1984 were of shorter duration (Table 2), and the methods were less consistent than in 1985 to 1993.

Table 2. Humpback whale summer study periods for the Glacier Bay-Icy Strait area, 1976-1984 (from Vequist and Baker, 1987).

1976	1977	1978	1979	1980	1981	1982	1983	1984
23 JUN- 01 JUL	12 JUN- 20 JUL	16 JUN- 07 JUL	23 JUN- 27 JUL	11 JUN- 02 AUG	14 JUL- 23 JUL	12 JUL- 15 AUG	16 JUL- 15 SEP	03 JUL- 12 SEP

The data collected from 1976 to 1984, were available from unpublished documents (Jurasz *et al.*, 1981; Vequist and Baker, 1987) and published reports (Baker *et al.*, 1987). The data from GBNP&P are used in this thesis with NPS permission. The data gathered up to 1979 were used only to extend sighting histories of two whales later identified as females. After 1979, the data were more complete, hence more useful for extending sighting histories of females for determination of birth intervals, reproductive rate, sexual maturity, and age; but not complete enough to be used in estimates of population size for the Glacier Bay-Icy Strait area.

Other areas

Survey efforts in the other areas were irregular and opportunistic. Efforts were often sporadic during the fall and winter, due to unfavorable weather and limited daylight (maximum 4hr/day useable light). On average, fall and winter work on the water was possible on one day in three.

Fiberglass, inflatable, and aluminum skiffs were used as survey vessels, ranging in size from 3.9m to 6.9m and powered by 25hp, 35hp, and 75hp outboard engines. Larger vessels (9.6m to 18.0m) were used as living platforms for surveys in Chatham Strait, Peril Strait, Frederick Sound, and Seymour Canal in 1985 to 1991 and for the Salisbury Sound survey in December 1991. The 1986, 1987, and 1988 summer Frederick Sound and Seymour Canal surveys were conducted from a 6.6m stern-drive vessel, and they began and ended in Juneau. Prior to 1985, surveys in Frederick Sound and Seymour Canal were primarily shore-based with occasional use of a 9.6m vessel.

The surveys in Peril Strait, Chatham Strait, and Stephens Passage were accomplished from 6.6m to 18m vessels while en route to Frederick Sound and Seymour Canal from Sitka or Juneau. The winter surveys in Lisianski Inlet and Ulloa Channel were brief and were conducted from a shore-based skiff.

Survey routes in Sitka Sound, Frederick Sound, lower Stephens Passage, and Seymour Canal were determined on the basis of reports via short-wave radio, telephone, and personal conversations from charter boat operators, pilots, fishermen, and whalewatchers. These people were contacted prior to or during each survey and requested to report the location of recent whale sightings. The sighting information was then used to plan the day's survey route. When no whales were reported, the day's survey route began where the previous day's survey had ended or where whales had previously been sighted.

<u>Photo-identification</u>

Individual humpback whales were identified from photographs of natural markings on the ventral surfaces of their flukes (Katona *et al.*, 1979).

Examples of the black and white photographs of humpback whale flukes used for identification purposes in this study are illustrated in Figure 2. Whales were approached slowly and cautiously from behind, at a steady speed of 1 to 4kt, beginning at a distance of 400m. Photographs were taken when the boat was positioned 10m to 30m directly behind the whale. A 35mm SLR camera (Olympus OM-1, Canon A-1 or Nikon 8008), equipped with a motordrive or winder and a 70-210mm or 300mm lens, was used to take the photographs. High speed black and white film (400 ASA, exposed at 800 or 1600 ASA) or color slide film (200 or 400 ASA) was used in the camera. Failure to photograph a whale was primarily due to the flukes not being shown, rough seas, or interruption of the encounter by a close approach of another vessel. If a photograph of the flukes was not obtained, a dorsal fin photograph was taken instead, if possible. This required a parallel approach to within 8m to 15m of the left or right side of the whale. An attempt was made to photograph both sides of the whale, but if only one side was available, the left was preferred to maintain consistency in data collection.

When more than one pod or group of whales was encountered, the number of whales in view was estimated from a distance. The pods were then approached, one by one, beginning from the closest pod and working

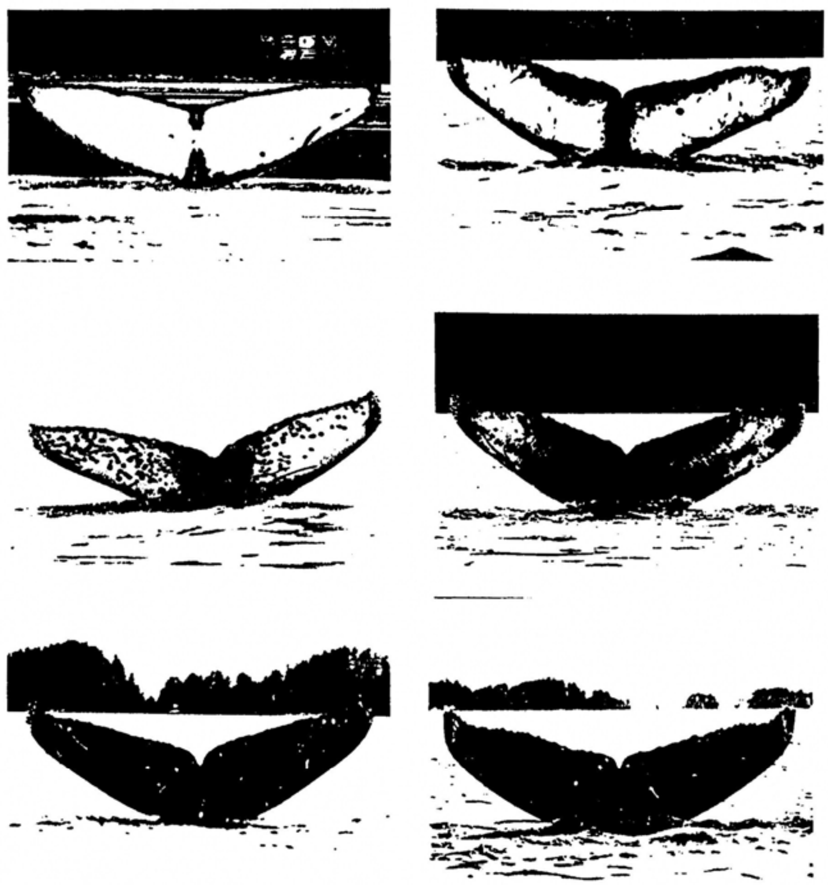

Figure 2. Examples of black and white photographs of the flukes of humpback whales. The distinctive characters useful for identification purposes are evident.

toward the farthest-away pod. While approaching one pod, the other pods were monitored as to their position and movements. Not more than one hour per day was devoted to any individual whale. All observations were made during the day, except on a few occasions when humpbacks were observed at night from a 9.6m vessel in Seymour Canal during the late fall and early winter.

The field data were recorded on waterproof notebook paper. Each day, the date, film roll number, weather, sea conditions, survey route, and reports from other observers were recorded. Time of departure and subsequent noteworthy times, such as stops, beginning and end times, and locations of pod encounters were listed. Pods were numbered consecutively (Pod 1, Pod 2, etc.) each day. Pod composition was noted, and each whale in the pod was given an alphabetical letter (A, B, C, etc.). A sketch of the flukes, dorsal fin, and distinct markings (scarring, wounds, etc.) was done for each whale, and the frame number for each corresponding photograph was noted near the sketch. The time of the end of the survey was recorded, and a preliminary tally of the number of whales approached and photographed was noted. Daily locations of whales and the survey routes were marked on charts and copies of United States Geological Survey (USGS) topographic maps used for the fall and winter Frederick Sound, Seymour Canal, and Ulloa Channel surveys.

Prior to 1988, all film was processed by a standard commercial photographic laboratory. Beginning in 1988, only black and white film was used and "push-processed" by Panda Lab, Seattle, WA, using a method developed by Elwood Miles, Nanaimo, BC, Canada (Miles, 1990). A 21.6cm x 27.9cm contact sheet was printed for each roll of film.

The black and white contact sheets and slides were used for preliminary data analyses. Each roll of film and slide was labelled with the film roll number, date, and location Each frame number was then labelled with the corresponding data obtained from the field notes. A print was made of the clearest photograph of each individual whale each year and the film roll number and frame number, date, whale identification number, and location were written on the photograph.

Each photograph was first compared with those in my reference catalog of fluke photographs from previous years, and then compared with photographic collections made available by other research groups in the North Pacific (i.e., Kewalo Basin Marine Mammal Laboratory, North Gulf Oceanic Society, and Ogasawara Marine Center). Primarily, comparisons were made with photographic collections of whales from Prince William Sound (von Ziegesar, 1992) and Hawaii, through the collection at Kewalo Basin Marine Mammal Laboratory (KBMML) at the University of Hawaii Manoa (Perry *et al.*, 1988). Photographs of individual whales seen each year also were filed with the North Pacific Humpback Whale Working Group catalog at the National Marine Mammal Laboratory (NMML), Seattle, WA.

Resighting of a whale was confirmed when two or more photographs showed the same black and white pattern on the flukes, and the same trailing edge and other distinctive markings were identical. Marks can be added to the black and white pattern, but rarely does a mark fade or disappear. Dark marks may be added to predominately white flukes, and white marks may be added to dark flukes. Such "marks" include lines, circles, and spots. Nicks can be added to the trailing edges, and sometimes, fluke edges and tips can become lost or eroded. If any ambiguity exists with a potential match-up of photographs, two trained observers are asked for their independent opinions. Total agreement is required for photographs to be identified as a match. Sometimes a possible match between two photographs will remain questionable until a third photograph is found that verifies the match.

Every fluke photograph has a unique film code. The film code designates area (e.g., SC = Seymour Canal, SS = Sitka Sound, GB = Glacier Bay-Icy Strait, etc.), year, film roll number, and frame number. The film code offers an initial determination of where and when the photograph was taken. When a whale was resighted (as confirmed by matching with a previous photograph), I gave the whale a permanent identification number;

otherwise, it was identified by its unique filmcode. Prior to 1986, I used the same permanent identification numbers issued by the University of Hawaii research group, because I was working in close collaboration with the KBMML researchers working in Alaska, and we were observing many of the same whales. These numbers range from 1 to 949. After 1986, I issued my own permanent identification numbers (higher than 949) to my catalog. Glacier Bay National Park humpback whales also were given permanent identification numbers in the same way: prior to 1986, they were the same as KBMML (1 to 949); since 1986, they have been numbers higher than 949. I was curator of the Glacier Bay National Park catalog for the years 1986 to 1990 and, for those years, identification numbers (from 950 to 1054) were the same as those in my catalog. After 1990, the permanent identification numbers (over 1055) in the NPS catalog were different from mine.

Times and locations of all sightings of each whale during a given year were compiled and then added to the long-term sighting history of that whale. Nearly all whales used in the present analyses, except for some calves, were photo-identified; visually identified whales were rarely included. The use of visually identified whales was allowed only when the pattern on the flukes was very distinctive. Every attempt was made to photograph both the flukes and dorsal fin of calves. Sometimes this was not possible, due to the protectiveness of the mother or the behavior of the calf (e.g., evasive, not showing the flukes upon diving, difficult to follow due to fast movements).

Photographs of the flukes were rated as "good," "fair," or "poor" quality, based on sharpness, contrast, and fluke angle. Good and fair photographs showed 50% of the flukes at an angle sufficient to show the shape of the trailing edge, the outline of which also was used as a natural, individual, identification "tag." Poor quality photographs and photographs of the flukes of calves were excluded from analysis involving resighted individuals in estimates of population size. The natural markings on calf flukes sometimes change, and unless the annual evolution of the pattern can be followed, identification may be difficult.

Determination of Reproductive Status, Age, and Sex

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 4-8m) 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 all whales known to be more than five years old, which has been determined as the average age at sexual maturity in the North Atlantic, South Pacific, and Indian Ocean (Chittleborough, 1958, 1959; Nishiwaki, 1959; Robins, 1960; Clapham and Mayo, 1987a; Clapham, 1992).

There is little sexual dimorphism in humpback whales. A small difference in size, with the female slightly larger than the males, is the only distinguishing characteristic between the sexes. A few calves were identified to sex by photographing the genital region while the calf rolled or flipped onto its back (True, 1904; Matthews, 1937; Glockner, 1983). Gender has been determined for some southeastern Alaskan humpback whales also through skin biopsy and cytogenetic analysis (Lambertsen *et al.*, 1988; Baker *et al.*, 1990; C. Baker, personal communication). Whales sighted at anytime accompanied by a calf were assumed to be females. Sexual maturity was determined from the year of the first pregnancy, which was the year prior to the first sighting with a calf.

Reproductive rates were measured by two methods. The first was the calving rate, which was the number of calves present each year divided by the sum of the known sexually mature females observed in that year. This proportion is considered to be the maximal calving rate for that year, because females for which gender and sexual maturity had not yet been confirmed were excluded from the calculation. The maximal calving rate across all years was calculated by dividing the total sightings of females with calves by the total sightings of known sexually mature females for all years. The minimal calving rate per year was calculated on the basis of all known females sighted in a given year, including those for which sexual maturity had not yet been established. Some of those females may have been immature. The minimal calving rate across all years was calculated by dividing the total sightings of females with calves by the total sightings of females for all years.

The second method for measuring reproductive rates was by determining the birth interval, which was defined as the number of years between successive calving events for each female For example, if an animal was seen in 1985 with a calf, in 1986 without a calf, and in 1987 with a calf, the birth interval would be two years. Only females with complete sighting histories during at least one birth interval were used for this calculation. That is, a whale had to be seen every year between the years when sighted with a calf. If a female was observed during two or more birth intervals, her mean birth interval was calculated.

Statistical Analyses

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 all of the study areas of southeastern Alaska combined. These sighting matrices summarized the numbers of adult humpback whales photo-identified each year and provided the basis for the "capture-recapture" data analyses. The "recaptured" whales were those sighted and photographed in previous years and resighted in the given year. 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, I calculated the sum of newly sighted whales across all years, which is a minimal estimate of the total number of individuals using the area. In addition, a sighting matrix was developed for data previously reported by Baker *et al.* (1992) from these same study areas of southeastern Alaska during 1979 to 1986.

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 annual estimates of population size, survival rate, the probability of capture, and the number of new animals (immigrants) that entered the population, based on the sighting matrices developed for each study area and the matrix developed from the data reported by Baker *et al.* (1992). Program JOLLY uses a series of open population models for multiple capture-recapture data (Jolly, 1982; Brownie *et al.*, 1986), based on the basic Jolly-Seber capture-recapture model (Seber, 1982; Pollock *et al.*, 1990). Modifications designed by Brownie *et al.* (1986) make the comparisons between models and the goodness-of-fit procedures for these models more efficient. The user selects the most appropriate model in program JOLLY by determining the most parsimonious model, i.e. the one that best fits the data with the fewest parameters (Pollock *et al.*, 1990). The estimated total number of whales present across all years was determined by summing the estimated number of new animals that entered the population each year and adding this number to the initial estimate of population size.

The models available from program JOLLY depend on several assumptions. These open population models allow for changes in the population over the time of the study. The population may be subject to birth, death, immigration, and emigration. Emigration is considered permanent, meaning once an animal leaves the population it is treated as a "death". If it enters the population again, it is considered a "new" animal. The assumptions for these open population models are (from Seber, 1982):

1. Animals have equal probability of capture each year.
2. Animals have equal probability of survival each year.
3. Animals have equal probability of being returned to the population.
4. Marks are not lost and marks are reported upon recovery.

5. All samples are instantaneous.

Three models are implemented in the JOLLY program; model A, model B, and model D. Model A is the original Jolly-Seber model and assumes time-specific survival and capture probabilities. Model B assumes constant survival rate per unit time and time-specific capture probabilities. Model D assumes constant survival rate per unit time and constant capture probabilities. The three models range from the most general (model A), with the highest number of parameters, to the most simple (model D), with the lowest number of parameters. Model B is the intermediate model. The program provides χ^2 goodness-of-fit tests for all models and χ^2 tests for comparing two models against each other (D vs. A, B vs. A, D vs. B). A fourth model is described, model C, with constant capture probabilities, but program JOLLY does not have a procedure to compute the estimates for this model.

Program CAPTURE (available from Colorado Cooperative Fish and Wildlife Research Unit, 201 Wager Building, Colorado State University, Fort Collins, CO 80523) was used to compute a closed estimate of population size for 1991 for all study areas combined in southeastern Alaska. This program is based on a closed population model, in which the population is assumed to remain unchanged during the study period. The assumptions for a closed population are (from Seber, 1982):

1. Animals have equal probability of capture.

2. Marking does not affect catchability.

3. Random sampling occurs at each sampling period.

4. Marks are not lost.

5. All marks are reported upon recovery.

Ten estimators of population size are available in program CAPTURE. The user can select the estimator or have the program determine the appropriate estimator. The different estimators include 2 for the model of time effects, 3 for the model of heterogeneity effects, and single estimators for models of behavior effect, time and heterogeneity effects, time and behavior effects, behavior and heterogeneity effects, and the null model of no time, behavior, or heterogeneity effects.

Use of capture-recapture methods to estimate population size for naturally marked whale populations is subject to violations of the model assumptions (Hammond, 1986). One of the most serious assumptions to be violated is equal probability of capture which, if violated, would cause underestimation of population size. The assumption of equal capture probabilities can be divided into three areas for naturally marked whale populations:

1. Equal probability of sighting, which is violated for the population of humpback whales in southeastern Alaska, because uniform mixing or

a random distribution of whales probably does not occur in the study areas. Within a specific study area, unequal sampling effort also will affect the probability of sighting.

2. Equal probability of photographing, which also is not true for southeastern Alaska, because individual whales do not behave in the same way when showing their flukes, and some whales are easier to approach and photograph than other whales.

3. Treatment of photographs, where each photograph is subject to quality guidelines that determine when the photograph should be included in the sample. Poor quality photographs are excluded, regardless of the ease of identification. This prevents the less distinctive and more difficult to identify flukes from being included in the sample as often as the more distinctive and easily identified flukes.

The assumption of homogeneity of capture probability is a violation of both the closed and the open population models for humpback whales in southeastern Alaska; hence both models give conservative estimates.

The open population models based on the Jolly-Seber method (Seber, 1982) have no available estimator of population size when there is variation in probability of capture. Closed population models do have some estimators available that take heterogeneity into account. The negative bias resulting from heterogeneity can be reduced and be less influential if the degree of variation in the capture probability among individuals is minimized (Carothers, 1973), or if the average capture probability is high, say ≥ 0.50 (Gilbert, 1973). Additionally, large samples increase the precision of the estimate of population size and make heterogeneity less important (Hammond, 1986).

The assumption that marks are not lost also could be violated with naturally marked whale populations, because the pattern on the ventral surface of the flukes can change over time, to the extent that individual whales can become unrecognizable. This will cause the population size to be overestimated. Misidentification of flukes can happen if many new scars are added or part of the flukes is deleted. The flukes of some calves change naturally over time, and because of this, all calves were excluded from the estimates of population size.

RESULTS

Distribution and Numbers of Whales

Numbers of whales observed through photo-identification

The sighting matrix developed for each primary study area provides information on the numbers of adult humpback whales photo-identified each year. The Glacier Bay-Icy Strait annual whale sightings ranged from a low of 38 individuals in 1985 to a high of 56 in 1987 (Table 3). In the Frederick Sound area, including Seymour Canal and Stephens Passage, yearly sightings ranged from 18 photo-identified whales in 1990 to 162 whales in 1986 (Table 4). In the Sitka Sound area, including Salisbury Sound, annual whale sightings ranged from 3 individuals in 1985 to 158 in 1991 (Table 5). The combined total for all southeastern Alaska study areas, including the three primary study areas, and Lisianski Inlet, Chatham Strait, and Peril Strait, ranged from a low of 82 photo-identified whales in 1990 to a high of 241 in 1991 (Table 6). Much of this difference, between minimum and maximum whale numbers, for the combined study areas was due to variation in effort among the years. Only the Glacier Bay-icy Strait area had consistent effort across all years.

Table 3. Humpback whale sighting matrix for the Glacier Bay-Icy Strait study area in southeastern Alaska, 1985-1992.

TIME OF LAST CAPTURE	TIME OF RECAPTURE: 1985	1986	1987	1988	1989	1990	1991	1992	TOTAL # WHALES (Σ NEWLY CAPTURED)
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	
NEWLY CAPTURED	38	15	20	13	8	9	8	8	119
TOTAL CAPTURED	38	39	56	48	38	45	48	51	

Table 4. Humpback whale sighting matrix for the Frederick Sound study area in southeastern Alaska, 1985-1992.

TIME OF LAST CAPTURE	TIME OF RECAPTURE: 1985	1986	1987	1988	1989	1990	1991	1992	TOTAL # WHALES (Σ NEWLY CAPTURED)
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	
NEWLY CAPTURED	139	103	36	10	32	6	12	34	372
TOTAL CAPTURED	139	162	63	26	72	18	29	67	

Table 5. Humpback whale sighting matrix for the Sitka Sound study area in southeastern Alaska, 1985-1992.

TIME OF LAST CAPTURE	TIME OF RECAPTURE: 1985	1986	1987	1988	1989	1990	1991	1992	TOTAL # WHALES (Σ NEWLY CAPTURED)
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	
NEWLY CAPTURED	3	11	42	37	14	6	114	48	275
TOTAL CAPTURED	3	12	47	55	31	15	158	124	

Table 6. Humpback whale sighting matrix for all study areas in southeastern Alaska, 1985-1992.

TIME OF LAST CAPTURE	TIME OF RECAPTURE: 1985	1986	1987	1988	1989	1990	1991	1992	TOTAL # WHALES (Σ NEWLY CAPTURED)
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	
NEWLY CAPTURED	182	122	72	50	41	21	98	62	648
TOTAL CAPTURED	182	211	155	125	138	82	241	235	

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 (Tables 3-5). In the other study areas, 15 whales were individually identified in Chatham Strait, 12 in Lisianski Inlet, and 3 in Peril Strait (Figure 3). A total of 648 whales were individually identified in all of the study areas of southeastern Alaska during this period (Table 6); this number is not the sum of individuals identified in all areas, because some whales were sighted in more than one area. The minimal estimate is 648 humpback whales for all study areas of southeastern Alaska, which is the total number of animals that were present over the study period.

The sum of individuals identified in all study areas during 1985 to 1992 was 796. Of these, 500 (62.8%) were seen only in one area, and 296 (37.2%) were seen in more than one study area. For a given area, the percentage of whales sighted in at least one other area ranged from 100% for Peril Strait to 28.5% for the Frederick Sound area (Table 7). The high percentage of whales seen only in the Frederick Sound and Sitka Sound study areas (Table 7) suggests that the degree of fidelity to specific study areas related to the number of whales using those areas. The degree of this fidelity is difficult to quantify, due to unequal sampling effort.

Table 7. 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 ONLY IN 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%)

Numbers of whales estimated through capture-recapture methods

Glacier Bay-Icy Strait

The three population models from program JOLLY showed little difference among average estimates of population size, survival, and probability of capture for the whales in the Glacier Bay-Icy Strait study area (Table 8), although annual estimates did vary somewhat.

Test comparisons between models resulted in no model being rejected at the 0.05 level of significance (Table 9). Model D was the most parsimonious model for the Glacier Bay-Icy Strait study area, because it has fewer parameters and does not fit the data significantly worse that the other two models. All goodness-of-fit tests were rejected, demonstrating that no model fits the data very well and that some assumptions of the open population model probably were violated.

Table 8. Estimated population size for humpback whales in the Glacier-Bay Icy Strait area, 1985-1992. Mean population size (N), standard error (SE), 95% confidence interval (CI), survival (ϕ), and probability of capture (ρ) are shown for the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D). An asterisk (*) denotes the most appropriate model selected to estimate population size and other parameters.

MODEL	N	SE	CI	ϕ (SE,CI)	ρ (SE,CI)
A	62	3.60	55-69	0.84 (0.02, 0.80-0.88)	0.73 (0.04, 0.74-0.88)
B	62	3.75	55-70	0.84 (0.02, 0.80-0.88)	0.75 (0.07, 0.61-0.89)
D*	64	4.72	55-73	0.85 (0.02, 0.81-0.89)	0.73 (0.03, 0.68-0.79)

Table 9. Tests of the capture-recapture models for the Glacier Bay-Icy Strait area. Shown are the χ^2 results from the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D). DF=degrees of freedom, P=probability.

TEST	χ^2	DF	P
GOODNESS-OF-FIT TO MODEL A	92.61	7	0.00
GOODNESS-OF-FIT TO MODEL B	98.49	12	0.00
GOODNESS-OF-FIT TO MODEL D	110.79	18	0.00
MODEL D VS. A	18.18	11	0.08
MODEL B VS. A	5.88	5	0.32
MODEL D VS. B	12.17	6	0.06

The annual estimates of population size and 95% confidence intervals, computed from program JOLLY model D, for the Glacier Bay-Icy Strait study area are presented in Figure 3, and the annual estimates of survival, probability of capture, number of new animals that entered the population, and standard errors for these parameters, are presented in Table 10. The estimated total was 121 whales present in the Glacier Bay-Icy Strait area across all years.

Table 10. Estimated annual population parameters for humpback whales in the Glacier Bay-Icy Strait area, 1986-1992. Shown are estimates of survival (ϕ), probability of capture (p), the number of new animals entering the population (B), and the standard errors (SE) under the JOLLY capture-recapture model D, with constant survival rate per unit time and constant capture probability.

YEAR	ϕ (SE)	ρ (SE)	B (SE)
1986	0.85 (0.02)	0.73 (0.03)	23 (4)
1987	0.85 (0.02)	0.73 (0.03)	12 (4)
1988	0.85 (0.02)	0.73 (0.03)	7 (3)
1989	0.85 (0.02)	0.73 (0.03)	10 (3)
1990	0.85 (0.02)	0.73 (0.03)	8 (3)
1991	0.85 (0.02)	0.73 (0.03)	8 (3)
1992	0.85 (0.02)	0.73 (0.03)	-
MEAN	0.85 (0.02)	0.73 (0.03)	11 (2)

Frederick Sound-Stephens Passage-Seymour Canal

The three models for this area were similar in their estimates of mean population size, survival, and probability of capture but varied in estimates of standard errors and confidence intervals (Table 11). Average probability of capture was very low at less than 20% for all models (Table 11).

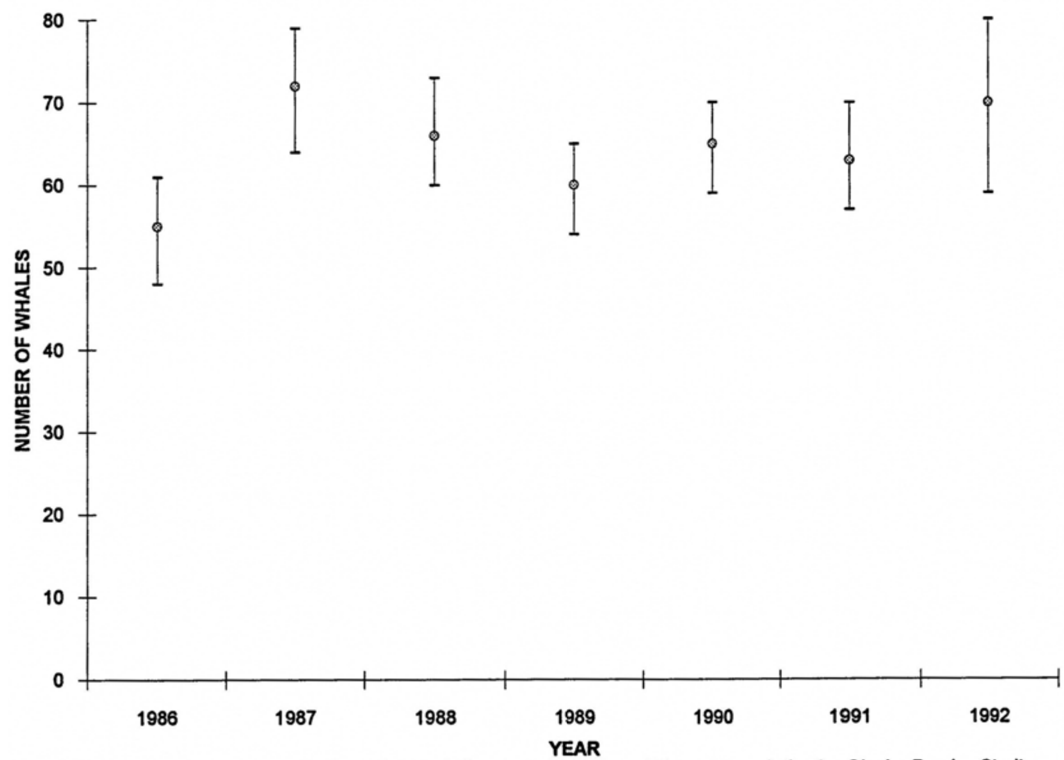

Figure 3. Estimates of open humpback whale population size with 95% confidence intervals for the Glacier Bay-Icy Strait area, 1986-1992.

Table 11. Estimated population size for humpback whales in the Frederick Sound area, 1985-1992. Mean population size (N), standard error (SE), 95% confidence interval (CI), survival (ϕ), and probability of capture (ρ) are shown for the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D). An asterisk (*) denotes the most appropriate model selected to estimate population size and related parameters.

MODEL	N	SE	CI	ϕ (SE,CI)	ρ (SE,CI)
A*	379	55.99	270-489	1.02 (0.16, 0.71-1.32)	0.18 (0.02, 0.03-0.11)
B	381	123.81	139-624	0.91 (0.04, 0.84-0.98)	0.17 (0.03, 0.10-0.23)
D	346	79.21	191-501	0.85 (0.20, 0.80-0.89)	0.18 (0.02, 0.15-0.22)

The test between models D and A rejected model D in favor of model A. Similarly, the test between models B and A rejected model B in favor of model A. The test between models D and B rejected model D in favor of model B (Table 12). All tests were performed at the 0.05 level of significance. Model D was ruled out as a reasonable model because the tests favored model A and model B, and the model selection decision was between these two models. The goodness-of-fit tests (Table 12) demonstrated that model B did not fit the data at the 0.05 significance level; while model A was not rejected. Therefore, model A was selected as the model that best describes the population.

Table 12. Tests of the capture-recapture models for the Frederick Sound area. Shown are the χ^2 results from the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D). DF=degrees of freedom, P=probability.

TEST	χ^2	DF	P
GOODNESS-OF-FIT TO MODEL A	13.47	8	0.10
GOODNESS-OF-FIT TO MODEL B	27.21	13	0.01
GOODNESS-OF-FIT TO MODEL D	136.55	19	0.00
MODEL D VS. A	123.08	11	0.00
MODEL B VS. A	13.74	5	0.02
MODEL D VS. B	106.68	6	0.00

The annual estimates computed from JOLLY model A for the Frederick Sound study area, along with 95% confidence intervals, are presented in Figure 4, and the annual estimates of survival, probability of capture, number of new animals that entered the population, and standard errors for these parameters are presented in Table 13. The estimated total was 695 whales present in the Frederick Sound area across all years.

Table 13. Estimated annual population parameters for humpback whales in the Frederick Sound area, 1986-1992. Shown are estimates of survival (ϕ), probability of capture (ρ), the number of new animals entering the population (B), and the standard error (SE) under the JOLLY capture-recapture model A.

YEAR	ϕ (SE)	ρ (SE)	B (SE)
1985	0.75 (0.06)	-	-
1986	1.46 (0.33)	0.57 (0.07)	280 (119)
1987	0.42 (0.12)	0.09 (0.03)	-55 (55)
1988	1.57 (0.47)	0.11 (0.03)	86 (71)
1989	0.49 (0.21)	0.16 (0.05)	-7 (40)
1990	1.43 (0.92)	0.08 (0.04)	100 (3)
1991	-	0.07 (0.04)	8 (93)
MEAN	1.02 (0.16)	0.18 (0.02)	81 (31)

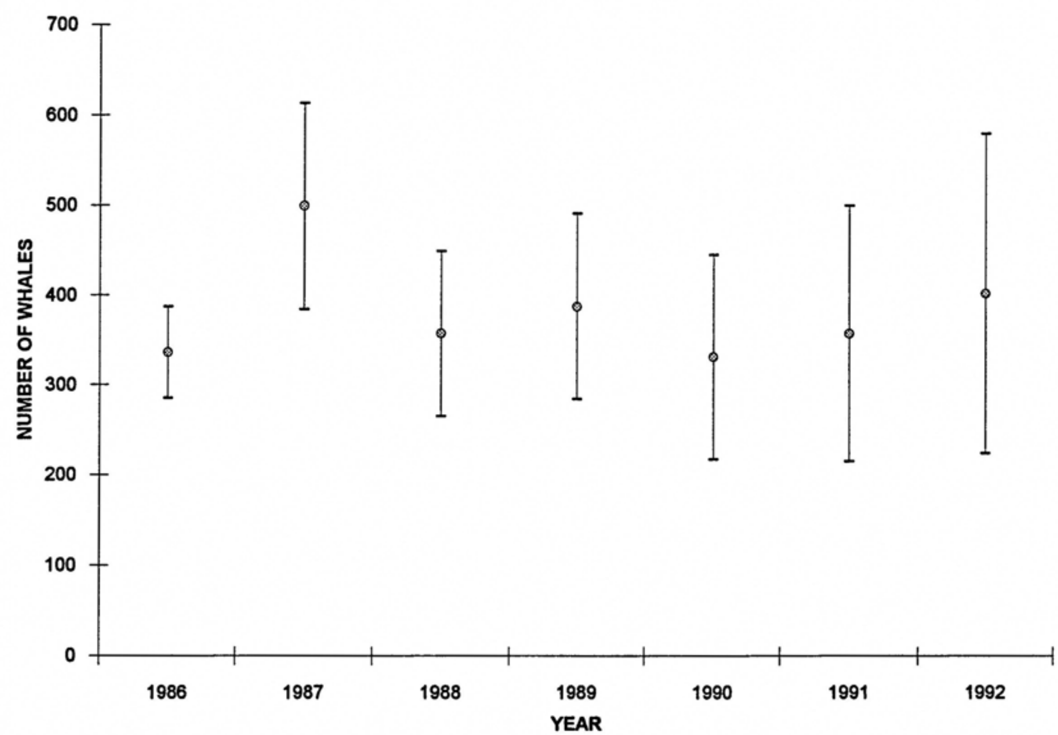

Figure 4. Estimates of open humpack whale population size with 95% confidence intervals for the Frederick Sound area, 1986-1992.

Sitka Sound-Salisbury Sound

There was some difference among the three models in mean estimates of population size, standard error, and 95% confidence intervals for this area (Table 14). Estimates of survival and probability of capture were similar between the models, with probability of capture all less than 50% (Table 14).

Table 14. Estimated population size for humpback whales in the Sitka Sound area, 1985-1992. Mean estimates of population size (N), standard error (SE), 95% confidence interval (CI), survival (ϕ), and probability of capture (ρ) are shown for the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D). An asterisk (*) denotes the most appropriate model selected to estimate population size and related parameters.

MODEL	N	SE	CI	ϕ (SE,CI)	ρ (SE,CI)
A	107	10.34	87-127	0.90 (0.05, 0.81-1.00)	0.39 (0.06, 0.58-0.83)
B*	133	24.46	85-181	0.82 (0.03, 0.76-0.87)	0.42 (0.13, 0.16-0.67)
D	156	28.91	99-213	0.85 (0.03, 0.80-0.91)	0.42 (0.03, 0.35-0.48)

Comparisons between models D and A rejected model D in favor of model A; tests of models B and A did not (barely) reject model B for model A, and the test of models D and B rejected model D in favor of model B (Table 15). Therefore, model B was selected because it is the most parsimonious model. The goodness-of-fit tests were all rejected, demonstrating that no model fits the data very well.

Table 15. Tests of the capture-recapture models for the Sitka Sound area. Shown are the χ^2 results from the Jolly-Seber model (A), The constant survival model (B), and the constant survival and capture model (D). DF=degrees of freedom, P=probability.

TEST	χ^2	DF	P
GOODNESS-OF-FIT TO MODEL A	45.88	7	0.00
GOODNESS-OF-FIT TO MODEL B	53.49	10	0.00
GOODNESS-OF-FIT TO MODEL D	107.70	16	0.00
MODEL D VS. A	61.82	9	0.00
MODEL B VS. A	7.61	3	0.05
MODEL D VS. B	53.15	4	0.00

Annual estimates for the Sitka Sound study area, computed from JOLLY model B, with 95% confidence intervals are presented in Figure 5, and the annual estimates of survival, probability of capture, the number of new animals that entered the population, and the standard errors for these parameters are presented in Table 16. The estimated total was 360 whales present in the Sitka Sound area across all years.

Table 16. Estimated annual population parameters for humpback whales in the Sitka Sound area, 1986-1992. Shown are estimates of survival (ϕ), probability of capture (p), the number of new animals entering the population (B), and the standard error (SE) under the JOLLY capture-recapture model B, with constant survival rate per unit time and constant capture probability.

YEAR	ϕ (SE)	p (SE)	B (SE)
1986	0.82 (0.03)	0.33 (0.27)	78 (42)
1987	0.82 (0.03)	0.44 (0.15)	39 (34)
1988	0.82 (0.03)	0.45 (0.08)	14 (22)
1989	0.82 (0.03)	0.27 (0.06)	12 (25)
1990	0.82 (0.03)	0.14 (0.04)	123 (23)
1991	0.82 (0.03)	0.74 (0.07)	57 (17)
1992	0.82 (0.03)	0.54 (0.05)	-
MEAN	0.82 (0.03)	0.42 (0.13)	54 (12)

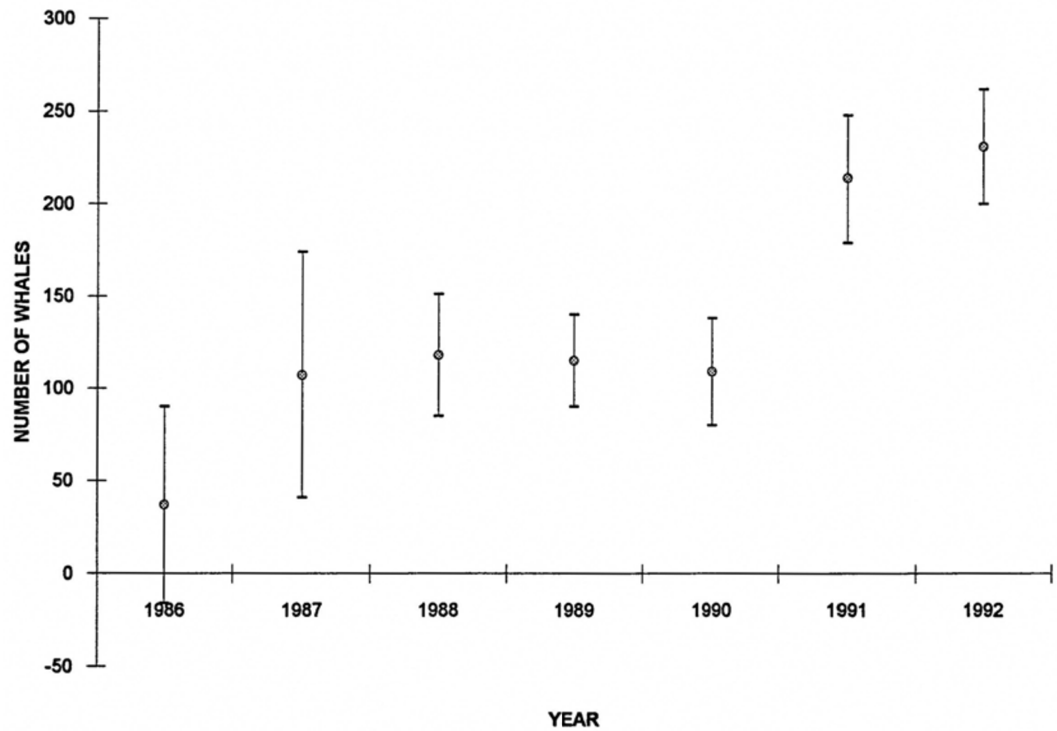

Figure 5. Estimates of open humpback whale population size with 95% confidence intervals for the Sitka Sound area, 1986-1992.

Southeastern Alaska as a whole

The analysis for southeastern Alaska included the pooled data from the three primary study areas and the data from Lisianski Inlet, Chatham Strait, and Peril Strait. There was some difference among the three models for the mean estimates of population size, standard errors, and 95% confidence intervals for southeastern Alaska as a whole (Table 17). Estimates of survival and probability of capture were similar, with probability of capture less than 50% for all models (Table 17).

Table 17. Estimated population size for humpback whales in all southeastern Alaskan study areas, 1985-1992. Mean estimates of population size (N), standard error (SE), 95% confidence interval (CI), survival (ϕ), and probability of capture (ρ) are shown for the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D). An asterisk (*) denotes the most appropriate model selected to estimate population size and related parameters.

MODEL	N	SE	CI	ϕ (SE,CI)	ρ (SE,CI)
A	400	15.09	370-429	0.86 (0.01, 0.84-0.89)	0.39 (0.01, 0.54-0.61)
B*	404	27.60	350-458	0.86 (0.01, 0.84-0.88)	0.42 (0.03, 0.35-0.49)
D	446	36.57	374-517	0.88 (0.01, 0.86-0.90)	0.40 (0.01, 0.37-0.43)

Comparisons between model D and A rejected model D in favor of model A, the test of models B and A did not reject model B for model A, and the test of models D and B rejected model D in favor of model B (Table 18). Therefore, model B was selected because it is the most parsimonious model. The goodness-of-fit tests were all rejected, demonstrating that no model fits the data very well.

Table 18. Tests of the capture-recapture models for all southeastern Alaskan study areas. Shown are the χ^2 results from the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D). DF=degrees of freedom, P=probability.

TEST	χ^2	DF	P
GOODNESS-OF-FIT TO MODEL A	169.49	16	0.00
GOODNESS-OF-FIT TO MODEL B	178.75	21	0.00
GOODNESS-OF-FIT TO MODEL D	305.96	27	0.00
MODEL D VS. A	136.47	11	0.00
MODEL B VS. A	9.25	5	0.10
MODEL D VS. B	126.43	6	0.00

Annual estimates of population size and 95% confidence intervals, computed from program JOLLY model B for all of southeastern Alaska are presented in Figure 6, and the annual estimates of survival, probability of capture, number of new animals that entered the population, and standard errors for these parameters are presented in Table 19. The estimated total was 743 whales present in all southeastern Alaskan study areas across all years.

Table 19. Estimated annual population parameters for humpback whales in all southeastern Alaskan study areas, 1986-1992. Shown are estimates of survival (ϕ), probability of capture (p), the number of new animals entering the population (B), and the standard error (SE) under the JOLLY capture-recapture model B, with constant survival rate per unit time and constant capture probability.

YEAR	ϕ (SE)	p (SE)	B (SE)
1986	0.86 (0.01)	0.56 (0.04)	128 (32)
1987	0.86 (0.01)	0.35 (0.03)	61 (36)
1988	0.86 (0.01)	0.28 (0.03)	7 (30)
1989	0.86 (0.01)	0.35 (0.03)	29 (26)
1990	0.86 (0.01)	0.23 (0.03)	109 (24)
1991	0.86 (0.01)	0.57 (0.04)	44 (17)
1992	0.86 (0.01)	0.58 (0.04)	-
MEAN	0.86 (0.01)	0.42 (0.03)	63 (9)

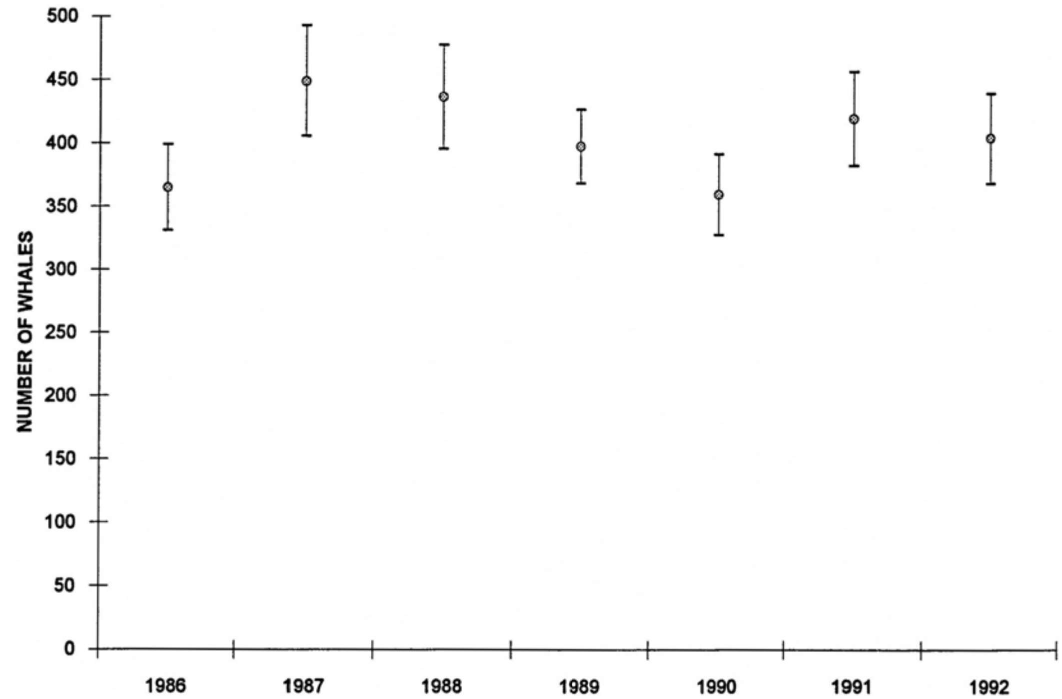

Figure 6. Estimates of open humpback whale population size with 95% confidence intervals for southeastern Alaska, 1986-1992.

Program CAPTURE computed the size of the 1991 closed population as 342 whales (SE=22.38, 95% confidence interval 307-396) for all study areas combined. The program selected the most appropriate model of M(th) with time-specific changes in capture probabilities during the year (influenced by unequal effort, weather changes, and sampling at different times of the day) and individual heterogeneity (behavioral variation) in capture probability. Although this estimate of the closed population in 1991 is lower and not within the bounds of the confidence intervals of the estimated 1991 open model B (Table 17), the open and closed estimates are comparable because their confidence intervals overlap. This comparison, however, is problematic because the open estimate intuitively should be lower, due to the negative bias from heterogeneity, than the closed estimate.

Southeastern Alaska, 1979 to 1986

Baker *et al.* (1992) estimated the population size of humpback whales in the northern part of southeastern Alaska, during 1979 to 1986, by using the Schnabel, multi-sample closed population estimator (Seber, 1982). This model, however, is unsuitable for use with data collected over a number of years, because it violates the assumption of a closed population and introduces a large positive bias to the estimate, which increases as the number of samples is increased (Seber, 1982; Hammond, 1986). A sighting matrix was developed from these data (Table 20), and this was used to compute estimates of open population size with program JOLLY.

Table 20. Humpback whale sighting matrix for southeastern Alaskan study areas from data of Baker et al. (1992), 1979-1986.

TIME OF LAST CAPTURE	TIME OF RECAPTURE: 1979	1980	1981	1982	1983	1984	1985	1986	TOTAL # WHALES (Σ NEWLY CAPTURED)
1979	0	32	19	11	1	1	2	0	
1980	0	0	58	20	1	9	3	6	
1981	0	0	0	85	5	17	11	4	
1982	0	0	0	0	31	57	29	15	
1983	0	0	0	0	0	35	5	1	
1984	0	0	0	0	0	0	80	25	
1985	0	0	0	0	0	0	0	79	
RECAPTURED	0	32	77	116	38	119	130	130	
NEWLY CAPTURED	83	92	72	71	13	82	75	127	615
TOTAL CAPTURED	83	124	149	187	51	201	205	257	

Model B was selected as the most parsimonious model. The result was a mean annual population estimate of 393 (SE = 32, 95% confidence interval 331-455) whales for southeastern Alaska during 1979 to 1986. Annual estimates of population size with standard errors and 95% confidence intervals; as well as survival, probability of capture, the number of new animals that entered the population each year, and the standard errors for these parameters are presented in Table 21.

Table 21. Estimated annual population size for humpback whales in southeastern Alaska, 1979-1986, from data of Baker et al. (1992). Shown are estimates of population size (N), standard error (SE) and 95% confidence interval (CI), and estimates of survival (ϕ), probability of capture (ρ), the number of new animals (B), and standard errors under the JOLLY capture-recapture model B, with constant survival rate per unit time and time-specific capture probability.

YEAR	N	SE, CI	ϕ (SE)	ρ (SE)	B (SE)
1980	288	30, 229-347	0.91 (0.01)	0.43 (0.06)	28 (35)
1981	285	13, 260-310	0.91 (0.01)	0.52 (0.04)	62 (19)
1982	326	11, 305-347	0.91 (0.01)	0.58 (0.04)	38 (28)
1983	337	16, 306-368	0.91 (0.01)	0.15 (0.02)	100 (29)
1984	411	17, 377-456	0.91 (0.01)	0.50 (0.04)	92 (24)
1985	448	21, 406-490	0.91 (0.01)	0.45 (0.03)	240 (37)
1986	655	36, 583-726	0.91 (0.01)	0.39 (0.03)	-
MEAN	393	32, 331-455	0.91 (0.01)	0.43 (0.04)	93 (19)

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 the same year (Appendix 1). These 92 whales were included in the 296 whales mentioned above as having been observed in one or more study areas during 1985 to 1992 (Table 7); they comprise the subset that was observed in two or more study areas within the same year. Of these 92 whales, 86 made at least one transit, 5 made at least two transits, and one whale made at least three transits between study areas within the same year (Table 22). In general, there was movement into the Frederick Sound-Seymour Canal area from all other areas, during late spring-early summer and mid-summer-fall (Figure 7). The seasonal movement in the fall and early winter was mainly to the Salisbury Sound-Sitka Sound area and Lisianski Inlet (Figure 8).

Table 22. Humpback whale seasonal movements between study areas, during the same year in southeastern Alaska, 1985-1992 (summarized from Appendix 1).

STUDY AREA FROM:	STUDY AREA TO:	NUMBER OF WHALES	SEASONAL MOVEMENT
SITKA SOUND	FREDERICK SOUND AND SEYMOUR CANAL	1	LATE SPRING TO SUMMER
GLACIER BAY AND ICY STRAIT	FREDERICK SOUND AND SEYMOUR CANAL	39	LATE SPRING AND SUMMER TO MID- LATE SUMMER AND FALL
SITKA SOUND	CHATHAM STRAIT	1	LATE SPRING TO FALL
GLACIER BAY AND ICY STRAIT	CHATHAM STRAIT	3	SUMMER
PERIL STRAIT	FREDERICK SOUND AND SEYMOUR CANAL	2	SUMMER
CHATHAM STRAIT	FREDERICK SOUND AND SEYMOUR CANAL	6	SUMMER AND FALL
FREDERICK SOUND AND SEYMOUR CANAL	GLACIER BAY AND ICY STRAIT	5	SUMMER AND SUMMER TO EARLY FALL
GLACIER BAY AND ICY STRAIT	SITKA SOUND AND SALISBURY SOUND	17	SUMMER TO FALL AND EARLY WINTER
FREDERICK SOUND AND SEYMOUR CANAL	SITKA SOUND AND SALISBURY SOUND	10	SUMMER TO FALL AND EARLY WINTER
CHATHAM STRAIT	SITKA SOUND AND SALISBURY SOUND	7	SUMMER TO FALL AND EARLY WINTER
PERIL STRAIT	SITKA SOUND AND SALISBURY SOUND	2	SUMMER TO FALL
GLACIER BAY AND ICY STRAIT	LISIANSKI INLET	2	LATE SPRING AND SUMMER TO EARLY WINTER
FREDERICK SOUND AND SEYMOUR CANAL	LISIANSKI INLET	1	SUMMER TO EARLY WINTER
SITKA SOUND AND SALISBURY SOUND	LISIANSKI INLET	3	FALL TO EARLY WINTER

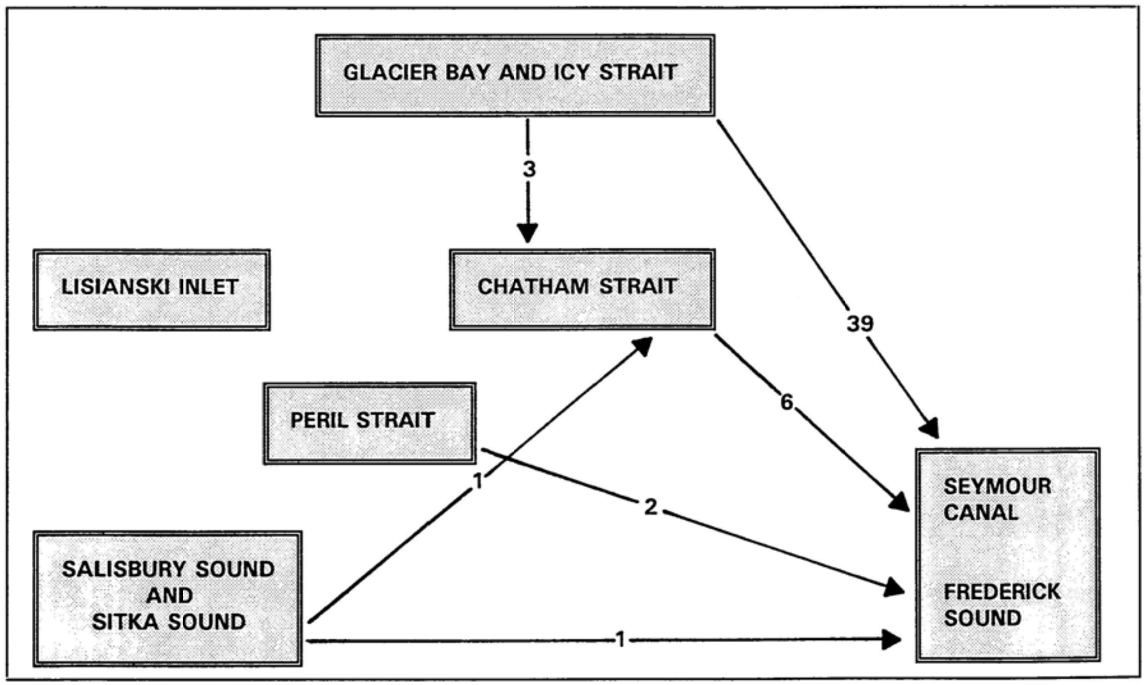

Figure 7. Seasonal movements of humpback whales during late spring to early summer and mid-summer to fall in southeastern Alaska, 1985-1992.

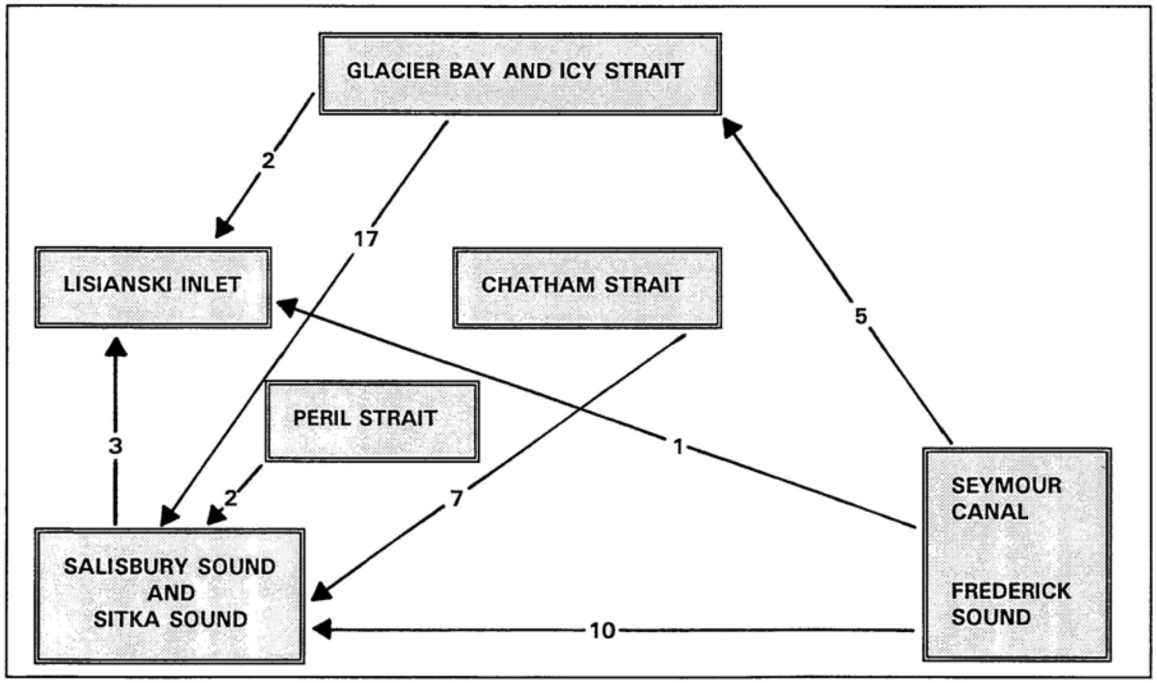

Figure 8. Seasonal movements of humpback whales during summer, fall, and early winter in southeastern Alaska, 1985-1992.

All other whales apparently remained in the same study areas across seasons. In 1985 and 1986 there were 21 whales sighted in Frederick Sound during the summer and resighted in the same study area in fall of the same year. The presence of humpback whales in the Frederick Sound study area during the late fall and early winter has been documented previously (Straley, 1990a). Due to infrequent surveys in recent years, the number of whales currently using this area in the fall and early winter is unknown.

Length of stay on the feeding grounds

During 1985 to 1992, 35 whales were documented to have stayed for over 100 days, and 55 whales were documented to have stayed less than 100 days in the southeastern Alaska study area (Appendix 1). The longest stay within one year was 206 days by whale #1073. 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 Lisianksi Inlet on December 26 (Appendix 1). This stay of 206 days (nearly 7 months) exceeds the previously reported maximum of 191 days (Baker *et al.*, 1992) by more than two weeks. There is a remote possibility this whale left and returned to southeastern Alaska during the 6 month span between 3 June and 15 December. One other whale is known to have changed feeding areas within the same year; this whale moved from Prince William Sound to southeastern Alaska during the summer of 1989 (Dahlheim and von Ziegesar, 1993).

This type of movement, however, is probably uncommon (Baker *et al.*, 1986, Calambokidis *et al.*, 1989, 1993, in preparation; von Ziegesar and Matkin, 1989; Perry *et al.*, 1990; J. Straley, unpublished data); as a rule the same whales return to the same feeding areas, year after year (Jurasz and Palmer, 1981; Martin *et al.*, 1984; Baker *et al.*, 1987; Clapham and Mayo, 1987b, 1990). If movement between feeding areas did occur with whale #1073, the length of stay of 206 days would still document the longest known stay on the North Pacific feeding grounds. It is unlikely that whale #1073 migrated to the breeding grounds and returned to southeastern Alaska during this time, because humpback whales do not occur on the Hawaiian breeding grounds from June to October (Herman and Antinoja, 1977) and rarely occur as far south as Mexico during these months (Urban and Aguayo, 1987).

Migration time to the Hawaiian breeding grounds

The shortest known migration time from the southeastern Alaskan feeding grounds to the Hawaiian breeding grounds was 39 days in 1988. 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. The match was made by Chris Gabriele of the University of Hawaii, during a photographic comparison of whales sighted from 1987 to 1989 in southeastern Alaska and Hawaii. Whale #339 has not been sighted in southeastern Alaska since 1988. There have been 5 other migration times previously reported from southeastern Alaska to Hawaii; these ranged from 79 to 117 days (Baker *et al.*, 1985). The migrational speed from Alaska to Hawaii (distance = 4500 km) for whale #339 was about 4.8 km/hour. This speed is 2 km/hour faster than the transits reported previously by Baker *et al.* (1985). The actual migrational speed probably was faster, because the whale probably did not swim in a straight line and was not photographed on the last day in Alaskan waters or on the first day in Hawaii. This speed also matches the slowest observed speed of migration of humpback whales along the western shore of Australia, in the Indian Ocean, reported by Chittleborough (1953). From aerial surveys, Chittleborough recorded speeds that ranged from 4.8 to 14.2 km/hour (mean = 8.0 km/hour, n = 25) for humpback whales migrating to the breeding grounds.

Reproduction and Calf Survival

Reproductive rate

From 1980 to 1992, a total of 136 of the photo-identified humpback whales in southeastern Alaska were identified as females. These were sighted 573 times, but the maturity of a few of them was in question at the time of some of those sightings. They were known to have been adult, sexually mature females at the time of 448 (8-60/year) of the sightings. In that same period, these females were sighted with 222 calves, hence the minimal mean calving rate implied was 222/573 or 0.39 ± 0.03 SE calves per female per year (Table 23). The maximal mean calving rate was 222/448 or 0.50 ± 0.03 SE calves per adult female per year (Table 24). The calves per adult female per year was quite stable throughout 1985 to 1992 (linear regression, $r^2=0.05$, d.f.$=11$; Zar, 1984), but the calves per female per year was not (linear regression, $r^2=0.57$, d.f.$=11$; Zar, 1984). Hence, the maximal rate appears to be the most reliable; the minimal rate appears to have been influenced by my ability to both identify females in general and to identify juvenile females, in particular. These data also demonstrated an increasing ability to distinguish adults, as indicated by the rising proportions of adults in the annual samples (linear regression, $r^2=0.78$, d.f.$=11$; Zar, 1984) (Table 25). This improvement in identification of adults partially can be attributed to increasing duration of longitudinal observations of the same whales, because the longer a female can be observed, the greater the chance of her being identified as such.

Table 23. Number of calves (n=222) sighted per female humpback whale (n=573) per year in southeastern Alaska, 1980-1992.

YEAR	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
CALVES PER ♀	3/28	12/45	16/42	6/17	18/52	7/37	30/61	20/50	20/49	17/47	13/29	27/60	33/56
RATE	0.11	0.27	0.38	0.35	0.35	0.19	0.49	0.40	0.41	0.36	0.45	0.45	0.59

Table 24. Number of calves (n=222) sighted per mature female humpback whale (n=448) per year in southeastern Alaska, 1980-1992.

YEAR	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
CALVES PER ♀	3/8	12/27	16/27	6/14	18/34	7/28	30/47	20/40	20/39	17/41	13/27	27/60	33/56
RATE	0.38	0.44	0.59	0.43	0.53	0.25	0.64	0.50	0.51	0.41	0.48	0.45	0.59

Table 25. Proportion of adult females (n=448) among all females (n=573) per year in southeastern Alaska, 1980-1992.

YEAR	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
ADULT♀ PER ALL ♀	8/28	27/45	27/42	14/17	34/52	28/37	47/61	40/50	39/49	41/47	27/29	60/60	56/56
PROPORTION	0.29	0.60	0.64	0.82	0.65	0.76	0.77	0.80	0.80	0.87	0.93	1.00	1.00

Of the 136 individual female humpback whales, 90 were seen once with a calf, 22 were seen twice with calves, 15 were seen three times with calves, 3 were seen four times with calves, 5 were seen five times with calves, and 1 whale was seen six times with calves in southeastern Alaska during 1980 to 1992. No female whale 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. Twenty-three others had incomplete records of sightings between the years when they were sighted with calves.

For the 23 females with complete sighting records, 46 birth intervals were measured. These ranged in length from one to five years (Table 26). 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 (Figure 9).

Table 26. Reproductive and sighting histories of female humpback whales (n=23) that returned to Alaskan waters with calves in two or more different years. Complete sighting records were available for each during one or more birth intervals. ⊙ = no calf ● = with calf

ID #	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
155					⊙	●		⊙	●	⊙	⊙	⊙	⊙	●	⊙	●
161	⊙	⊙	⊙	⊙	⊙	⊙	●	⊙	⊙	●	⊙	⊙	●	⊙		⊙
193					⊙	●	⊙	⊙	⊙	●	⊙	⊙	⊙	●	●	●
219						⊙			⊙	⊙	⊙	●	⊙	●	⊙	●
231			⊙	⊙		⊙		●	⊙	⊙	●	⊙				
235	⊙		⊙	⊙	●			●		⊙	●	●	⊙	⊙	●	⊙
236		⊙				●	⊙	●	⊙	⊙	●	⊙	●	⊙	⊙	●
268		⊙		●	⊙	⊙		●	⊙	⊙	●					
454					⊙		⊙	⊙			●	⊙	●		●	⊙
467								⊙		●	⊙	●	⊙	●	⊙	●
508				⊙	●	●										
530					⊙	●	⊙	●	⊙	●	⊙	●	⊙	●	⊙	●
539		⊙	⊙	⊙	⊙	●	⊙	⊙	●	⊙	⊙		⊙	⊙	●	⊙
560					⊙	●		●	⊙	●	⊙					
566		⊙	⊙		⊙			⊙	⊙	●	⊙	⊙	●	⊙		●
573				●	⊙		⊙	●	⊙	●	⊙	●	⊙	●	⊙	⊙
581					⊙	⊙	⊙	●	⊙	⊙	●	●	●	⊙	●	⊙
587	●	⊙		⊙	⊙	⊙	⊙	●	⊙	●	⊙	●	⊙	⊙	⊙	●
801									⊙		⊙			●	⊙	●
895										●	●					
959								⊙			⊙	⊙	●	⊙	⊙	●
961										⊙	●	⊙	●		●	
1121															●	●

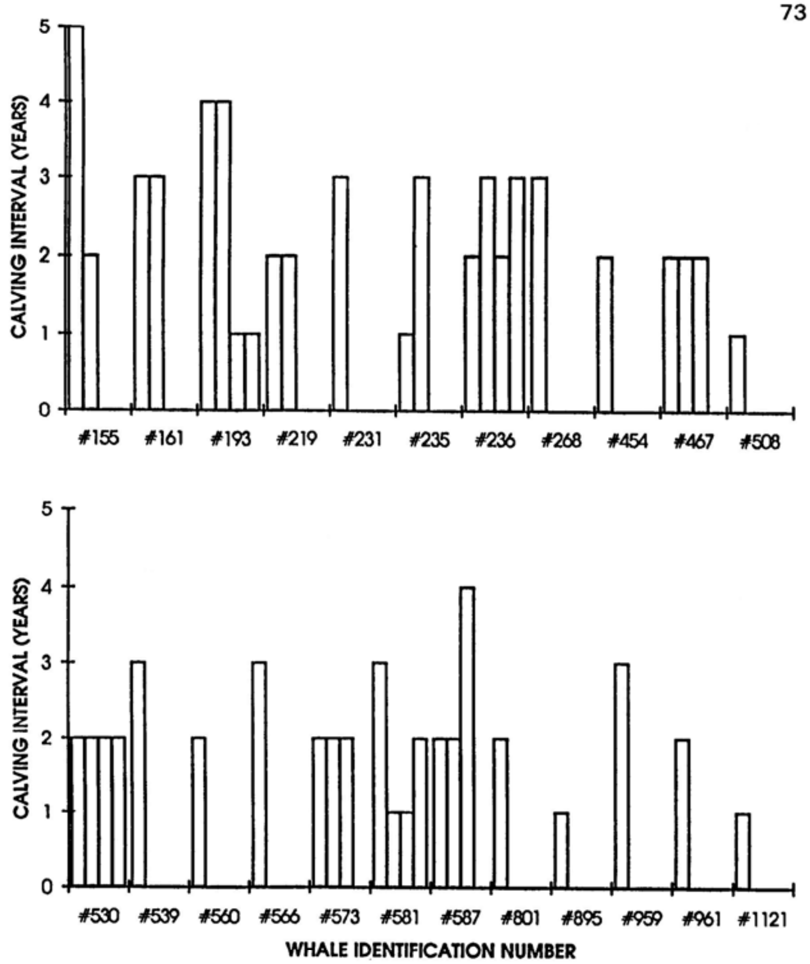

Figure 9. Consecutive birth intervals of individual female humpback whales of southeastern Alaskan waters, 1980-1992.

For the 23 females with one or more completely documented birth intervals, the mean interval was 2.26 ± 0.13 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.

Separation of mother and calf

Observations of females with calves on the feeding grounds is suggestive that the calves are still taking milk. Later sighting of a calf not with its mother is evidence that weaning has taken place.

One case of separation was confirmed on the southeastern Alaskan feeding grounds, and 3 other possible cases were observed but not completely verified. One calf (the 1988 calf of whale #900) was observed on 5 December 1988 with its mother and then alone on 21 December 1988. The mother and calf were not sighted again in that feeding season. This calf (#995) was resighted in 1992 as a 4-year old, and its mother was resighted several times in 1991 and in 1992. Three other calves were observed with their mothers at various times during the summer, fall, and early winter, and the mothers were later observed (in January) unaccompanied by their calves. The sighting histories of these mothers and calves were: 1) whale #961 was seen with a calf on 28 December 1987 and on 3 and 4 January 1988;

then the mother was seen alone on 6 January 1988. 2) whale #959 was seen with a calf on 13 and 15 October and on 7 December 1989; then the mother was seen alone on the 3, 8, and 12 January 1990. 3) whale #580 was seen with a calf on 8 August and on 9 December 1991; then the mother was seen alone on 16 January 1992. These three calves have not been sighted since the birth year (all were photographed), hence it is possible that they died before separation from the mother. Until these whales are resighted and documented to have survived, their weaning cannot be confirmed. The mothers have all been resighted in later years.

Calf mortality

Mortality can be documented on the feeding grounds by finding a dead calf. It also can be presumed by resighting the mother without the calf when complete weaning and total independence from the mother would be unexpected. During the course of this study there were three cases of presumed calf mortality, one case of possible mortality, and confirmed deaths of three other calves. Two of the three cases of presumed mortality were determined from observations of a mother and calf together early in the summer and then, a little later, of the mother without the calf. These events took place during the summers of 1986 and 1988 in Icy Strait. The disappearance of one of these calves (#587's 1986 calf) was reported previously (Baker *et al.*, 1987, 1992), and the disappearance of the other

(#573's 1988 calf) was reported in an unpublished annual report of GBNP&P (Baker and Straley, 1988). A third calf was seen with its mother (#1037) in Hawaiian waters in February 1987 by University of Hawaii researchers but was not seen with the mother when she was resighted in Alaska in July 1987. This calf is presumed to have died sometime during the interval between sightings. A fourth calf was seen with its mother (#972) near the island of Kauai, Hawaii in April 1991 by S. Cerchio of Moss Landing Marine Laboratory, but was not seen with the mother when she was resighted near Sitka in December 1991 and January 1992. This case is less clear than the others, because the resighting of the mother was late enough that the calf could have been weaned and separated from the mother.

Three male calves were found dead in southeastern Alaska in 1987, 1991, and 1992. One found floating in Sitka Sound was towed to Sitka by NMFS Law Enforcement personnel on 1 August 1987. It was presumed to have had died very recently, because no skin had sloughed, and the pigmentation pattern on the flukes was very distinct. Measurements (total length = 7.3m) were taken. Extensive bruising was noted forward and to the left of the blowhole, but cause of death was not determined. By matching dorsal fin photographs, this whale was identified as the calf of a female seen in Sitka Sound in May of that year.

The second dead calf was found floating near Big Port Walter in southern Chatham Strait by NMFS Auke Bay Laboratory personnel on 6 August 1991. This whale was towed to shore, and a preliminary examination was performed on 7 August. A more complete necropsy was done on 10 August. Measurements (total length = 7.5m) and blubber and tissue samples were taken. Most of the ventral skin surface was smooth and dark without scars, scratches or blemishes. The skin was eroded off most of the dorsal surface, the pectoral fins and the flukes, hence nothing remained of the pigmentation pattern on the ventral surface of the flukes. There were no lesions or tumors observed inside the body cavity, and all organs appeared normal, with no discoloration, inflammation, or excessive fluid. The stomach was empty, and only foul-smelling, mustard-brown ooze was present in the intestines. The skull was completely shattered, from the top of the cranium to the base of the skull. Because bruising was not detected, this impact could have happened after death by smashing onto rocks or from a collision with a vessel. The parts of the body of the whale that were visible (it was positioned ventral side up) were not damaged. This whale probably had died not more than two weeks earlier.

The third dead calf was found on the southern shore of Hood Bay, Admiralty Island. It was reported to the NMFS Alaska Region on 22 September 1992, and an examination was done on 24 September. This whale was very bloated; 95% of its skin had sloughed off, and there were no visible scars or damages to the body. There was no pigmentation present on the flukes, but the distinctive trailing edge (many points and scalloped edges) was intact, as was the notch between the flukes. A photographic match was not found, however, between this whale and any of the 1992 calves photographed. Measurements (total length = 8.3m) and blubber samples were taken. An unconfirmed local report placed time of death at two weeks prior to my observations. The cause of death was attributed to exhaustion following pursuit by killer whales (*Orcinus orca*).

Calf survival, recruitment, and return

Of the 222 calves observed from 1980 to 1992 in southeastern Alaska, 105 were successfully photographed for identification purposes.

Of these 105 photographed calves, 85 were re-photographed in subsequent years. Of these 85, 21 were resighted in southeastern Alaska as juveniles and adults (Table 27). 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 (Chittleborough, 1958; Nishiwaki, 1959; Robins, 1960; Clapham and Mayo, 1987a; Clapham, 1992), but only two of them (#353 and #967) have been

Table 27. Calves that have been resighted (n=21) as known-age whales in southeastern Alaska since 1980.[1]
FS=Frederick Sound, GB=Glacier Bay, IS=Icy Strait, LI=Lisianski Inlet, ND=Not Determined, SS=Sitka Sound, SP=Stephens Passage.

ID #	BIRTH YEAR	MOTHER ID #	AREA(S) OBSERVED	YEAR(S) RESIGHTED	AREA(S) OBSERVED	RESIGHTED AGE: FIRST	LAST	COMMENTS
967	1980	268	FS	1988,1991,1992	SS,SS	8	12	FEMALE OBSERVED WITH CALF IN 1992
186	1982	530	IS	1986-1992	FS,GB,IS	4	10	FEEDING IN IS NEAR MOTHER ALL YEARS
198	1982	539	GB,FS,SC	1985,1986	SC,FS	3	4	
416	1983	541	FS	1985,1991	FS	2	8	FEEDING IN FS NEAR MOTHER IN 1991
349	1984	535	GB,SP	1989	IS	5	5	
352	1984	530	IS	1987-1992	IS,GB	3	8	FEEDING IN IS NEAR MOTHER ALL YEARS
353	1984	581	IS	1987-1992	IS	3	8	FEMALE OBSERVED WITH CALF IN 1992, FEEDING IN IS NEAR MOTHER ALL YEARS
891	1986	556	FS	1987	SS	1	1	
893	1986	1180	SS	1991	SS	5	5	
933	1986	566	GB,FS	1988,1992	FS	2	6	
945	1986	573	IS	1990	IS	4	4	FEEDING IN IS NEAR MOTHER IN 1990
1042	1987	581	IS	1990-1992	IS	3	5	FEEDING IN IS NEAR MOTHER ALL YEARS
1091	1987	1176	FS	1988,1990	FS	1	4	
1164	1987	895	FS	1990	GB	3	3	
992	1988	991	SS	1991,1992	SS	3	4	FEEDING IN SS NEAR MOTHER IN 1992
995	1988	900	SS	1992	SS	4	4	FEEDING IN SS NEAR MOTHER IN 1992
1031	1988	219	IS	1991	IS	3	3	FEEDING IN IS NEAR MOTHER IN 1991
1069	1988	ND	FS	1991	LI	3	3	
977	1989	969	SS	1991,1992	SS	2	3	
1014	1989	236	IS	1991,1992	LI,IS,GB	2	3	MALE, FEEDING IN IS NEAR MOTHER ALL YEARS
1057GB	1991	539	IS	1992	IS	1	1	FEEDING IN IS NEAR MOTHER 1992

[1]GB or IS sightings from Glacier Bay National Park unpublished reports.

observed with calves. These were at ages of 8 and 12 years, respectively (Table 27). 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 (Gabriele, 1992a). 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, however, 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 (#186, #198, and #416) in 1980 to 1985 (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 known to have returned to the southeastern Alaskan feeding ground, 11 were seen feeding as juveniles and adults near, but not with, their mothers (Table 27). These observations were in areas where they were initially observed with their mothers as calves. This further corroborates the fidelity of the whales to the same subregion within a feeding ground, as previously reported by Jurasz and Palmer (1981) and Baker *et al.* (1987) for the North Pacific, and by Martin *et al.* (1984) and Clapham and Mayo (1987b, 1990) for the North Atlantic.

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. This was true even in the Glacier Bay-Icy Strait area, where effort was most consistent among years and numbers of whales sighted per year did not fluctuate much. 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. The latter could not have been a major cause, as most of the whales did eventually reappear. I think fewer whales were missed in Glacier Bay-Icy Strait than elsewhere because of the consistent and systematic coverage, hence I conclude that most of the "missed" whales simply did not return ever year. This conclusion was 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. These whales evidently were familiar with the Glacier Bay-Icy Strait area but, for whatever reasons, did not feed there every year. The Glacier Bay-Icy Strait 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, I think a high proportion of whales could have been missed during the sampling effort. The Frederick Sound study area is much larger and more complex than Glacier Bay-Icy Strait, hence is more difficult to survey adequately, which is evident by the lower estimated probability of capture there than in the other areas. The fact that nearly three-fourths of the Frederick Sound whales were seen only in this area helps to support the conclusion that the whales were there but not observed. Fidelity to an area increased with the number of whales identified there and may be a function of numbers--the more whales there are in an area the better the chance to see those whales again. The two areas with the most whales identified and the highest fidelity also have had the most abundant food resources in recent years (Bryant *et al.*, 1981; Wing and Krieger, 1983; Dolphin, 1987b; Larson *et al.*, 1991). It would seem likely that the whales that find plentiful food in one year would return to check out the same area for a similar availability of food the next year. This would increase the chance of resighting whales in the same area if they remained in the area, which would be dependent upon the whales finding sufficient food.

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. Given that the Sitka Sound whales had a comparatively high fidelity to this area, I think that the increase in numbers during the last two years of the study was due to some whales coming from unstudied areas, such as the waters offshore of Baranof Island, to feed in the Sitka Sound area. I also think that 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, rough seas, and limited daylight. The increase in whales to the Sitka Sound study area coincides with an increase in the herring stock overwintering there during the fall and early winter of the late 1980s and early 1990s (Larson *et al.*, 1991; B. DeJong, personal communication). There was a lag time, however, for the whales to "discover" the increase in herring in Sitka Sound.

The difference between the estimated total number of whales present in southeastern Alaska during 1985 to 1992 (743) and the estimate of the mean annual population (404) says that some whales do not return to this region every year due to mortality, emigration, and immigration. Some proportion of the whales in any study area will be missed, depending on whale behavior and the degree of sampling effort, which is often dependent on weather and sea conditions. Some of the missing whales also could have been present in other areas of southeastern Alaska, where humpback whales have been reported but not studied. The effect of temporary migration from those areas on open population estimators is difficult to ascertain (Pollock *et al.*, 1990). These unstudied areas are the waters offshore of Baranof Island, along the western shore of Prince of Wales Island, the inside waters of the southern part of southeastern Alaska, the waters near the city of Juneau, and Lynn Canal. The missing whales also could have been outside of southeastern Alaska. Recent studies conducted on humpback whales in northern British Columbian waters have resulted so far in three matches between whales in that area and those in southeastern Alaska (G. Ellis and J. Straley, unpublished data). It is likely that there is considerable movement of whales between northern British Columbia and southeastern Alaska. Movement of whales to other areas, such as the waters around Kodiak and the Aleutian Islands, is less probable, because the feeding aggregations of geographically isolated areas are known to be essentially discrete (Baker *et al.* 1986, 1992; von Ziegesar and Matkin, 1989; Perry *et al.*, 1990).

Baker *et al.* (1992) estimated the population size of humpback whales in the northern part of southeastern Alaska, during 1979 to 1986, to be 547 (95% confidence interval 504-590) individuals, using the Schnabel, multi-sample, closed population estimator (Seber, 1982). When the data of Baker *et al.* (1992) are used in open population models for multiple capture-recapture data, the result is a mean annual population estimate of 393 (95% confidence interval 331-455) whales for southeastern Alaska during 1979 to 1986, and this is comparable with the mean annual population estimate of 404 (95% confidence interval 350-458) for the whales present during 1986 to 1992, as described in this thesis. The similarity of these population estimates suggests that the population of humpback whales in southeastern Alaska was neither increasing nor decreasing from 1979 to 1992 or that growth was so slow that it was indiscernible. Slow population growth is characteristic of large mammals that are long-lived and have low reproductive rates, such as humpback whales (Eisenberg, 1981).

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 of those assumptions. The Jolly-Seber models presented in this thesis were accompanied by goodness-of-fit test statistics that helped the user in choosing the most appropriate model that best fits the data. For the Glacier Bay-Icy Strait area, Sitka Sound area, and the combined southeastern Alaskan study areas, all of the goodness-of-fit tests were significant, indicating that no model fitted the data very well and that some underlying assumptions of each model were violated. The nonsignificant goodness-of-fit test for the Frederick Sound study area, cannot be used to imply that the data met all of the model assumptions, because this test can have low power, especially with low capture probabilities and survival rates (Pollock *et al.*, 1990), which were extremely low in this study area.

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. Some whales could not be identified, because they never showed their flukes well enough for photo-identification. The assumption that the pattern on the ventral surface of the flukes did not change over time, I think, was less problematic, because many of the same whales were observed every year or two, hence any gradual changes were taken into account and the whales were equally identifiable over time. The most likely source of new scars added between sampling periods would be predation marks resulting from killer whale attacks, but these were uncommon. 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, while 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 that 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. The other study areas had reasonably large sample sizes, however, so that the effect of heterogeneity may not be too large (Hammond, 1986). A comparison of the estimates from both open and closed models for the combined study areas in southeastern Alaska in 1991 indicated that the negative bias resulting from unequal capture probabilities was not significant. The closed population estimator, however, which corrects for heterogeneity, is lower than the open population estimator, which does not correct for heterogeneity (and should result in an underestimation of population size). This suggests that the result from the heterogeneity model may not be comparable to open population models.

The coefficient of variation (CV) is a measure of the relative variability of an estimate (Zar, 1984). A CV of less than 20%, is sometimes considered a reasonable level of precision (Pollock *et al.*, 1990). All of the CV's for the estimates of population size for the primary study areas, were less than 20%. The Glacier Bay-Icy Strait and the combined southeastern Alaska study areas had more precise estimates, with CV's of 7%, than did the Sitka Sound and Frederick Sound study areas, the estimates for which had CV's of 18% and 15%, respectively.

The estimates of survival were lower than expected for the whales in all study areas except Frederick Sound. Elsewhere, the survival rate of adult whales has been found to be within the range of 90-96% per year (Allen, 1980). Temporary or permanent emigration can lower estimates of survival. The low estimated survival rates, in the 80% range, for whales in three of the study areas may be reflective of temporary emigration mimicking mortality. The Frederick Sound whales had an estimated mean survival rate of greater than 100%, which, of course, is a real-world impossibility. In this case, re-immigration possibly mimicked survival or heterogeneous capture probabilities.

Seasonal Movements and Migration

The seasonal movement 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 reported previously (Baker *et al.*, 1992). A similar seasonal shift from other areas to Frederick Sound, which had not been documented previously, established that the whales travel the inside waters of southeastern Alaska, rather than take the more direct route, south of Baranof Island. Seasonal observations also established the use of northern Chatham Strait as the route to Frederick Sound by whales from Glacier Bay-Icy Strait. The possibility of transit through northern Stephens Passage cannot be discounted, however, because observations from there were not included in this study.

Five whales, two of which were reported earlier by Baker *et al.* (1992), made the reverse transit from Frederick Sound to Glacier Bay-Icy Strait in late summer and early fall. These five whales may have had an individual preference for feeding on schooling fishes such as herring, which are present in Icy Strait but infrequently in Frederick Sound. Fishes are present in some years in the Frederick Sound area, in addition to euphausiids, but the latter is the predominate prey there of the whales (Andrews, 1909; Wing and Krieger, 1983; Kreiger and Wing, 1984, 1986; Dolphin, 1987a, 1987b). Four of these five whales have had long sighting histories (since 1975, 1979, 1980, and 1982) in southeastern Alaska and are believed to be males, because none of them has ever been observed with a calf.

The fall movement of whales to the Sitka Sound area and Lisianski Inlet is a seasonal response to herring schools, which move in from the open passages to overwinter in the deep, sheltered bays and sounds of southeastern Alaska. Herring move into these sheltered areas when the surface waters become cooler and the turbulence from fall storms results in thorough mixing of the water column to near-uniform temperatures (Carlson, 1984). Sitka Sound and Lisianski Inlet are both areas where herring congregate at that time (Funk, 1991; 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 Sitka Sound, and back north to Lisianski Inlet. During the fall and early winter of 1991 and 1992, there was a significant increase in the use of the Sitka Sound area by humpback whales. This increase follows an increase in the Sitka Sound herring stock during the 1980s and early 1990s (Larson *et al.*, 1991). The whales utilizing these herring may be those needing additional energy reserves for the migrations to and from the breeding grounds. In years when there are abundant resources, female humpback whales may stay longer to gain additional energy stores for improving their reproductive potential. 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. There are at least five other areas where herring are known to overwinter in southeastern Alaska and where whales have been reported during the fall and early winter (lower Lynn Canal, Tenakee Inlet, Whale Bay, Bucareli Bay, and the waters near Ketchikan). 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 breeding grounds.

Earlier, I speculated (Straley,1990a) that the whales present in southeastern Alaska during the fall and winter were late migrants--part of a staggered or irregular migrational pattern, in which the whales that arrived early departed early, and these fall-winter animals reached southeastern Alaska later and returned later to the breeding 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 early winter. Humpback whales could stay on the feeding grounds for 8 to 9 months, leave in January, and still reach the Hawaiian breeding grounds in time for peak breeding activities in February and March (Gabriele, 1992b). This would still allow enough time to return to southeastern Alaska for the next summer's feeding season, for the migrational speed from Hawaii to southeastern Alaska probably is equal to, or possible faster, than 39 days. Other studies have demonstrated much shorter stays on the feeding grounds of 4.5 months for mothers with calves and 6.5 months for pregnant females in Antarctic waters (Dawbin, 1966), and just over 6 months for various age classes in southeastern Alaska (Baker *et al.*, 1992). Even the 7-month stay documented here is considerably 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.

The segregation of whales by age, sex, and reproductive status during and prior to migration has been demonstrated for humpback whales of the South Pacific and Indian Ocean (Chittleborough, 1958; Dawbin, 1966), as well as for North Pacific humpback whales arriving on the Hawaiian breeding grounds (Gabriele, 1992b). No comparable segregation was evident among humpback whales in southeastern Alaska during the fall and early winter, just before the southward migration (Straley, 1990a). Once a whale leaves a feeding area in the fall, however, it does not necessarily make the final southbound departure for the breeding grounds. Until there is a complete study of all areas where the humpback whales congregate in the fall and early winter, it will be unknown whether segregation by age, sex, and reproductive status takes place before migration from southeastern Alaska.

Reproduction and Calf Survival

The minimal and maximal calving rates estimated in this thesis are comparable with those determined from previous longitudinal studies of humpback whales in the North Atlantic of 0.41 calves/year (Clapham and Mayo, 1990), and are close to pregnancy rates derived from whaling data of 0.37 to 0.47 calves/year (Omura, 1953; Nishiwaki, 1959; Rice, 1963; Chittleborough, 1965). The previously determined North Pacific calving rates of 0.36 (Baker *et al.*, 1992) and 0.37 calves/year (Baker *et al.*, 1987) are lower than the minimal rate reported here. This difference may be accountable to the larger sample used in this study and not due to any change in the calving rate with time. In this study, the rates were calculated from 222 sightings of females with calves, compared with 49 and 58 sightings used in Baker *et al.* (1987, 1992), respectively.

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 (Chittleborough, 1958). Other studies have used incomplete sighting histories to determine average birth intervals. Both Clapham and Mayo (1987b) and Baker *et al.* (1987) calculated birth intervals based on females with incomplete sighting histories and made untenable assumptions for the years when not sighted. The data used here 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 years between calves 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 in all the studies on birth intervals. 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 made it through the migration and to the feeding grounds, and not the actual birth interval observed on the breeding 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. The energetic demands of the reproductive cycle are high, especially for lactation (Lockyer, 1984). 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. If whale numbers are high when resources are scarce, reproduction will be suppressed. Essentially, whale reproductive rates will vary as an adaption, or in response, to changes in their environment (i.e., fluctuations in food availability). The females with the longest intervals (4 or 5 years) between births may have had extreme 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. This is consistent with the theory proposed by Ralls (1976) that females compete for resources, such as food, and a larger mother is a better mother. 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 (Clutton-Brock, 1988).

The return of known-aged whales 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 area also has been documented (Martin *et al.*, 1984; Clapham and Mayo, 1987b, 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 also could be attributed to more thorough sampling in Massachusetts Bay, compared with southeastern Alaska, because of (1) more researchers there and consequently more effort given to studying humpback whales, and (2) a smaller and simpler geographical area, where whales may be sighted more easily than in the complex archipelago of 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 five years (Chittleborough, 1958; Nishiwaki, 1959; Robins, 1960; Clapham and Mayo, 1987a; Clapham, 1992) the earliest average age at first birth would be 6 years, because a pregnancy lasts 12 months (Chittleborough, 1958). 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 at the time (Gabriele, 1992a). 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. Continued observations of whales of known age returning with their offspring are needed to establish the average age at first birth for North Pacific humpback whales.

In this thesis I have provided information regarding the seasonal distribution and population characteristics for humpback whales in southeastern Alaska. Clearly, there are pieces missing from the puzzle, but our understanding of the natural history and biology of this species in southeastern Alaska and the North Pacific in general is advancing rapidly through observational programs such as this one.

The recovery of humpback whales of the North Pacific will only occur though an increase in the population. Currently, we do not know the 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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Appendix 1. Sighting histories and regional movements of whales seen in more than one area during the same year in southeastern Alaska, 1985-1992.

NUMBER	WHALE ID #	YEAR	AREA	SIGHTING DATES	DAYS BETWEEN FIRST AND LAST SIGHTING
1.	22	1987	SITKA SOUND FREDERICK SOUND FREDERICK SOUND	MAY 13 AUGUST 31 SEPTEMBER 1	111
2.	43	1985	ICY STRAIT FREDERICK SOUND	JUNE 7,15 AUGUST 5	59
3.	68	1985	CHATHAM STRAIT SEYMOUR CANAL	NOVEMBER[1] DECEMBER 7	UNKNOWN
4.	117[2]	1986	GLACIER BAY GLACIER BAY ICY STRAIT FREDERICK SOUND	JUNE 15,20,25,30 JULY 16,19,22 JULY 25 AUGUST 30	76
5.	117	1988	GLACIER BAY GLACIER BAY ICY STRAIT GLACIER BAY FREDERICK SOUND GLACIER BAY	JUNE 6,14 JULY 3 JULY 21 JULY 26,30 AUGUST 4 AUGUST 26	81
6.	155	1985	ICY STRAIT ICY STRAIT ICY STRAIT FREDERICK SOUND	JUNE 21,27,30 JULY 11,15,24 AUGUST 8 AUGUST 30	70
7.	155[2]	1986	ICY STRAIT GLACIER BAY GLACIER BAY ICY STRAIT GLACIER BAY FREDERICK SOUND	JUNE 18 JUNE 30 JULY 6,8 JULY 8 JULY 10,12,13,14,15,21,22 AUGUST 30	73
8.	159	1987	ICY STRAIT GLACIER BAY GLACIER BAY SITKA SOUND	JULY 14,22,31 AUGUST 14,19,25 SEPTEMBER 1 DECEMBER 23	162
9.	159	1989	GLACIER BAY SITKA SOUND	AUGUST 17,14,23 DECEMBER 27	132
10.	159	1991	GLACIER BAY GLACIER BAY SALISBURY SOUND LISIANSKI INLET	JULY 13,25 AUGUST 5,16 NOVEMBER 13 DECEMBER 26	166
11.	161	1985	ICY STRAIT FREDERICK SOUND FREDERICK SOUND	JUNE 15 AUGUST 31 SEPTEMBER 1	78
12.	161	1986	GLACIER BAY GLACIER BAY FREDERICK SOUND SEYMOUR CANAL	JUNE 28,30 JULY 3,21,22 AUGUST 2,31 DECEMBER 4	159

NUMBER	WHALE ID #	YEAR	AREA	SIGHTING DATES	DAYS BETWEEN FIRST AND LAST SIGHTING
13.	161	1989	GLACIER BAY GLACIER BAY SEYMOUR CANAL SEYMOUR CANAL	JUNE 21 JULY 19 NOVEMBER 29 DECEMBER 2,3	165
14.	193	1985	ICY STRAIT FREDERICK SOUND	JUNE 4 AUGUST 6	63
15.	196[2]	1986	FREDERICK SOUND ICY STRAIT	JULY 31 AUGUST 8	8
16.	196	1989	GLACIER BAY GLACIER BAY SEYMOUR CANAL	JUNE 30 JULY 1 NOVEMBER 30	153
17.	219	1985	ICY STRAIT FREDERICK SOUND	JULY 15,18,24 SEPTEMBER 2	49
18.	221	1985	GLACIER BAY FREDERICK SOUND FREDERICK SOUND	JULY 11,17 AUGUST 5,6 SEPTEMBER 1	52
19.	221[2]	1986	GLACIER BAY ICY STRAIT GLACIER BAY FREDERICK SOUND	JULY 3 JULY 8 JULY 22,29 AUGUST 31	59
20.	221	1987	GLACIER BAY GLACIER BAY ICY STRAIT GLACIER BAY SEYMOUR CANAL	JUNE 15,18,24,29 JULY 1,2,6,13 JULY 16 JULY 20,23 SEPTEMBER 6	83
21.	221	1991	ICY STRAIT SALISBURY SOUND	AUGUST 27 OCTOBER 30	64
22.	235	1987	GLACIER BAY GLACIER BAY FREDERICK SOUND	JUNE 29 JULY 2,6,8,13,20,25 SEPTEMBER 7	70
23.	237	1987	GLACIER BAY GLACIER BAY ICY STRAIT ICY STRAIT FREDERICK SOUND	JUNE 26 JULY 8,13 JULY 22 AUGUST 8 SEPTEMBER 5	71
24.	262	1986	GLACIER BAY CHATHAM STRAIT FREDERICK SOUND	JULY 16,19 JULY 29 AUGUST 2	17
25.	262	1987	GLACIER BAY GLACIER BAY FREDERICK SOUND	JUNE 26,29 JULY 8,15,16 SEPTEMBER 9	75
26.	268	1986	SITKA SOUND CHATHAM STRAIT	JUNE 15 NOVEMBER 29	167
27.	274	1992/93	FREDERICK SOUND SITKA SOUND SITKA SOUND SITKA SOUND	AUGUST 4 OCTOBER 28 NOVEMBER 7 JANUARY 10,27	176

NUMBER	WHALE ID #	YEAR	AREA	SIGHTING DATES	DAYS BETWEEN FIRST AND LAST SIGHTING
28.	281	1985	GLACIER BAY FREDERICK SOUND	JUNE 6,24,26,28 JULY 11	35
29.	350[2]	1986	GLACIER BAY GLACIER BAY FREDERICK SOUND FREDERICK SOUND	JUNE 30 JULY 21 AUGUST 30 DECEMBER 3	156
30.	351	1992	GLACIER BAY SITKA SOUND	AUG 4 NOVEMBER 7	95
31.	397	1987	SITKA SOUND FREDERICK SOUND	JUNE 21 SEPTEMBER 7	78
32.	397	1991	CHATHAM STRAIT SALISBURY SOUND	AUGUST 8 DECEMBER 6	120
33.	397	1992	ICY STRAIT SITKA SOUND	JULY 31 NOV 2	94
34.	416	1985	ICY STRAIT FREDERICK SOUND	JULY 15 SEPTEMBER 1	48
35.	441	1986	GLACIER BAY FREDERICK SOUND	JUNE 15,19 DECEMBER 7	175
36.	455	1992	ICY STRAIT SALISBURY SOUND	JUNE 24 NOVEMBER 12	141
37.	461	1992	CHATHAM STRAIT SALISBURY SOUND SITKA SOUND	AUGUST 2 OCTOBER 9 OCTOBER 30	89
38.	507	1990	CHATHAM STRAIT FREDERICK SOUND	JULY 14 JULY 22	8
39.	539	1985	ICY STRAIT FREDERICK SOUND	JUNE 27 AUGUST 6	40
40.	539	1987	ICY STRAIT ICY STRAIT ICY STRAIT FREDERICK SOUND	JUNE 25,30 JULY 3,7,14,16,22,28,31 AUGUST 8,12 AUGUST 22	58
41.	541	1991	FREDERICK SOUND LISIANSKI INLET	AUGUST 11,12 DECEMBER 26	137
42.	545	1991/92	ICY STRAIT ICY STRAIT SITKA SOUND	JUNE 20 AUGUST 8,27 JANUARY 3, 1992	70
43.	553	1987	FREDERICK SOUND ICY STRAIT	AUGUST 23 SEPTEMBER 28	37
44.	560	1985	CHATHAM STRAIT SEYMOUR CANAL	NOVEMBER[1] DECEMBER 7	UNKNOWN
45.	564	1985	GLACIER BAY GLACIER BAY FREDERICK SOUND FREDERICK SOUND	JUNE 10,26 JULY 1 AUGUST 4,5 SEPTEMBER 1	83

NUMBER	WHALE ID #	YEAR	AREA	SIGHTING DATES	DAYS BETWEEN FIRST AND LAST SIGHTING
46.	564	1986	GLACIER BAY ICY STRAIT GLACIER BAY FREDERICK SOUND	JUNE 25,30 JULY 8 JULY 16,19,22 AUGUST 29	65
47.	566	1986	GLACIER BAY ICY STRAIT FREDERICK SOUND FREDERICK SOUND	JULY 16,17,22,28 AUGUST 18 AUGUST 30 SEPTEMBER 13,14	60
48.	577	1991	ICY STRAIT SALISBURY SOUND	JUNE 3,13,17,20 SEPTEMBER 27	116
49.	580	1991/92	CHATHAM STRAIT SALISBURY SOUND SITKA SOUND	AUGUST 8 DECEMBER 9 JANUARY 16, 1992	161
50.	580	1992	FREDERICK SOUND SITKA SOUND	AUGUST 4 OCTOBER 14	71
51.	581	1992	ICY STRAIT ICY STRAIT ICY STRAIT CHATHAM STRAIT	JUNE 5,6 JULY 2,8,16,31 AUGUST 7 AUGUST 30	86
52.	586	1991	ICY STRAIT CHATHAM STRAIT SITKA SOUND	JUNE 3 AUGUST 8 OCTOBER 30	149
53.	587[2]	1986	GLACIER BAY ICY STRAIT ICY STRAIT FREDERICK SOUND	JUNE 11,15,20 AUGUST 5,8,14 SEPTEMBER 1? DECEMBER 4	176
54.	593	1987	GLACIER BAY GLACIER BAY FREDERICK SOUND	JUNE 26 JULY 7 SEPTEMBER 9	75
55.	593	1992	GLACIER BAY GLACIER BAY FREDERICK SOUND	JUNE 17,30 JULY 1 AUGUST 4,5	49
56.	598	1991	PERIL STRAIT FREDERICK SOUND	AUGUST 4 AUGUST 12	8
57.	616[2]	1986	ICY STRAIT GLACIER BAY FREDERICK SOUND GLACIER BAY FREDERICK SOUND SEYMOUR CANAL	MAY 27 JULY 16 JULY 31 AUGUST 14 AUGUST 30 DECEMBER 4	191
58.	817	1985	ICY STRAIT FREDERICK SOUND	JUNE 8 AUGUST 4	57
59.	875	1989	ICY STRAIT SEYMOUR CANAL	JUNE 17 DECEMBER 3	169
60.	899	1991	ICY STRAIT FREDERICK SOUND	JULY 23 AUGUST 11	19

NUMBER	WHALE ID #	YEAR	AREA	SIGHTING DATES	DAYS BETWEEN FIRST AND LAST SIGHTING
61.	911	1992	FREDERICK SOUND SITKA SOUND	AUGUST 4 NOVEMBER 6	94
62.	913	1991	FREDERICK SOUND SITKA SOUND	AUGUST 12 DECEMBER 27	137
63.	933	1986	GLACIER BAY ICY STRAIT FREDERICK SOUND FREDERICK SOUND	JULY 16,17,22,28 AUGUST 18 AUGUST 30 SEPTEMBER 13,14	60
64.	937	1987	GLACIER BAY FREDERICK SOUND	JULY 15,20,23 SEPTEMBER 7,8	55
65.	941	1988	GLACIER BAY SITKA SOUND	JUNE 30 DECEMBER 22	175
66.	941	1991	ICY STRAIT ICY STRAIT SALISBURY SOUND	JULY 23 AUGUST 13 NOVEMBER 13	113
67.	941	1992	ICY STRAIT SITKA SOUND	JULY 2,31 NOVEMBER 20	141
68.	963	1992	FREDERICK SOUND SITKA SOUND	AUGUST 5 SEPTEMBER 23	49
69.	971	1992	FREDERICK SOUND SITKA SOUND SITKA SOUND	AUGUST 31 SEPTEMBER 23 OCTOBER 3	33
70.	986	1989	GLACIER BAY GLACIER BAY SEYMOUR CANAL SEYMOUR CANAL	JUNE 21 JULY 19 NOVEMBER 29 DECEMBER 2,3	165
71.	988	1988	GLACIER BAY SITKA SOUND	JUNE 28 NOVEMBER 12	137
72.	1014	1991	GLACIER BAY GLACIER BAY GLACIER BAY LISIANSKI INLET	JUNE 25 JULY 5,9,12,13 AUGUST 3 DECEMBER 26	184
73.	160	1987	ICY STRAIT GLACIER BAY SEYMOUR CANAL	MAY 29 JULY 1,2 AUGUST 22	85
74.	160	1991	GLACIER BAY GLACIER BAY ICY STRAIT GLACIER BAY LISIANSKI INLET	JUNE 24,28 JULY 3,5,21,24 AUGUST 8 AUGUST 13,14,16,22,27 DECEMBER 26	185
75.	1029	1988	FREDERICK SOUND ICY STRAIT	AUGUST 5 AUGUST 16	11
76.	1033	1988	GLACIER BAY SITKA SOUND	JUNE 30 DECEMBER 22	175

NUMBER	WHALE ID #	YEAR	AREA	SIGHTING DATES	DAYS BETWEEN FIRST AND LAST SIGHTING
77.	1062GB	1991	GLACIER BAY GLACIER BAY SALISBURY SOUND SITKA SOUND	JULY 23 AUGUST 8 NOVEMBER 13 DECEMBER 10	140
78.	1067	1987	SEYMOUR CANAL SITKA SOUND	SEPTEMBER 6 DECEMBER 28	113
79.	1073	1991	ICY STRAIT SITKA SOUND LISIANSKI INLET	JUNE 3 DECEMBER 15 DECEMBER 26	206
80.	1079	1987	CHATHAM STRAIT FREDERICK SOUND	JUNE 23 SEPTEMBER 7	76
81.	1086	1991	PERIL STRAIT FREDERICK SOUND	AUGUST 4 AUGUST 12	8
82.	1087	1991	CHATHAM STRAIT SALISBURY SOUND	AUGUST 8 DECEMBER 9	123
83.	1088	1991	CHATHAM STRAIT SALISBURY SOUND	AUGUST 8 DECEMBER 8	122
84.	1102	1992	CHATHAM STRAIT SITKA SOUND	SEPTEMBER 1 OCTOBER 26	55
85.	1103	1991	SITKA SOUND LISIANSKI INLET	OCTOBER 10,11 DECEMBER 26	77
86.	1108	1992	PERIL STRAIT SITKA SOUND	AUGUST 29 OCTOBER 14,28	46
87.	1109	1992	PERIL STRAIT SITKA SOUND	AUGUST 29 OCTOBER 14,28	60
88.	1110	1991	FREDERICK SOUND SITKA SOUND	AUGUST 3 OCTOBER 1,28	86
89.	1124	1992	FREDERICK SOUND SITKA SOUND	AUGUST 5 NOVEMBER 7	94
90.	1165	1985	ICY STRAIT FREDERICK SOUND	JUNE 8 SEPTEMBER 3	87
91.	1179	1992	GLACIER BAY SITKA SOUND	AUGUST 18 OCTOBER 30	73
92.	1204	1992/93	FREDERICK SOUND SITKA SOUND	AUGUST 6 JANUARY 16, 1993	163

[1] PHOTO COURTESY OF NOAA SHIP FAIRWEATHER, EXACT DATE UNKNOWN.
[2] MOVEMENT FROM GLACIER BAY TO FREDERICK SOUND AND FREDERICK SOUND TO GLACIER BAY PREVIOUSLY REPORTED IN BAKER et al., 1992.