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POPULATION CHARACTERISTICS AND MIGRATION OF SUMMER AND LATE-SEASON HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN SOUTHEASTERN ALASKA

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Abstract

A total of 326 humpback whales (*Megaptera novaeangliae*) were individually identified in southeastern Alaska during five summer seasons (July to September) and four late seasons (November to February) spanning the years 1979 to 1983. Peak numbers of whales were found late in August or early in September. Whales arrived 1–2 wk later in 1982 than in 1981. Whales sighted in both the summer and late seasons of 1981 and 1982 remained about 3.7 mo and one whale remained for at least 4.9 mo. Humpback whales from southeastern Alaska wintered in Hawaiian or Mexican waters, but generally did not travel to other feeding regions. The most rapid migratory transit between Hawaii and southeastern Alaska was 79 d. Based on mark-recapture analyses of the photographic data, we estimate a population of 270–372 whales in the southeastern Alaska feeding herd.

Key words: humpback whales, photographic identification, southeastern Alaska, overwintering, feeding herd, migration, mark-recapture, abundance.

The North Pacific population of humpback whales feeds in the summer and fall along the upper rim of the North Pacific Ocean. Known feeding areas include sites along the coasts of British Columbia, southeastern Alaska (the Alexander Archipelago), the Gulf of Alaska and the Aleutian Islands (Nemoto 1957, Pike and MacAskie 1969, Hall 1979, Rice and Wolman 1982). Humpback whales also summer in the southern Bering Sea, the waters near the Kamchatka Peninsula and the Farallon Islands of central California (Omura 1955, Tomilin 1957, Nasu 1963, Dohl 1983).

Humpback whales in the North Pacific are thought to number around 1,200 animals (Rice and Wolman 1982), but the distribution of these animals on the summer grounds is poorly understood. Of the known feeding areas in the North Pacific, only two have been reasonably well studied in recent years: Prince William Sound and southeastern Alaska. Work in Price William Sound has concentrated on assessing the distribution and abundance of humpbacks through vessel surveys and photographic identification (Hall 1979, Rice and Wolman 1982). These reports suggest that 40–60 humpbacks return annually to this region.

Humpback whales in southeastern Alaska have been the subject of more extensive population studies. Their abundance has been estimated from survey "indices" of Japanese whalers (Rice 1978), direct photographic identification counts (Jurasz *et al.* 1981, Baker *et al.* 1982, Baker *et al.* 1983, Darling and McSweeney 1983) and mark-recapture methods based on photographic identification (Baker *et al.* 1982, Baker *et al.* 1983). These estimates range from a low of 60 whales, based on indices of abundance (Rice 1978), to 414 ± 54 whales, based on the mark-recapture analysis of photographs collected in 1981 and 1982 (Baker *et al.* 1983).

Here we report some of the combined results from three independent studies, spanning five consecutive years, of humpback whales in southeastern Alaska. The results provide insight into the seasonal influx, duration of occupancy and abundance of whales in southeastern Alaska. Data on concentrations of late-season humpback whales found in southeastern Alaska during November, December, January and February are examined in relation to data from summer months. Finally, observations are presented on the migratory destinations and migratory rates of southeastern Alaska whales.

Materials and Methods

Each of the three studies summarized in this paper provided information from different years or times of year during the period 1979–1983. The combined data provided a more complete picture of the population characteristics of humpback whales in southeastern Alaska than would have been possible from any single study. Data on seasonal influx, periods of occupancy and abundance were drawn from studies during the summers of 1981, 1982 and 1983 (Baker *et al.* 1982, Baker *et al.* 1983). Additional data on abundance were drawn from work during the summers of 1979 and 1980 (Lawton 1979). Late-season aggregations of whales were studied during the fall and winters of

1979 through 1982 (Straley and Straley 1983). Although the study areas and study periods differed somewhat each year, the general methods of data collection were similar in the three studies.

Photographic Methods

Humpback whales were observed and photographed by teams of two or three researchers operating from small outboard-driven boats. Photographs of whales were taken with 35-mm single-lens reflex cameras equipped with motor drives and 300-mm telephoto or 70- to 210-mm zoom lenses. High-speed black-and-white or color film was used. In all cases we attempted to obtain clear photographs of the ventral surface of the tail flukes. The unique coloration, shapes and scarring patterns of the flukes allowed for reliable identification of individuals (Katona *et al.* 1979).

From each observation of a whale or group of whales, the best photograph of each individual's flukes was assigned a "fluke observation" number. Information on the location, date of sighting and social affiliation of each fluke observation was stored on computer at the Kewalo Basin Marine Mammal Laboratory, University of Hawaii. At present, this library contains 2,020 fluke observations of 1,039 individual whales identified in the central and eastern North Pacific from 1976 to 1983. Some of the photographic data used in this paper are also on file with the Photographic Identification Storage and Retrieval System (PISAR) at the National Marine Mammal Laboratory, Seattle, Washington.

All fluke observation photographs were judged to be of either good, fair or poor quality. Good and fair photographs showed at least 50 percent of each fluke at an angle sufficiently vertical to distinguish the shape of the flukes' trailing edge. For the purposes of this study, only good and fair quality photographs were used.

Mark-Recapture Methods

Mark-recapture formulae were applied to the individual identification data in order to estimate the abundance of whales in southeastern Alaska. For these analyses an animal was considered "marked" or "sighted" when it was photographically identified. Any subsequent resighting of that individual was considered a "recapture" or "resighting." Two mark-recapture methods were used: the Petersen estimate and the Jolly-Seber method (Caughley 1977, Begon 1979). The Petersen method requires marking on only one occasion and a single recapture. The Jolly-Seber method makes use of the information on multiple captures available in the data. The Jolly-Seber population estimates were consistent with the Petersen estimates and are not reported here. The assumptions based on the Petersen mark-recapture method are presented in the discussion.

Study Periods and Locations

Research effort was concentrated in three study areas within southeastern Alaska (Fig. 1): (1) the confluence of Frederick Sound and Stephens Passage;

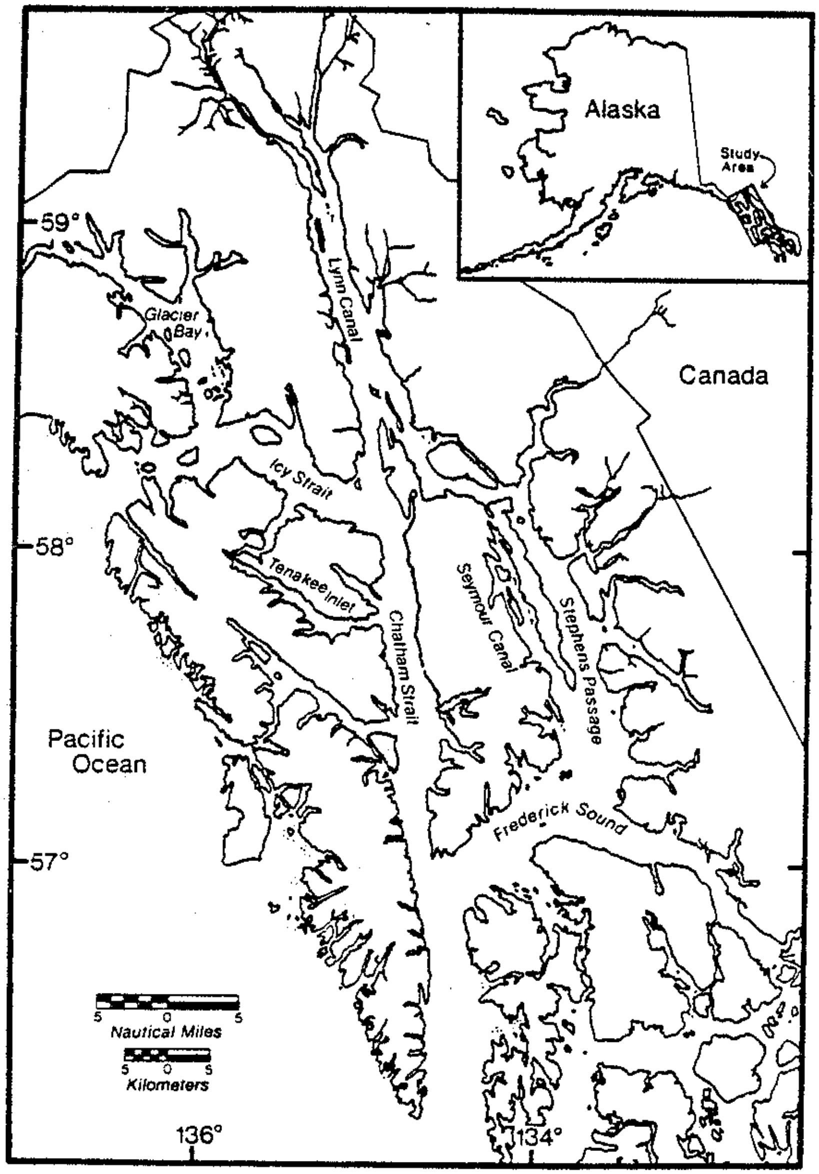

Figure 1. The southeastern Alaska study area.

(2) Glacier Bay within the Glacier Bay National Park and Preserve and parts of Icy Strait adjacent to the mouth of the bay; and (3) Seymour Canal, a long narrow inlet open at its southern end to Stephens Passage and bordered by the Admiralty Island National Monument. Other areas occasionally surveyed during the summer studies included Chatham Strait, northern Stephens Passage and eastern Icy Strait. All late-season studies were conducted in Seymour Canal.

Table 1. Seasonal study periods and locations in southeastern Alaska.

Summer		
Year	Dates	Location
1979	18 Jun–25 Aug	Frederick Sound—Stephens Passage
1980	01 Jul–14 Sep	Frederick Sound—Stephens Passage
	12 Aug–21 Aug	Chatham Strait
1981	29 Jun–03 Sep	Frederick Sound—Stephens Passage
	15 Jul–23 Jul	Glacier Bay—Icy Strait
	04 Sep–08 Sep	Chatham Strait
1982	09 Jul–01 Sep	Frederick Sound—Stephens Passage
	12 Jul–15 Aug	Glacier Bay—Icy Strait
1983	05 Jul–13 Sep	Glacier Bay—Icy Strait
	01 Sep–09 Sep	Frederick Sound—Stephens Passage

Late-season		
Years	Dates	Location
1979–1980	18 Nov–07 Mar	Seymour Canal
1980–1981	18 Nov–07 Jan	Seymour Canal
1981	18 Nov–04 Dec	Seymour Canal
1982	23 Nov–10 Dec	Seymour Canal

Study periods spanned roughly a 2-mo period from early July to early September in each of the five summer seasons (Table 1). Late-season study periods were more variable, spanning from November to March in the 1979–1980 season and from 23 November to 10 December in 1982.

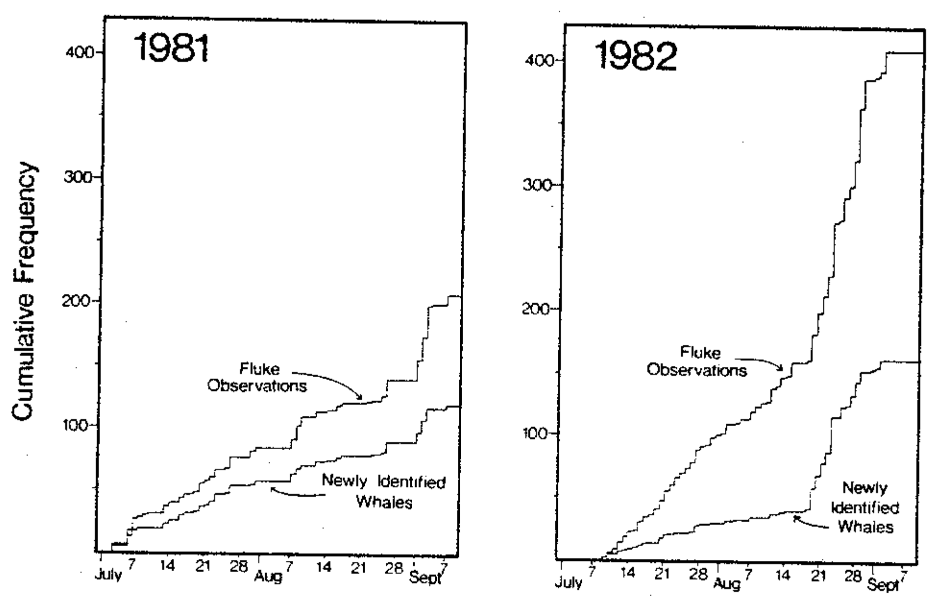

Figure 2. The cumulative frequency of fluke observations and newly identified whales (whales not previously identified that season) for 1981 and 1982.

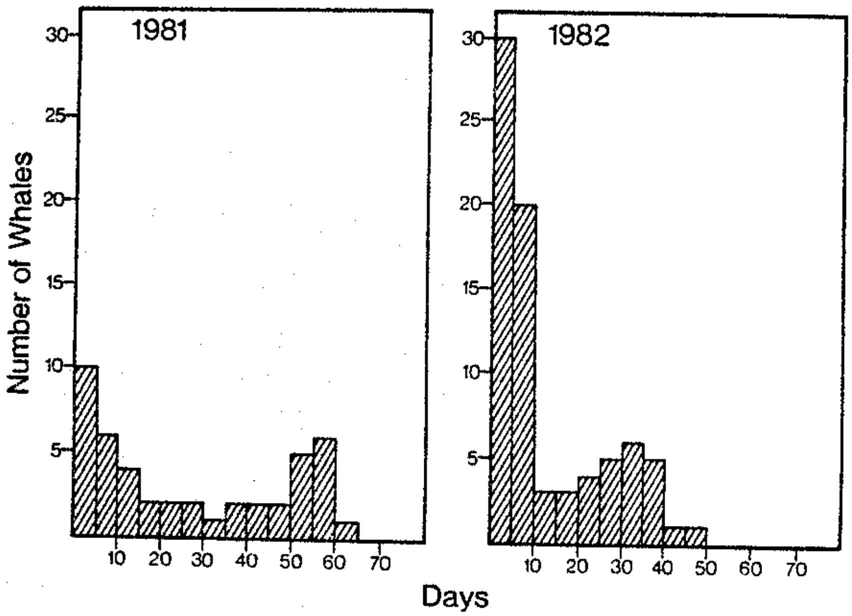

Figure 3. Occupancies (the interval between first and last sightings) of individually identified whales during 1981 and 1982.

Results

Seasonal Influx

Summer—The rate at which fluke observations were collected during 1981 and 1982 provided an indication of the seasonal changes in abundance. A total of 620 fluke observations was collected during 1981 and 1982 (Fig. 2). Fluke observations were collected on 35 d in 1981 and 51 d in 1982. The largest numbers of whales photographed on a single day were 25 on 3 September 1981, and 43 on 23 August 1982. The rate at which whales were photographed per day in 1981 remained fairly steady through the second week of August. There was a slight decrease in the fluke observations per day in the third week of August due to bad weather, followed by an increase early in September. In 1982 the rate of whales photographed per day remained steady until about 20 August, when it increased sharply.

Figure 2 also shows the cumulative total of individual whales identified on each day that had not been identified previously that season (newly sighted whales). A total of 124 individuals were identified in 1981 and 144 in 1982. The largest numbers of new whales photographed on a single day were 10 on 2 September 1981, and 28 on 23 August 1982.

The cumulative frequency of newly sighted whales in 1981 showed a steady increase throughout the season. The increased rate of fluke observations early in September 1981 was not reflected markedly in the number of new whales. The rate of increase in new whales in 1982 declined between about 18 July and 20 August, followed by a sharp increase that nearly paralleled the increase in fluke observations.

Using only the dates encompassed by the study periods in both years (9 July–2 September), the median date on which whales were newly sighted was 7 August in 1981, significantly earlier than the median date of 22 August in 1982 (Wilcoxon two-sample test, $P = 0.002$). This shift in seasonal influx was also reflected in the date of first sighting of the 54 individual whales seen in both years. A pair-wise comparison showed that these whales were first sighted, on average, 7.8 d earlier in 1981 ($SD = 23.6$, $t(52) = 2.43$, $P = 0.019$).

Late season—Due to inclement weather and short daylength during the late-season studies, photographic observations could not be collected as consistently as during the summer seasons. Consequently, changes in late-season abundance cannot be determined reliably from the photographic data. Instead, we present some results based on opportunistic boat and shore-based surveys.

The largest daily count in Seymour Canal was 35 whales on 25 November 1979. The number of whales observed slowly declined throughout December and January. No whales were seen after 12 February to the end of the study on 7 March. A total of eight whales were individually identified. Trends were similar during the 1980 late season. The largest daily count was 34 whales on 21 November and at least three whales were present on 7 January 1981, when the study ended. A total of nine whales were individually identified.

During the short 1981 study period, the largest daily count was 28 whales on 23 November. A total of 27 whales remained on 3 December. Forty-four whales were individually identified this season. A much larger number of whales was found in Seymour Canal during the 1982 late season than in the three previous seasons. The largest count of 61 whales occurred on 4 December. This number declined rapidly and only 17 whales were counted on 10 December. Sixty-one whales were individually identified during this late-season period.

Occupancy

Summer—In 1981, 45 (36 percent) of the 124 individual whales were sighted on more than one day. In 1982, 78 (54 percent) of the 144 individual whales were sighted on more than one day. The interval between first and last sighting of a whale during a single season provided an estimate of its minimum period of occupancy in an area (Fig. 3). The distribution of occupancy intervals during the summer of 1981 was distinctly bimodal. The distribution of intervals during the summer of 1982 was also bimodal but showed a much greater proportion of shorter intervals. The longest periods after which an identified whale was resighted within a season were 63 d in 1981 and 46 d in 1982.

Late season—The first and last photographic sightings of whales seen in both the summer and late season of a given year provided an expanded estimate of occupancy in southeastern Alaska. Only one whale sighted in the summer of 1979 was subsequently found during the late season that year. No whales sighted in the summer of 1980 were found that fall or winter. Twenty of the 44 late-season whales in 1981 had been seen earlier that summer. Their average

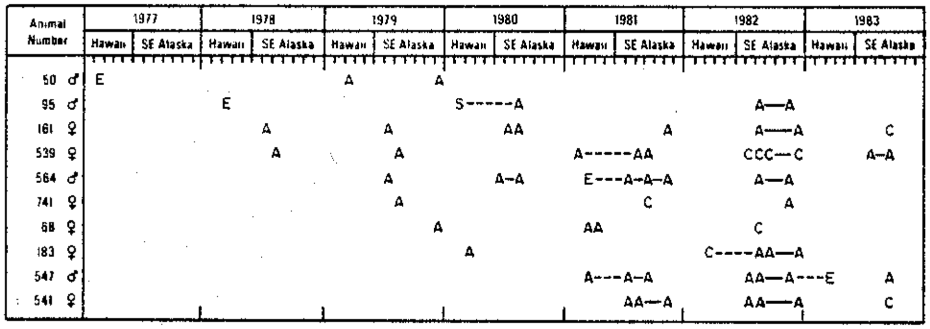

Figure 4. The resighting histories of late-season whales of known sex. Individually identified whales are designated by their sex and animal number. Monthly sightings are shown across rows. Solid lines or adjacent letters indicate presumed regional occupancy. Broken lines indicate presumed migratory transits. Letters indicate behavioral roles: A, adult; C, cow with calf; E, escort; S, singer.

occupancy was 113.6 d (SD = 23.7 d) and the maximum occupancy was 145 d. Twenty-seven of the 62 late-season whales in 1982 had been seen earlier that summer. Their average occupancy was 110.9 d (SD = 16.6 d) with a maximum of 148 d.

To determine if the age-sex class of an individual affected its tendency to remain in southeastern Alaska during the late season, we examined the resighting histories of 10 late-season whales whose sex was known or surmised (Fig. 4). Six animals were thought to be reproductively mature females based on their close association with a calf in Alaska or Hawaii during one or more years. Mature females were observed in at least four reproductive stages: (1) resting just prior to conception (#541 in 1981, #161 in 1981); (2) pregnant (#541 in 1982, #161 in 1982); (3) presumably still lactating (#539 with calf in 1982); and (4) following the apparent loss of a calf (#183 in 1982).

Four individuals were thought to be mature males based on their roles as singers or escorts in Hawaii. Singing and escorting during the winter breeding

Table 2. The number of years individual whales were sighted in each seasonal study.[1]

Seasonal habitat	Years sighted 1	2	3	4	5	Total whales
Summer	162 (55.7)	70 (24.0)	39 (13.4)	18 (6.2)	2 (0.7)	291
Late-season	83 (81.4)	18 (17.6)	1 (1.0)			102
Combined	172 (52.8)	88 (27.0)	43 (13.2)	20 (6.1)	3 (0.9)	326

[1] Percentages of total whales are shown in parentheses.

Table 3. Across-year resighting of whales in southeastern Alaska during summer seasons.[1]

Sighting (year)	Resighting year				
	1979	1980	1981	1982	1983
1979 (n = 75)	(22)	29	35	37	10
1980 (n = 114)		(43)	52	39	9
1981 (n = 124)			(31)	57	21
1982 (n = 144)				(55)	26
1983 (n = 44)					(11)

[1] The number of whales sighted in only one study year is shown in parentheses.

season are thought to be behaviors sex-specific to mature males (Winn *et al.* 1973, Glockner-Ferrari and Ferrari 1981, Baker and Herman 1984*a*). On 29 December 1979, and 5 January 1980, loud singing was heard from one or more of the five whales in Seymour Canal. It seems probable that one of the singing whales was animal #50, a presumed male.

Abundance

After accounting for across-year resightings, 291 whales were identified during the five summer seasons and 102 were identified during the four late seasons (Table 2). Sixty-seven (66 percent) of the late-season whales were sighted in at least one summer season. Adding the remaining 35 late-season whales to the 291 summer whales gave a grand total of 326 individuals identified across the five-year study. From this combined total of identified whales, 154 (47 percent) were sighted in southeastern Alaska during more than one year.

Mark-recapture methods were applied to the yearly resighting data in order to estimate the abundance of humpback whales in southeastern Alaska. To satisfy some of the assumptions of the mark-recapture methods, only data from the summer study periods were used in these estimates (Table 3). The four Petersen estimates for each pair of contiguous years were consistent, ranging from 240 to 310 animals (Table 4). The 95 percent confidence intervals, based on Cochran's normal approximation (Seber 1982), range from a low of 197 in 1983 to a high of 402 in 1980, and all show a considerable amount of overlap.

Migratory Destinations

Photographs from known summering and wintering grounds in the North Pacific were compared to determine the migratory destinations of southeastern Alaska humpback whales (Table 5). The six regions used in the comparison include two wintering grounds (Hawaii and Mexico) and four other feeding regions (Yakutat Bay, Prince William Sound, the Gulf of Alaska west of Prince William Sound and the Farallon Islands). Although the migratory destinations of southeastern Alaska summer and late-season whales were similar, they are shown separately for comparison in Table 5.

Table 4. Petersen mark-recapture population estimates.

Years	*n*	95% confidence limits
1979–1980	288	233–402
1980–1981	269	234–325
1981–1982	310	270–372
1982–1983	240	197–320

Of the 326 whales identified in southeastern Alaska during the five study years, 46 were also identified in Hawaii during at least one winter. One whale sighted in southeastern Alaska during the summer and late season was sighted near the Islas de Revillagigedo, Mexico, during the winter of 1980.

To determine if southeastern Alaska humpback whales have a preferred migratory destination, we calculated the probability of resighting between seasonal habitats as

$$P = R/(N_1)(N_2)$$

where R is the number of resights between southeastern Alaska and either Hawaii or Mexico, N_1 is the number of photographs from southeastern Alaska and N_2 is the combined sample from the wintering grounds (Hawaii and Mexico). This probability (0.00023) is equivalent to the inverse of the uncorrected Petersen population estimate based on the samples from the two seasonal habitats (Begon 1979). Using this common resighting probability, the expected resights between southeastern Alaska and each wintering ground were calculated separately (southeastern Alaska to Hawaii = [326][583][0.00023] = 43.7; southeastern Alaska to Mexico = [326][43][0.00023] = 3.2). Comparing the observed number of resights to the expected, it was not possible to reject the null hypothesis that whales from southeastern Alaska were equally represented on each wintering ground (Chi-square [1] = 1.66, $P > 0.10$).

During this study, no matches were made between southeastern Alaska and the following feeding regions: Prince William Sound, the Gulf of Alaska west of Prince William Sound and the Farallon Islands. One individual was sighted in Yakutat Bay on 24 June 1980, and in Glacier Bay (southeastern Alaska) on 11 August 1982. A 1984 survey of southeastern Alaska, however, resulted in two matches with whales photographed previously in Prince William Sound.[1]

Migratory Rates

Five whales were found in southeastern Alaska during the fall or winter and in Hawaii later that same winter (Table 6). The most rapid migratory transit was recorded for animal #203, last seen in southeastern Alaska on 8 December 1982, and first seen in Hawaii on 25 February 1983. Using the minimum

[1] The 1984 photographs were collected by one of the authors (Baker) as part of a research project directed by Ken Krieger and Bruce Wing of the Auke Bay Laboratory, National Marine Fisheries Service.

Table 5. Number of whales from southeastern Alaska resighted in other regions of the North Pacific.[a]

	Southeastern Alaska		
	Summer 1979–1983 $n = 291$	Late season 1979–1982 $n = 102$	Total 1979–1983 $n = 326$
Hawaii 1976–1982 $n = 583$[b]	43	14	46
Mexico 1978–1980 $n = 43$[c]	1	1	1
Western Gulf of Alaska 1980 $n = 15$[d]	0	0	0
Prince William Sound 1977–1982 $n = 55$[d,e]	0	0	0[f]
Yakutat Bay 1980 $n = 5$[d]	1	0	1
Farallon Islands 1983 $n = 8$[g]	0	0	0

[a] n is the number of individual whales photo-identified in each region. The body of the table shows the number of resights between southeastern Alaska and the other region.

[b] Photographs courtesy of the Kewalo Basin Marine Mammal Laboratory, the authors (Baker and Herman) and Greg Kaufman, the Pacific Whale Foundation.

[c] Photographs courtesy of Dr. Howard Winn, University of Rhode Island, and the authors (Lawton).

[d] Photographs courtesy of Allen Wolman, Dale Rice, Marilyn Dahlheim and Mark Towner, National Marine Mammal Laboratory.

[e] Photographs courtesy of Dr. John Hall, John Reinke, Brad Hanson and Colin Miller.

[f] Two matches were made between whales from Prince William Sound and whales photographed in southeastern Alaska during 1984 (see text for details).

[g] Photographs courtesy of Jan Ostman, Gulf of Farallones Research Group.

distance between Hawaii and southeastern Alaska (about 4,500 km) and the shortest period of transit (79 d) yielded a minimum migratory speed of 2.38 km/h, traveling 24 h a day. The average migratory speed of the five whales was 1.88 km/h (SD = 0.29).

Discussion

Seasonal Influx

Both in 1981 and 1982 the largest numbers of whales were found in late August and early September, primarily in Frederick Sound and Stephens Pas-

Table 6. Migratory transits of late-season whales.

Animal number	Last sighting Southeastern Alaska	First sighting Hawaii	Migratory transit (d)	Minimum speed (km/h)
#553	24 Nov 1981	21 Mar 1982	117	1.60
#542	24 Nov 1981	15 Mar 1982	111	1.69
#232	29 Nov 1981	15 Mar 1982	106	1.77
#547	29 Nov 1982	7 Mar 1983	98	1.92
#203	8 Dec 1982	25 Feb 1983	79	2.38

sage. The steady increase in newly identified whales suggested that humpback whales moved into southeastern Alaska and the study areas throughout the summers of 1981 and 1982. Three patterns of whale movement could have contributed to the late-summer peak in the abundance of whales: (1) arrival from the breeding grounds; (2) movement from other feeding grounds; or (3) local movement from unstudied areas in southeastern Alaska.

The peak numbers of humpbacks are found in Hawaii from mid-February to mid-March and a substantial number remain through April (Herman and Antinoja 1977, Herman *et al.* 1980, Baker and Herman 1981). Using Dawbin's (1966) calculated migratory rate of 15 degrees of latitude per month for a direct north–south migration route, humpback whales traveling from Hawaii to southeastern Alaska should take approximately 3 mo. Using our migratory rate determined from photographic resighting, the journey would take slightly less time. Either migratory rate would place the whales' arrival in southeastern Alaska somewhere between mid-June and late July. This is somewhat early to account for the late-summer influx. It is interesting, however, that the peak number of whales was found in southeastern Alaska just six months offset from the period of peak abundance on the Hawaiian breeding grounds. The possibility cannot be excluded that some whales continued to arrive in southeastern Alaska late in the summer after feeding and migrating slowly from areas to the south.

Presently available data (reviewed later) indicate that the waters of southeastern Alaska encompass the summer range of a segregated feeding herd. However, the exact geographical boundaries of this range are unknown. Our surveys in Glacier Bay, Icy Strait, Chatham Strait, Stephens Passage and Frederick Sound have covered only a portion of the available habitat. Humpback whales are reported from many unstudied areas, including the Fairweather Grounds, Sitka Sound, Lynn Canal, Sumner Strait and Dixon Entrance. Surveys by one of the authors (Lawton) during the summer of 1984 found 60–70 animals along the west coast of Prince of Wales Island, just south of our study area. It seems likely, therefore, that much of the influx into Frederick Sound and Stephens Passage during late summer was the result of movement from these adjacent areas.

The date of first sighting for all whales and the pair-wise comparison of individuals seen in 1981 and 1982 indicated that individual whales arrived, on average, about 1–2 wk later in 1982 than in 1981. Similar shifts in the migratory timing of humpbacks have been reported in other parts of the Northern Hemisphere (Nishiwaki 1960, Baker and Herman 1981, Whitehead *et al.* 1982). More dramatic evidence of variability in migratory timing comes from our late-season sightings of whales in southeastern Alaska. Groups of late-season whales were found in Seymour Canal in each of the study years. The largest number, nearly twice that counted in previous years, was found during December 1982. In each year the whales were vigorously feeding during the daylight hours. Analyses of feces (Krieger and Wing 1984) and visual observations indicated that the predominant prey included both schooling fish and euphausiids.

The environmental cues influencing the timing of humpback-whale migration remain grounds for speculation. Dawbin (1966) proposed that seasonal changes in length of daylight initiate migration and account for the invariant migratory cycle observed in the Southern Hemisphere. This proposal is contradicted by the reported variance in the timing of migration in the Northern Hemisphere. Nishiwaki (1960) proposed that lunar cycles or changes in surface sea temperatures influence the timing of humpback whale arrival on the wintering grounds. Neither of these factors can account for the variable departure times of late-season whales in southeastern Alaska.

An important but poorly understood factor determining the departure of humpback whales from the summering grounds is the abundance and availability of a late-season food source. Brodie (1975) speculated that the energetic costs of remaining in cold water could be more than offset by finding and exploiting a rich food source. This proposal is strongly supported by our observations of whales feeding in southeastern Alaska until at least early February.

Other factors influencing departure from the feeding grounds may be the age, sex and reproductive strategy of an individual. Among humpback whales, the timing of migratory departures from seasonal habitats is related to the age-sex class of an individual (Nishiwaki 1960, Chittleborough 1965, Dawbin 1966). However, we did not find any strict segregation of this kind in our late-season groups. Late-season whales included calves less than one year old, mature males and mature females in several reproductive stages.

Although most mating and calving are thought to take place in transit to or on the breeding grounds (Chittleborough 1965), our reports of singing by late-season whales suggest that some behavioral and physiological changes thought to be associated with breeding can proceed in northern waters. Whether singing in northern waters results in breeding and reproductive success is unknown. We can only conclude that the decision to migrate is complex, involving both environmental and biological factors, and is subject to considerable individual variability.

Occupancy

It is difficult to estimate an average occupancy period for whales in southeastern Alaska based only on summer studies. Summer occupanies are underestimates resulting from the limited timeframes of the study periods. The average occupancy derived from the combined summer and late-season studies, about 3.7 mo (113.6 d in 1981 and 110.9 d in 1982), is a better estimate, and the maximum observed resighting interval of 4.9 mo (148 d) is not an unreasonable estimate.

Late-season sightings have been used to suggest that humpback whales commonly overwinter in southeastern Alaska and other feeding areas. Cuccarese and Evans (1981), citing Berzin and Rovnin's (1966) report of humpbacks near the eastern Aleutians during December, assumed that these whales were foregoing migration to southerly wintering grounds. Our observations of rapid migratory transits caution against this assumption. Humpback whales can be found in Hawaii as early as October or as late as the first week of June. Given this broad range of sighting dates on the wintering grounds, it cannot be assumed that whales seen in southeastern Alaska during the late fall, winter or early spring have not or will not travel south that year. Although humpbacks are sighted in southeastern Alaska during all months of the year, no single individual has yet been documented to remain throughout the winter. If overwintering occurs in southeastern Alaska, it is probably not as common as late-season sightings would suggest.

The bimodal distribution of occupancies suggests some whales established preferred ranges within the study area while others were relatively transient. If individuals were uniformly available for sighting at all times during a season, a Poisson distribution of resighting intervals would be expected.

The local movement of whales in southeastern Alaska may reflect complex foraging strategies to exploit seasonal changes in the distribution and abundance of prey species. Early in the summer, when large concentrations of prey are not available, whales may continue to arrive in southeastern Alaska and remain dispersed or scattered in small pockets throughout the region. The relatively early arrival of whales in Glacier Bay (Jurasz and Palmer 1981, Baker *et al.* 1983) indicates that it is an important area for early-summer feeding. In late August and early September, when swarms of euphausiids are common in Frederick Sound and Stephens Passage (Wing and Krieger 1983), whales congregate there in large numbers. Later in the fall and winter some whales remain in areas like Seymour Canal, where concentrations of late-season prey such as schooling herring and adult euphausiids are available.

Migratory Destinations

Humpback whales from southeastern Alaska migrated to at least two geographically distinct wintering grounds separated from each other by more than 4,800 km: the main Hawaiian Islands and the west coast of Mexico. These observations corroborate other recent data on humpback whale migration in the North Pacific (Lawton *et al.* 1979, Baker *et al.* 1982, Darling and Jurasz 1983).

Using only the observations of early whalers, Kellogg (1929) suggested that humpback whales in the North Pacific were divided into an American stock and an Asian stock. He proposed that the American stock breeds in the islands near Mexico and travels northward along the coast of western North America to feeding grounds in the Gulf of Alaska and the Aleutians. The Asian stock was thought to winter near the islands south of Japan and travel north along the coast of Japan to feeding areas in the Sea of Okhotsk and along the Kamchatka Peninsula. Kellogg did not consider a migratory route for the Hawaiian group and may have been unaware of this group's existence (Herman 1979).

Based on Kellogg's proposal, a greater proportion of photographic matches would be expected between southeastern Alaska and Mexico than between southeastern Alaska and Hawaii. This was not the case. Although a proportionately larger number of southeastern Alaska whales migrated to Hawaii, we could not determine a preferred wintering ground from the available photographic data.

Humpback whales in southeastern Alaska and other areas in the North Pacific may form discrete feeding herds similar to those formed by humpback whales in the northwest Atlantic (Whitehead 1982, Katona *et al.* 1983). The number of whales documented moving between southeastern Alaska, Prince William Sound and Yakutat Bay was small in comparison to the number returning to southeastern Alaska. Strong fidelity to specific feeding areas, including southeastern Alaska (Jurasz and Palmer 1981, this paper), Prince William Sound (Hall 1979) and other parts of the Gulf of Alaska (Rice and Wolman 1982) is shown by the resightings of individuals in the same region across many years. Further evidence of some segregation among feeding regions in the eastern and central North Pacific comes from an analysis of humpback whale fluke coloration. Data from the Kewalo Basin Marine Laboratory show that the flukes of humpback whales in southeastern Alaska are darker than the flukes of whales from more westerly feeding regions. Earlier, Herman and Antinoja (1977) reviewed data showing that the dorsal coloration of humpback whales' flippers varied across regions of the North Pacific. Similar distinctions are found between stocks of humpback whales in the Southern Hemisphere (Omura 1953).

Migratory Rates

Chittleborough (1953) estimated a migratory rate of 8 km/h for humpback whales based on short-term observations of swimming speed. Dawbin (1966) used the time delay between seasonal peaks in the catches of shore-based whaling stations at different latitudes to estimate an average rate of 2.28 km/h (15 degrees per month) for the entire migratory transit. The fastest documented migratory rate of southeastern Alaska whales, 2.38 km/h, agrees closely with Dawbin's estimate. However, our estimate, like Dawbin's, makes the unlikely assumption that the migrating whales followed a straight-line path between seasonal habitats. It is also unlikely that migrating whales were photographed on their last day in southeastern Alaska or on their first day in Hawaii. The actual time in migratory transit may be considerably less than implied by the photographic data.

Abundance

The Petersen mark-recapture model is based on the following assumptions (Caughley 1977, Begon 1979): (1) all marks are permanent and are noted correctly on recapture; (2) all individuals, whether marked or unmarked, have an equal chance of being caught during each sample; (3) sampling periods are short in relation to the time between sampling periods; and (4) there are no births or immigrations and no deaths or emigrations between mark and recapture. Although mark-recapture methods based on fluke photographs have been used previously to estimate populations of humpback whales (Baker *et al.* 1982, Whitehead 1982, Baker *et al.* 1983, Darling *et al.* 1983), it is important to examine the degree to which the southeastern Alaska data satisfy these assumptions before considering the estimates.

The markings and shape of the flukes of humpback whales remain stable over periods of at least five years (Katona *et al.* 1979, Jurasz and Palmer 1981). Although a recent study by Carlson and Mayo (1983) showed that in some cases the coloration of the flukes changes during the first year or two after birth, the characteristic shape of the flukes is not affected.

A photographic mark can be improperly noted in two ways. Photographs of different whales could be counted as a single whale, resulting in a negative bias in the population estimate, or photographs of a single whale could be counted as different individuals, resulting in a positive bias. We were very stringent in the requirements for a match and it is improbable that two different whales were considered to be the same individual. Although this is a conservative approach to the identification process, it could lead to an inflated population estimate. The use of only good and fair quality photographs in the comparisons should serve to counter this bias.

Several aspects of the ecology and behavior of whales could affect the assumption of equal catchability in the yearly samples: (a) animals may travel to southeastern Alaska in some years but not others; (b) animals may arrive during the sampled period in some years but not in others; (c) animals may have preferred ranges that were not uniformly sampled; (d) animals may show repeated associations or preferred companions resulting in a "group bias" (Caughley 1977).

Each of these potential biases can be discounted, to some degree, by available data. Whales in southeastern Alaska seem to form a discrete feeding herd and generally do not travel to other known feeding regions. The large congregations of whales found in Frederick Sound and Stephens Passage during late August and early September indicated that most individuals had arrived in southeastern Alaska and abandoned other preferred ranges during this period. Although humpback whales in southeastern Alaska are known to associate repeatedly within a summer season and across years (Baker and Herman 1984*b*), the large proportion of the population photographed during each sample year should have prevented a serious group bias.

The choice of yearly sampling satisfies assumption (3); the approximately two-month summer studies were short in comparison to the intervening 10 mo. Unfortunately, it also results in some violation of assumption (4); births and deaths during the intervening year could have biased the estimates upwards in proportion to the rate of replacement. Whitehead (1982), using data from Chittleborough (1965), assumed a replacement rate of 0.10 for his estimates of humpback populations in the northwest Atlantic. Baker (dissertation in preparation), using the reproductive histories of individual females, found a calving rate of 8.8–10.6 percent among humpback whales in southeastern Alaska. Assuming these estimates are correct, it is unlikely that the Petersen estimates, based on contiguous years, are inflated by more than 8.8–10.6 percent due to births and deaths.

Considering the large sample size, the consistent sampling methods and the narrow confidence limits, we believe that the 1981–1982 Petersen estimate of 310 whales (95 percent confidence interval = 270–372) is our best available estimate of the southeastern Alaska herd. Although this is somewhat less than the total of 326 individuals photo-identified over the five-year study, the loss to a population from deaths or emigration must be considered in a count taken over a number of years. Our estimate is also more than five times larger than some of the previous estimates for this region (Rice 1978). Much of the discrepancy between these estimates may be explained by an increased regional and seasonal effort as well as improved techniques. However, some true increase in the southeastern Alaska herd may have resulted from births or immigration during the past 5–7 yr.

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