

**Abstract.**—In the summer and fall of 1986 a total of 257 humpback whales *Megaptera novaeangliae* were individually identified during nonsystematic vessel surveys of southeastern Alaska. The majority of adult animals ( $n = 130$ , 54.6%) identified in 1986 had been identified previously in southeastern Alaska during the years 1979–85. Capture-recapture estimates suggested that this regional subpopulation increased in abundance from 1979 to 1986, and included 547 individual whales (95% CL: 504–590) at the time of the 1986 surveys. An average reproduction rate of 0.36 calves/mature female-year<sup>-1</sup> (95% CL: 0.28–0.43) was estimated for this regional subpopulation using individual identification records collected during 1980–86. In the Frederick Sound–Stephens Passage area, the largest number of whales was found during August and their predominant prey appeared to be euphausiids. In the Glacier Bay–Icy Strait area, the relative abundance of whales was greatest in June and July and their predominant prey appeared to be schooling fish. Low levels of interchange between surveyed areas for much of the summer season indicated strong preferences for local habitats among individual whales. The documented presence of some individual whales for at least 6 months is evidence that southeastern Alaska is the primary feeding ground for many of the whales identified in these surveys.

## Population characteristics of individually identified humpback whales in southeastern Alaska: Summer and fall 1986

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Humpback whales *Megaptera novaeangliae* in the central and eastern North Pacific, like those in the western North Atlantic (Katona and Beard 1990), appear to form several geographically-isolated subpopulations during the summer and fall feeding season (Baker et al. 1986, Perry et al. 1990). Following their yearly migration south, individuals from these feeding herds intermingle in the waters of either Hawaii or Mexico during the winter breeding season (Darling and Jurasz 1983, Baker et al. 1985, Darling and McSweeney 1985, Baker et al. 1986).

The coastal waters of southeastern Alaska (56–59°N lat.) seem to encompass the primary feeding ground of a single 'herd' or regional subpopulation estimated to number between 327 and 421 individual whales as of 1983 (Baker et al. 1986). Although the exact geographic boundaries of each herd are unknown, whales from southeastern Alaska appear to remain segregated from those that summer to the west in the Gulf of Alaska, including Prince William Sound, and those which summer to the south along the coast of central California (Baker et al. 1986, Perry et al. 1990). Fidelity to a particular

feeding ground appears to be maternally directed (Martin et al. 1984, Baker et al. 1987, Clapham and Mayo 1987) and may persist across many generations, as suggested by geographic segregation of mitochondrial DNA haplotypes (Baker et al. 1990).

Within southeastern Alaska, however, the distribution of whales is not homogeneous and intermingling of individuals is not random (Baker 1985a, Baker et al. 1985). Some whales return with considerable fidelity to specific areas or 'neighborhoods' such as Glacier Bay, Sitka Sound or Frederick Sound and, at least during part of the feeding season, may establish restricted local ranges (Jurasz and Palmer 1981, Perry et al. 1985, Baker et al. 1988, Straley 1990). Changes in distribution and local movement within a season appear to reflect changes in prey availability. The relatively early arrival of whales into the Glacier Bay area indicates that this may be an important area for early-summer feeding on schooling fish, including capelin *Mallotus villosus*, sand lance *Ammodytes hexapterus*, and Pacific herring *Clupea harengus* (Wing and Krieger 1983, Krieger and Wing 1984 and 1986, Perry et al. 1985).

By late summer, whales typically congregate in Frederick Sound and Stephens Passage where large swarms of euphausiids, primarily *Thysanoessa raschii* and *Euphausia pacifica*, are common (Krieger and Wing 1984, 1986). Some whales feed throughout fall and early winter in areas such as Seymour Canal and Sitka Sound where euphausiids and schooling herring appear to remain available (Baker et al. 1985, Straley 1990).

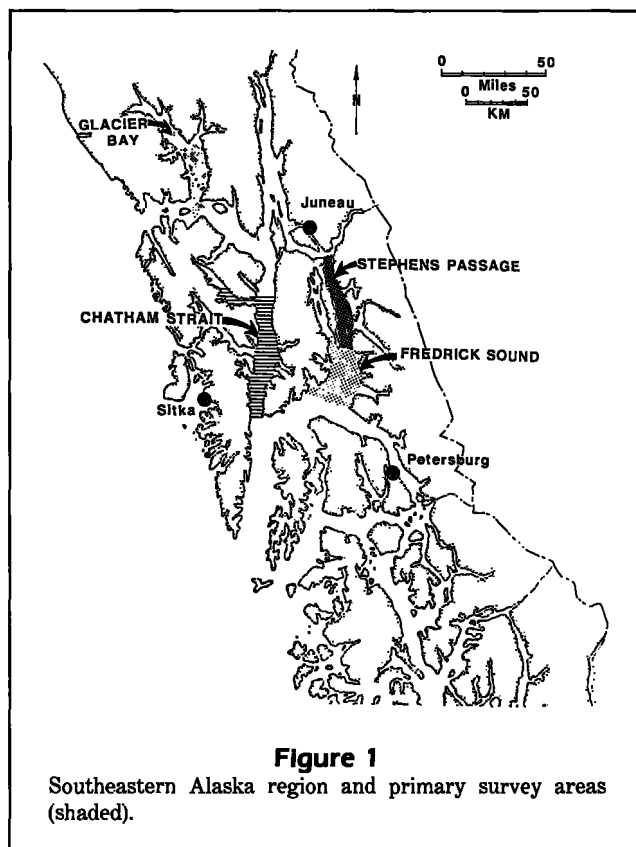
Here we summarize the results of nonsystematic surveys of individually identified humpback whales in southeastern Alaska during the summer and through late fall of 1986. The 1986 surveys were designed to overlap in geographic range and seasonal timing with previous coverage during the years 1979–85 (Baker et al. 1985, Baker 1985b). In keeping with recommended management plans (Anonymous 1984), our surveys documented regional abundance and distribution of humpback whales in areas that may be impacted directly or indirectly by vessel activity in Glacier Bay National Park. More specifically, we sought to evaluate trends in the abundance, reproductive rates, and primary prey of humpback whales in southeastern Alaska across the years 1979–86. Documentation of long-term trends in these population characteristics are valuable for assessing the influences of human activity, such as mining, logging, or petroleum exploration and development, or natural environmental fluctuations such as El Niño events, on the habitat use and recovery of this endangered species (National Marine Fisheries Service 1991).

## Methods

### Vessel surveys

Humpback whales were observed and individually identified primarily in two areas or subregions of southeastern Alaska (Fig. 1): Glacier Bay and the adjacent waters of Icy Strait (referred to collectively as Glacier Bay); and the contiguous waters of Stephens Passage and Frederick Sound, including Seymour Canal (referred to collectively as Frederick Sound). Photographs of whales were also collected in Chatham Strait and Sitka Sound on an opportunistic basis throughout the summer and fall.

Whales in Glacier Bay were censused by one of us (CSB) from 22 May to 10 September under the auspices of the National Park Service. A total of 42 one-day surveys were conducted aboard a 17-foot fiberglass boat powered by a 50-hp outboard motor. The lower and middle bay (i.e., from Bartlett Cove to the mouths of Muir Inlet and the West Arm) were surveyed not less than twice and not more than three times a week. The mouth of Glacier Bay and the adjacent waters of



**Figure 1**

Southeastern Alaska region and primary survey areas (shaded).

Icy Strait were surveyed at least once and not more than twice a week. Study period and survey coverage were designed to overlap and extend previous coverage during the summers of 1982–85 (Baker et al. 1985, Baker 1985b).

Whales in Frederick Sound were censused during three summer surveys: 31 July–3 August; 29 August–1 September; and 12 September–15 September. These survey cruises were conducted aboard the RV *Sashin*, a 22-foot stern-drive vessel provided by the Auke Bay Laboratory, National Marine Fisheries Service. Each cruise originated and ended in Juneau and surveyed the length of Stephens Passage and Frederick Sound south to Cape Fanshaw and west to Pybus Bay (see shaded area, Fig. 1). A fourth survey of Frederick Sound was conducted from 29 November to 9 December aboard the MV *Fairweather*, a 43-foot, diesel-powered cabin cruiser. This cruise originated and ended in Sitka, Alaska, and surveyed the southern half of Chatham Strait and Frederick Sound, north to Seymour Canal. The dates and geographic coverage of Frederick Sound surveys were chosen to coincide with those of similar previous surveys during the summers of 1984–85 (Krieger and Wing 1986, CSB unpubl. data), the fall or winters of 1979–85 (Straley 1990),

and with field efforts during the summers of 1981–82 (Baker et al. 1985).

### Prey assessment

Humpback whale prey species were assessed in Glacier Bay with a Ross Fineline 250C recording fathometer equipped with a 22° beam, 105-kHz transducer. In Frederick Sound, prey were assessed with a Lowrance recording fathometer equipped with a 250-kHz transducer. Putative identification of primary prey species type (e.g., euphausiids vs. schooling fish) was based on qualitative differences in target strength, as judged from the relative intensity of fathometer recordings, and the size, shape, and depth of prey schools. These interpretations were based on reference to previous documentation of humpback whale prey using quantitative hydroacoustics and net sampling (Wing and Krieger 1983, Krieger and Wing 1984 and 1986). On occasion, observations of feces from feeding whales or the presence of prey species at the surface provided direct confirmation of primary prey species type.

### Individual identification

We attempted to individually identify all humpback whales encountered by collecting photographs of the ventral surface of the whales' flukes. The uniqueness of the coloration, shape, and scarring pattern of the flukes' ventral side allowed for the reliable identification of individual whales (Katona et al. 1979). Because our primary objective was to collect individual identification photographs for use in capture-recapture analyses and the estimation of long-term reproductive rates, we did not attempt to count unidentified whales along the survey tracks. Consequently, all references to 'sightings' or 'observations' of whales are based only on photographs of unique individuals.

Methods for processing and comparison of fluke photographs followed that described by Perry et al. (1988). Photographs of whales were taken with a 35 mm single-lens reflex camera equipped with a motor drive and a 300 mm telephoto or 70–210 mm zoom lens. High-speed (ASA 400–1600) black-and-white film was used. From each observation of a whale or group of whales, the best photograph of each individual's flukes was printed and assigned a "fluke observation" or identification number. Information on the location, date, and social affiliation of each fluke identification was stored in a data retrieval file at the University of Hawaii Computing Center. During the matching of fluke photographs, a whale that was identified on more than one occasion was also assigned an "animal" number. This number allowed us to reference all fluke observations, or identifications, of that individual. All

**Table 1**

Between-years reidentification and the Petersen population estimate using Bailey's correction (in parentheses) of humpback whales *Megaptera novaeangliae* in southeastern Alaska.

Year	Identified: no. [newly]	Reidentification year						
		1980	1981	1982	1983	1984	1985	1986
1979	83 [83]	32 (307)	41 (294)	48 (310)	11 (353)	36 (435)	33 (498)	40 (484)
1980	121 [89]	—	58 (306)	53 (410)	11 (514)	48 (479)	53 (457)	51 (556)
1981	148 [71]	—	—	85 (315)	26 (280)	73 (388)	66 (451)	63 (553)
1982	182 [66]	—	—	—	31 (290)	80 (436)	81 (453)	79 (544)
1983	50 [12]	—	—	—	—	35 (269)	29 (340)	23 (498)
1984	193 [76]	—	—	—	—	—	80 (486)	76 (599)
1985	203 [74]	—	—	—	—	—	—	79 (606)
1986	238 [108]	—	—	—	—	—	—	—
Sum	579							

fluke photographs were judged to be of either good, fair, or poor quality. Good- and fair-quality photographs showed at least 50% of both flukes at an angle sufficiently vertical to distinguish the shape of the flukes' trailing edges. For this study, poor-quality photographs were deleted from the data set.

## Results

### Abundance and regional fidelity

A total of 257 humpback whales, including 19 calves, were individually identified in southeastern Alaska during 1986. This total includes 29 adults identified only in Glacier Bay, 183 identified only in Frederick Sound, 16 identified only in Sitka Sound or Chatham Strait, and 10 adults common to more than one subregion. The majority ( $n = 130$ , 54.6%) of the 238 adults identified in 1986 had been identified in southeastern Alaska previously, based on comparison with photographs collected by University of Hawaii researchers and associates during the years 1979–85 (Perry et al. 1988). The addition of the 108 newly identified individuals to the existing catalogue of photographs resulted in a cumulative total of 579 adult whales identified in southeastern Alaska across the 8 study years (Table 1).

To determine the fidelity of humpback whales to regional feeding grounds, photographs collected from southeastern Alaska during 1986 were compared with

photographs of 95 individuals from the western Gulf of Alaska (von Ziegesar and Matkin 1989), 18 from central California collected during 1977–85 (Perry et al. 1988), and 225 individuals from central California identified during 1987–88 (Calambokidis et al. 1990). This comparison provided no evidence of movement by individual whales between these three feeding regions. Two whales previously identified in both southeastern Alaska and Prince William Sound (Baker et al. 1986) were not reidentified in southeastern Alaska in 1986, suggesting that their immigration to southeastern Alaska may have been temporary.

The identification and reidentification of individual animals across years lends itself to the estimation of abundance using capture-recapture formulae (e.g., Hammond 1986). Table 1 summarizes abundance estimates of the southeastern Alaska feeding herd from a pair-wise comparison of all yearly samples using the Petersen estimate with Bailey's correction (Caughley 1977). The yearly estimates range from a low of 269 (1983–84) to a high of 606 (1985–86). The weighted mean of the Petersen estimate (i.e., the Schnabel estimate; Seber 1982) across the 8-year study indicated

that this regional subpopulation has included 547 animals (95% CL: 504–590).

Possible inequalities of individual reidentification probabilities were examined by calculating the identification frequencies for individual whales across the 8 study years (Table 2). The observed frequency distribution showed fewer 2- or 3-year reidentification records and more single identifications and reidentification records of extreme frequencies than expected when compared with a zero-truncated Poisson distribution calculated according to Caughley (1977). The significant departure of the observed from the expected distribution ( $\chi^2$  [4] 291,  $p < 0.001$ ) suggests that all individual whales were not equally available for reidentification during the study period. Possible causes of this unequal 'catchability' include births, deaths, and permanent emigration across the 8-year study, as well as heterogeneity of reidentification probabilities due to local habitat preferences and the limited range of surveys.

### Reproductive rates

Among the 238 adults individually identified in 1986, there were 32 cows accompanied by calves assumed to be less than a year old. Using this census information we estimated the crude birth rate in 1986 to be 0.125, calculated as the total number of identified cows ( $n$  32) divided by the total number of identified whales of all classes ( $n$  257, including only identified calves). This estimate, however, may have been biased by the greater visibility of cow/calf pairs and by additional effort directed towards individually identifying members of this age/sex class.

An alternate estimate of annual reproductive rates was calculated using the identification histories of individual females known to be reproductively mature prior to the 1986 surveys (Baker et al. 1987). Of the 41 mature females previously identified by Baker et al. (1987), 24 were reidentified during the 1986 surveys and 9 were accompanied by a calf, yielding an estimate of 0.375 calves/mature female·year<sup>-1</sup>. The addition of the 1986 identifications provides an updated estimate of the long-term calving rates for 41 females previously discussed by Baker et al. (1987) (Table 3). Between 1980 and 1986, these 41 females were observed with 58 individual calves across 162 seasonal identifications. Although annual calving rates appeared to alternate

**Table 2**

Observed and expected frequency of yearly identifications for 579 adult humpback whales *Megaptera novaeangliae* in southeastern Alaska during the years 1979–86.

	Identification frequency (years)						
	1	2	3	4	5	6	7+
Observed	330	81	56	46	32	24	10
Expected	216	186	108	47	16	6	—

Note: Expected frequencies were calculated from the zero-truncated Poisson distribution according to the methods described by Caughley (1977).

**Table 3**

Calving rates of mature female humpback whales *Megaptera novaeangliae* in southeastern Alaska, based on reproductive histories of 41 individuals identified in two or more summer seasons (see Baker et al. 1987).

	Identification year							Sum
	1980	1981	1982	1983	1984	1985	1986	
Females identified	8	33	33	12	31	21	24	162
Total calves	2	9	15	3	15	5	9*	58
Calves/female	0.25	0.27	0.45	0.25	0.48	0.24	0.38	0.36

\* Includes one calf thought to have died during the summer. See text for details.

**Table 4**

Within-year (between-survey) reidentification and the Petersen population estimates with Bailey's correction (in parentheses) of adult humpback whales *Megaptera novaeangliae* in Glacier Bay, 1986.

Survey month	Identified: no. [newly]	No. reidentified			
		June	July	Aug	Sept
June	27 [27]	—	17 (42)	12 (39)	7 (37)
July	27 [10]	—	—	12 (39)	9 (30)
August	18 [3]	—	—	—	10 (18)
September	10 [0]	—	—	—	—
Sum	40				

**Table 5**

Within-year (between-survey) reidentification and the Petersen population estimates with Bailey's correction (in parentheses) of adult humpback whales *Megaptera novaeangliae* in Frederick Sound, 1986.

Survey dates	Identified: no. [newly]	No. reidentified			
		1	2	3	4
31 July-3 Aug	72 [72]	—	22 (247)	19 (234)	13 (283)
29 Aug-1 Sept	78 [56]	—	—	23 (211)	9 (429)
12-15 Sept	64 [30]	—	—	—	4 (704)
29 Nov-7 Dec	54 [36]	—	—	—	—
Sum	194				

between high and low years from 1981 to 1986, a Test of Independence indicated that these year-to-year differences were not significant ( $\chi^2$  [6] 6.88,  $p$  0.332). Average calving rate across the 7-year study was 0.36 calves/year (95% binomial CL: 0.284-0.432), similar to the previously reported rate of 0.37 for the years 1980-85 (Baker et al. 1987).

### Local abundance and Interchange

Capture-recapture estimates of seasonal abundance for the Glacier Bay and Frederick Sound subregions were calculated using the Petersen formula with Bailey's correction and treating each survey or survey period as a sample (Tables 4 and 5). In Glacier Bay, the number of individual whales identified was greatest during June and July and declined through August and September

**Table 6**

Local movement of humpback whales *Megaptera novaeangliae* between Glacier Bay (GB) and Frederick Sound (FS) during the summer and fall of 1986.

Animal no.	From Last ident. date	To First ident. date	Interval (days)
#117	GB, 25 July	FS, 30 Aug	36
#161	GB, 22 July	FS, 2 Aug	8
#155	GB, 22 July	FS, 30 Aug	39
#196	FS, 31 July	GB, 8 Aug	8
#221	GB, 29 July	FS, 31 Aug	33
#350	GB, 21 July	FS, 30 Aug	40
#564	GB, 22 July	FS, 26 Aug	35
#566	GB, 11 July	FS, 30 Aug	50
#587	GB, 14 Aug	FS, 4 Dec	112
#616	GB, 16 July	FS, 31 July	15
#616	FS, 31 July	GB, 14 Aug	14
#616	GB, 14 Aug	FS, 30 Aug	16

(Table 4). The percentage of newly-identified whales declined rapidly through the summer, suggesting that the census of identified individuals approached a complete count of the whales in this subregion. Capture-recapture estimates based on monthly censuses ranged from 18 to 42 and agreed closely with the total number of 40 adults identified in this subregion.

In Frederick Sound, the number of individual whales identified during each survey remained constant from late July to mid-September and declined by late fall (Table 5). The percentage of newly-identified whales decreased through the three summer surveys but increased in the late-fall survey. The Frederick Sound capture-recapture estimates from the three summer surveys ranged from 211 to 247, exceeding the total of 158 individuals identified during this period but not approaching the between-year estimates of regional abundance (see Table 1). Capture-recapture estimates increased considerably when summer surveys were compared with the fall surveys. Ranging from 283 to 704, the fall estimates agreed more closely with across-year estimates for the entire southeastern Alaska region. The larger capture-recapture estimates from the fall survey and the increase in percentage of newly identified whales suggested the dissolution of population stratification observed during the summer months or the arrival of individuals from unsurveyed areas of southeastern Alaska.

Documented interchange between the southeastern Alaska subregions was limited to 12 transits by 10 individual whales (Table 6). Eight one-way transits were from Glacier Bay to Frederick Sound, and a single one-way transit was from Frederick Sound to Glacier Bay. One individual, animal #616, traveled from Glacier

Bay to Frederick Sound and back between 16 July and 14 August. Animal #616 was last identified in Frederick Sound on 30 August.

### Regional occupancy

The interval between the first and last identification of an individual whale provided a minimum estimate of its occupancy in southeastern Alaska (Baker et al. 1985). Although it was not possible to document continuous residency of individual whales in either of the primary study areas (i.e., Glacier Bay or Frederick Sound), there was no evidence that individuals migrated to other known feeding regions between surveys (see 'Abundance and regional fidelity'). The longest documented regional occupancy was 192 days for animal #587. This individual was first identified on 1 June in Glacier Bay and last identified on 9 December in Frederick Sound. Animal #587's identification record, discussed by Baker et al. (1987), showed that she lost a calf sometime during the summer of 1986. Three other adults and one calf had documented occupancies of nearly equivalent length: 191 days for #616, an animal of unknown age-sex class (see also Table 6); 183 days for #350, an animal of unknown age-sex class; and 186 days for #161 and her calf.

### Foraging behavior

During summer surveys, whales in Frederick Sound tended to occur in aggregations of 20 to 80 animals often clustered along submerged ridges and mounts, as determined by reference to fathometer recordings and navigational charts. Observations of whale feces and fathometer recordings of dense scattering layers below feeding whales indicated that euphausiids were the primary prey for these aggregations. During the late-fall survey, we were unable to collect fathometer recordings or to observe whale feces in order to confirm the primary prey species. However, the surface-movement and diving patterns of whales and the location of feeding aggregations were similar to that observed during summer surveys, suggesting that euphausiids were again the primary prey.

The predominant prey of humpback whales in Glacier Bay was schooling fish, as evidenced by fathometer recordings and observations of schooling fish at the surface. Within the Bay, whales fed singly or in pairs on dense schools of capelin and sandlance. Outside the Bay, in the adjacent waters of Icy Strait, the predominant prey of humpback whales appeared to be herring as demonstrated in previous years using hydroacoustic techniques and net tows (Wing and Krieger 1983, Krieger and Wing 1984 and 1986). As in previous years (Baker 1985a), whales near Icy Strait formed a social-

ly cohesive pod of 7 to 9 individuals that appeared to cooperate in foraging on schools of herring.

## Discussion

### Population characteristics

The number of individual whales photographically identified during the 1986 surveys, 238 adults and 19 calves, can be considered a minimum estimate of abundance for the southeastern Alaska feeding herd. Capture-recapture analyses of across-year identification records, however, provide estimates of this regional population that are two or three times larger than that based on the 1986 census alone. Although these analyses are more likely than simple counts to provide realistic estimates of regional abundance, they should be interpreted with caution since the behavior of whales seldom conforms strictly to the theoretical assumptions underlying these models (e.g., Hammond 1986, Perry et al. 1990). Violation of the assumption of equal catchability among southeastern Alaska whales, for example, is indicated by the analysis of reidentification frequencies across the 8-year study period. Births, deaths and permanent emigration obviously contribute to this unequal catchability (i.e., reidentification inequality). Another probable source of unequal catchability is heterogeneity due to local habitat preference by individual whales and the variable and limited geographic coverage of the surveys. While births and deaths cause a positive bias in the Petersen estimate of abundance, reidentification heterogeneity causes a negative bias (Hammond 1986 and 1990).

Assuming, however, that adult mortality among humpback whales is low (e.g., Buckland 1990) and that permanent emigration to other feeding regions is infrequent (e.g., Perry et al. 1990), the weighted Petersen estimate of 547 whales (95% CL: 503-590) may be our most robust for the southeastern Alaska subpopulation in 1986. By using the cumulative reidentification records of individuals across years and weighting the final estimate by the largest sample year, the weighted Petersen should be less biased than the between-year Petersen estimates by heterogeneity due to local habitat preferences or variation in survey effort. Births during the study period are included in the cumulative population estimate when the calves mature sufficiently to become available for individual identification. The weighted Petersen is also consistent with other estimates derived from the individual identification records. The upper confidence interval of this estimate overlaps with the total count of 579 whales identified during the 8-year study and agrees closely with the unbiased Petersen estimates from the pair-

wise comparisons of years with the largest sample of identified whales, 1984–86 and 1985–86 (see Table 1).

Regardless of the exact number of individuals inhabiting this region, the individual identification surveys and mark-recapture estimates suggest that the southeastern Alaska herd increased from 1979 to 1986. In Frederick Sound, overall survey effort decreased since 1981–82 but, with the exception of 1983 when only a single 4-day survey was conducted, the number of identified whales increased. As confirmed by photographic documentation, a general increase in the number of whales in the Glacier Bay area during the last few years was the result of the continued return of past residents and the recruitment of their offspring (Baker et al. 1988). In terms of overall regional abundance, the mark-recapture estimates from pair-wise comparisons of 1986 to previous years suggest an increase from 484 to 606 across 1979–86, while estimates from contiguous years suggest an increase from 307 to 606 (Table 1). Requiring an annual rate of increase from 3.4 to 10.4%, these trends in estimated abundance are within the range reported for population growth of other unexploited baleen whales based on individual identification data (e.g., Hammond 1990, Best and Underhill 1990, Bannister 1990). More accurate estimates of the current abundance and the true rate of increase in the southeastern Alaska subpopulation will require further detailed analyses of survival rates and the biases introduced by heterogeneity of identification records.

Although apparently sufficient to sustain some degree of population growth, the observed reproduction rate of humpback whales in southeastern Alaska seemed low in comparison with other studied populations and to the maximum reproductive potential of 0.50, or even 1.00 (calves/mature female·year<sup>-1</sup>) as observed in some individually identified females (Darling 1983, Glockner-Ferrari and Ferrari 1984 and 1990, Baker et al. 1987, Clapham and Mayo 1987 and 1990, Straley 1989). The estimated calving rate of 0.36 (calves/mature female·year<sup>-1</sup>) across the 1980–86 study suggests that females from this region give birth to a calf that survives its first migration from the wintering grounds about once every 2.8 years. In the Gulf of Maine, Clapham and Mayo (1990) report an average reproduction rate of 0.41 (calves/mature female·year<sup>-1</sup>) and an average calving interval of 2.35 years for the period 1979–87, using individual identification methods similar to those used here. Pregnancy rates from exploited populations, as summarized by Baker et al. (1987), all exceed the estimated calving rate for southeastern Alaska, although this historical comparison is confounded by differences in methodology.

### Seasonal trends and foraging strategies

The number of whales identified in Glacier Bay and Icy Strait was greatest during late June and early July, and declined through August and September. Since survey effort in Glacier Bay was high relative to total number of whales identified, and constant throughout the study period, we believe that trends in the monthly censuses or counts of individuals reflected changes in seasonal abundance for this subregion. Although surveys of Frederick Sound were not frequent enough to track the seasonal increase in whales during early summer, the greatest numbers of whales were found during late July and August, approximately 1 month after the local peak in Glacier Bay.

We could not determine if these seasonal trends reflect primarily changes in the timing of migratory arrival on the feeding grounds or the pattern of local movement among subregions of southeastern Alaska. Within the geographic limits of our surveys, seasonal changes in influx were accompanied by some local movement between subregions; the decline in numbers of whales in Glacier Bay was, in part, the result of their relocation to Frederick Sound. Studies in previous years also demonstrated that local movement between these subregions tends to be one-directional, resulting in the whales congregating in Frederick Sound during late summer and fall (Baker 1984, Perry et al. 1985, Krieger and Wing 1986). Large areas of available habitat in southeastern Alaska remain entirely unsurveyed (see Fig. 1), including the outer coast of Baranof Island and the inside passage to the south of Frederick Sound. The increase in percentage of newly-identified whales during the late-fall survey of 1986 suggests local movement from these unsurveyed areas.

Local movement may be an attempt to take advantage of seasonal changes in prey availability. Humpback whales in Frederick Sound fed almost entirely on euphausiids while those in Glacier Bay fed almost entirely on schooling fish. Movement from Glacier Bay to Frederick Sound was presumably accompanied by a shift in primary prey species. Similar contrasts in the primary prey species of whales in these two subregions have been documented in previous years (Krieger and Wing 1984 and 1986). Some whales, however, showed a strong preference for particular prey species or local habitat throughout the summer. This was indicated by the persistence of certain individual whales feeding on herring in Icy Strait late through the summer, when other whales had moved to feed on euphausiids in Frederick Sound.

## Stock Identity and management

The summer and late-season surveys of 1986 and previous years (Baker et al. 1985) demonstrated that many whales remained to feed in southeastern Alaska for much of the summer and into late fall. Intervals between first identification and last reidentification of some individual whales indicated seasonal occupancies of at least 6 months. Since no surveys were conducted from 15 September to 29 November, it was not possible to document continuous residency of individual whales in either of the primary study areas (i.e., Glacier Bay or Frederick Sound). However, comparisons of individual identification photographs collected in the central and western Gulf of Alaska, including Prince William Sound, and along the coast of central California indicate that whales which summer in southeastern Alaska seldom migrate to alternate feeding grounds within seasons or across years (Baker et al. 1986, Perry et al. 1990). These observations are strong evidence that southeastern Alaska is the migratory terminus and primary feeding ground for a distinct herd or seasonal subpopulation of humpback whales.

Comparisons of individual identification photographs and analysis of mitochondrial DNA haplotypes demonstrate that many members of the southeastern Alaska feeding herd migrate to wintering grounds near the islands of Hawaii (Darling and Jurasz 1983, Baker et al. 1986, Perry et al. 1990, Baker et al. 1990). The migratory connection between these primary seasonal habitats provides a unique opportunity to study and protect a population of humpback whales that spends the majority of its time within U.S. coastal waters (National Marine Fisheries Service 1991).

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## Citations

### Anonymous

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### Baker, C.S.

1984 Population characteristics and feeding behavior of humpback whales in southeastern Alaska during 1984. Unpubl. rep. to NMFS Auke Bay Lab., Auke Bay, AK, 44 p.

1985a The population structure and social organization of the humpback whale (*Megaptera novaeangliae*) in the central and eastern North Pacific. Ph.D. diss., Univ. Hawaii, Honolulu, 307 p.

1985b The humpback whales of Glacier Bay and adjacent waters: Summer 1985. Unpubl. rep. to Glacier Bay Natl. Park, Gustavus, AK, 33 p.

### Baker, C.S., L.M. Herman, A. Perry, W.S. Lawton, J.M. Straley, and J.H. Straley

1985 Population characteristics and migration of humpback whales in southeastern Alaska. Mar. Mammal Sci. 1:304-323.

### Baker, C.S., L.M. Herman, A. Perry, W.S. Lawton, J.M. Straley, A.A. Wolman, G.D. Kaufman, H.E. Winn, J.D. Hall, J.M. Reinke, and J. Ostman

1986 Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. Mar. Ecol. Prog. Ser. 31:105-119.

### Baker, C.S., A. Perry, and L.M. Herman

1987 Reproductive histories of female humpback whales (*Megaptera novaeangliae*) in the North Pacific. Mar. Ecol. Prog. Ser. 41:103-114.

### Baker, C.S., A. Perry, and G. Vequist

1988 Humpback whales of Glacier Bay, Alaska. Whale-watcher 22(3):13-17.

### Baker, C.S., S.R. Palumbi, R.H. Lambertsen, M.T. Weinrich, J. Calambokidis, and S.J. O'Brien

1990 The influence of seasonal migration on the geographic distribution of mitochondrial DNA haplotypes in humpback whales. Nature (Lond.) 344:238-240.

### Bannister, J.

1990 Southern right whales off western Australia. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 279-288. Rep. Int. Whaling Comm. Spec. Issue 12.

### Best, P.B., and L.G. Underhill

1990 Estimating population size in southern right whales (*Eubalaena australis*) using naturally marked animals. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 183-190. Rep. Int. Whaling Comm. Spec. Issue 12.



**Buckland, S.T.**

1990 Estimation of survival rates from sightings of individually identified whales. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 149-154. Rep. Int. Whaling Comm. Spec. Issue 12.

**Calambokidis, J., J.C. Cabbage, G.H. Steiger, K.C. Balcomb, and P. Bloedel**

1990 Population estimates of humpback whales in the Gulf of the Farallones. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 325-334. Rep. Int. Whaling Comm. Spec. Issue 12.

**Caughley, G.**

1977 Analysis of vertebrate populations. Wiley, NY, 288 p.

**Clapham, P.J., and C.A. Mayo**

1987 Reproduction and recruitment of individually-identified humpback whales, *Megaptera novaeangliae*, in Massachusetts Bay: 1979-1985. Can. J. Zool. 65:2853-2863.

1990 Reproduction of humpback whales (*Megaptera novaeangliae*) observed in the Gulf of Maine. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 171-176. Rep. Int. Whaling Comm. Spec. Issue 12.

**Darling, J.D.**

1983 Migration, abundance and behavior of Hawaiian humpback whales, *Megaptera novaeangliae* (Borowski). Ph.D. diss., Univ. Calif., Santa Cruz, 147 p.

**Darling, J.D., and C.M. Jurasz**

1983 Migratory destinations of North Pacific humpback whales (*Megaptera novaeangliae*). In Payne, R. (ed.), Communication and behavior of whales, p. 359-368. Westview Press, Boulder.

**Darling, J.D., and D.J. McSweeney**

1985 Observations on the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). Can. J. Zool. 63: 308-314.

**Glockner-Ferrari, D., and M. Ferrari**

1984 Reproduction in humpback whales, *Megaptera novaeangliae*, in Hawaiian waters. In Perrin, W.P., et al. (eds.), Reproduction in whales, dolphins, and porpoises, p. 237-242. Rep. Int. Whaling Comm. Spec. Issue 6.

1990 Reproduction in the humpback whales (*Megaptera novaeangliae*) in Hawaiian waters, 1975-1988: The life history, reproductive rates, and behavior of known individuals identified through surface and underwater photography. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 161-169. Rep. Int. Whaling Comm. Spec. Issue 12.

**Hammond, P.S.**

1986 Estimating the size of naturally marked whale populations using capture-recapture techniques. In Donovan, G.P., (ed.), Behavior of whales in relation to management, p. 253-282. Rep. Int. Whaling Comm. Spec. Issue 8.

1990 Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 135-140. Rep. Int. Whaling Comm. Spec. Issue 12.

**Jurasz, C.M., and V.P. Palmer**

1981 Censusing and establishing age composition of humpback whales (*Megaptera novaeangliae*) employing photodocumentation in Glacier Bay National Monument, Alaska. Unpubl. rep. to Natl. Park Serv., Alaska Reg. Office, Anchorage, 44 p.

**Katona, S.K., and J.A. Beard**

1990 Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 295-307. Rep. Int. Whaling Comm. Spec. Issue 12.

**Katona, S., B. Baxter, O. Brazier, S. Kraus, J. Perkins, and H. Whitehead**

1979 Identification of humpback whales by fluke photographs. In Winn, H.E., and B.L. Olla (eds.), Behavior of marine animals, vol. 3, p. 33-44. Plenum Press, NY.

**Krieger, K., and B.L. Wing**

1984 Hydroacoustic surveys and identification of humpback whale forage in Glacier Bay, Stephens Passage and Frederick Sound, southeastern Alaska, Summer 1983. NMFS Auke Bay Lab., Juneau, 60 p.

1986 Hydroacoustic monitoring of prey to determine humpback whale movements. NOAA Tech. Memo. NMFS F/NWC-66, NMFS Auke Bay Lab., Juneau, 62 p.

**Martin, A.R., S.K. Katona, D. Matilla, D. Hembree, and T.D. Waters**

1984 Migration of humpback whales between the Caribbean and Iceland. J. Mammal. 65:330-333.

**National Marine Fisheries Service**

1991 Recovery plan for the humpback whale (*Megaptera novaeangliae*). Prepared by the Humpback Whale Recovery Team for the Natl. Mar. Fish. Serv., Silver Spring, MD, 105 p.

**Perry, A., C.S. Baker, and L.M. Herman**

1985 The natural history of humpback whales in Glacier Bay, Alaska. Final rep. to Natl. Park Serv., Alaska Reg. Office, Anchorage, 22 p.

1990 Population characteristics of individually identified humpback whales in the central and eastern North Pacific: A summary and critique. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 307-318. Rep. Int. Whaling Comm. Spec. Issue 12.

**Perry, A., J.R. Mobley, C.S. Baker, and L.M. Herman**

1988 Humpback whales of the central and eastern North Pacific: A catalog of individual identification photographs. Sea Grant Misc. Rep. UNIH-SEAGRANT-MR-88-02, Univ. Hawaii, Honolulu, 37 p.

**Seber, G.A.F.**

1982 The estimation of animal abundance and related parameters. Macmillan, NY, 654 p.

**Straley, J.M.**

1989 Population characteristics of humpback whales (*Megaptera novaeangliae*) in Glacier Bay and adjacent waters: 1989. Unpubl. rep. to Glacier Bay Natl. Park, Gustavus, AK, 33 p.

1990 Fall and winter occurrences of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. In Hammond, P.S., et al. (eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters, p. 319-324. Rep. Int. Whaling Comm. Spec. Issue 12.

**Von Ziegeler, O., and C.O. Matkin**

1989 A catalogue of Prince Williams Sound humpback whales identified by fluke photographs between the years 1977 and 1988. North Gulf Oceanic Soc., P.O. Box 15244, Homer, AK, 28 p.

**Wing, B.L., and K. Krieger**

1983 Humpback whale prey studies in southeastern Alaska, summer 1982. Unpubl. rep. to NMFS Auke Bay Lab., Juneau, 60 p.