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Population Estimates of Humpback Whales in the Gulf of the Farallones, California

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ABSTRACT

We examined population estimates of humpback whales (*Megaptera novaeangliae*) based on photo-identification and aerial surveys in the Gulf of the Farallones, California. Population estimates for 1986–8 were made within years, between years and among years; methods used to estimate population size included the total number of individuals identified, the rate of discovery, mark-recapture estimators (Petersen estimator with the Chapman and Bailey modifications and Jolly-Seber method) and aerial line-transect calculations. We found a number of violations of mark-recapture assumptions in our data; the most serious was the lack of a defined closed population. Heterogeneity of capture probability was observed, particularly in the occurrence of a sub-group of whales that was more likely than others to return to the region. Assuming that within-year estimates were accurate, 22% and 17% of whales present in 1986 and 1987, respectively, did not return the following year; 54% and 35% of whales present in 1987 and 1988, respectively, had not been present the previous year. All abundance estimates based on photo-identification, including the number of individuals identified, were higher than estimates from aerial line-transects even when an attempt was made to correct the latter for whales submerged and undetected. Estimates of abundance based on between-year samples at a feeding area may be seriously biased unless whales in the entire region are sampled randomly.

INTRODUCTION

Cetacean abundance has been estimated using mark-recapture techniques based on individually identified whales of several different species including humpback whales (e.g. Whitehead, 1982; Katona and Beard, 1990). The calculations and assumptions of the various mark-recapture models have been reviewed by Seber (1982) and their application to individually identified cetaceans reported by Hammond (1986). In the North Atlantic, methods for estimating humpback whale abundance have varied both in the estimators employed and the sampling strategy. The most commonly used procedures to estimate humpback whale populations have been the two-sample Petersen estimate (Whitehead, 1982; Whitehead, Chu, Perkins, Bryant and Nichols, 1983; Balcomb and Breiwick, 1984; Perkins, Balcomb, Nichols and DeAvilla, 1984; Perkins, Balcomb, Nichols, Hall, Smultea and Thumser, 1985; Whitehead and Glass, 1986; Balcomb, Katona and Hammond, 1986; Baker and Herman, 1987; Alvarez, Aguayo, Rueda and Urbán, 1990; Katona and Beard, 1990) and the Jolly-Seber multiple sample model (Whitehead, 1982; Hammond and Larsen, 1985; Whitehead and Glass, 1985; Baker and Herman, 1987). Other methods include the Schnabel estimator (Perkins and Whitehead, 1977; Whitehead *et al.*, 1983) and the estimate for the saturation number for the rate of discovery of new whales (Darling and Morowitz, 1986; Alvarez *et al.*, 1990; Katona and Beard, 1990). Even with a given procedure such as the Petersen estimate, however, strategies for delineating the two samples have varied. These pairs of samples have included: (1) within-year samples at a feeding or breeding area during two time periods in one season; (2) within-year samples in an area using different vessels from which photos were taken as the samples; (3) within-year samples in a region using specific locations as the division between samples; (4) between-year samples for the same breeding or feeding location; and (5) feeding and breeding area samples in adjacent seasons.

These procedures involve different potential violations of one of the principal assumptions of the Petersen estimate, namely that the population is closed. Similarly, the samples must be taken from a clearly-defined population so that the estimates have practical meaning. Between-year estimates of humpback whales on North Atlantic feeding grounds have relied on the general site fidelity of humpback whales at these areas (Perkins *et al.*, 1984; Katona and Beard, 1990). The population of the whales in these areas was thereby considered defined and closed (with the exception of natality and mortality between samples).

Humpback whales have been studied and individually identified at feeding areas in the eastern North Pacific including the Gulf of Alaska (Baker, Herman, Perry, Lawton, Straley, Wolman, Kaufman, Winn, Hall, Reinke and Ostman, 1986), southeastern Alaska (Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.*, 1986), Prince William Sound (Darling and McSweeney, 1985; von Ziegesar and Matkin, 1986; Baker *et al.*, 1986), Vancouver Island (Darling and McSweeney, 1985), and central California (Baker *et al.*, 1986; Calambokidis, Steiger, Cubbage, Balcomb and Bloedel, 1989). Some individuals from all these feeding areas have been identified at breeding grounds in Mexico and Hawaii (Darling and McSweeney, 1985; Baker *et al.*, 1986; Urbán, Balcomb, Alvarez, Bloedel, Cubbage, Calambokidis, Steiger and Aguayo, 1987; Calambokidis *et al.*, 1989). Some interchange has occurred between some areas in Alaska and off Vancouver Island across years (Darling and McSweeney, 1985) but no interchange has yet been observed between feeding areas off California and those in Alaska (Baker *et al.*, 1986; Calambokidis *et al.*, 1989).

Although the humpback whales that summer along the California coast may represent a discrete feeding herd, they do not redistribute randomly between years within this region as evidenced by the decreasing proportion of matches with increasing distance between areas (Calambokidis *et al.*, 1989).

We estimate humpback whale population size with data gathered over a three-year period in the Gulf of the Farallones, California. Sampling effort in this region was thorough which resulted in a high proportion of the animals present being identified. We compare various mark-recapture estimates, consider some of the problems associated with these estimates, and compare the mark-recapture estimates with aerial line-transect estimates for the same region.

METHODS

Individual identification

The study area extended from the southern border of the Gulf of the Farallones National Marine Sanctuary (37°30′N) north to 38°30′N (off Bodega Bay, California) west to 122°30′W and included the Farallon Islands, Cordell Bank and Bodega Canyon (Fig. 1). Three primary vessels were used to photograph whales: a 44ft motor sailer (the *Noctilio*), a 19ft Boston Whaler and 14–16ft inflatable boats. Total vessel effort was 513 hours in 1986, 460 hours in 1987 and 484 hours in 1988. In 1986, vessel effort was conducted in a 7-week period from 23 July to 15 September; the 1987 surveys were conducted during two three-week sessions between 17 August-4 September and 25 September-17 October; the 1988 surveys were conducted in two three-week sessions between 19 August-5 September and 21 September-17 October, as well as a late season effort from 27 October to 2 November.

Whales were identified using photographs of the underside of the flukes. We used motor-advance 35mm cameras with lenses from 180mm f2.8 to 300mm f4.5 and *Kodak* Tri-X or *Ilford* HP-5 film black and white film pushed for ISO rating 1000 to 1600. A catalog of individual whales identified during the study was developed by comparing all photographs taken of individual whales.

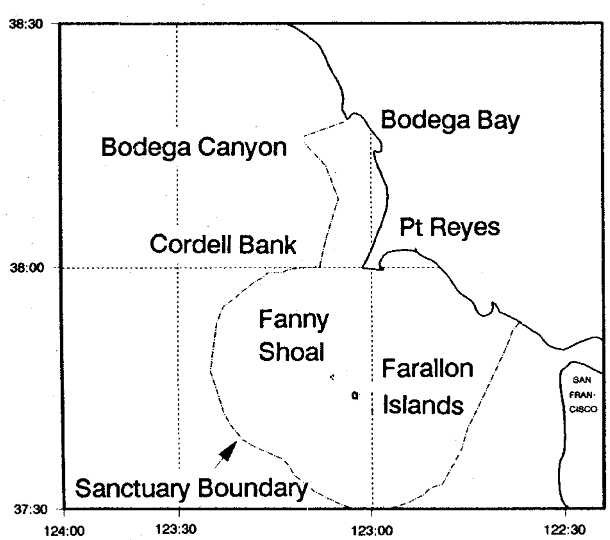

Fig. 1. Study area off central California showing the Gulf of the Farallones National Marine Sanctuary.

Mark-recapture estimates

Population estimates of humpback whales in the Gulf of the Farallones were derived with mark-recapture methods based on resighting rates of identified individuals. Estimates were made with the following procedures: (1) total individuals identified (number of unique individuals in a time period); (2) Chapman modification of the Petersen estimate (Seber, 1982, p.60; Chapman, 1951) for sampling without replacement (multiple captures of the same animal in the second sample were ignored); (3) Bailey modification of the Petersen estimate (Seber, 1982; Bailey, 1951) for sampling with replacement (an animal captured on several days in the second sample was counted each time (see Seber, 1982, pp.110-11)); (4) Jolly-Seber model (Seber, 1982, p. 219–20); and (5) rate of discovery (Darling and Morowitz, 1986).

Assumptions of the models are reported in Seber (1982) for the Petersen estimator (p. 59) and the Jolly-Seber method (p. 196).

Several sampling schemes were used for the mark-recapture calculations. Petersen estimates were computed using both within-year samples and between-year samples. Within-year samples were divided by date and alternatively by vessel and by region. The date used to divide samples was straightforward in 1987 and 1988 because the field season was divided into two sessions separated by a three-week interval; for 1986 a division date was chosen (19 August) that roughly divided the sample in half and occurred during a period of 7 days of no effort. Identifications made from the vessel having the largest sample were compared to identifications from all other vessels for each year. Identifications made in the southern portion of the study area were compared to those from the northern portion. The specific boundary of the separation was chosen as the 10 min latitude that separated the sample into the most similar sample sizes for each year. The Jolly-Seber estimate was made using each year as a sample.

Rate of discovery estimates were calculated using the generalized saturation curve suggested by Darling and Morowitz (1986), however, we used only daily totals of whales identified (whales identified multiple times in a single day were counted only once) instead of treating each identification as a sample. SYSTAT (Wilkinson, 1988) was used to fit the best parameters to the observed discovery rate. Rates of discovery were calculated for each year and for all three years combined. To help evaluate the observed discovery rate and the fitted curves, we also computed expected rates of discovery for the calculated saturation points, assuming whales were sampled randomly each day.

Estimates of emigration/mortality and immigration/natality were made using the single-year Petersen estimates as the assumed number of animals present each year in the Gulf of the Farallones. Portions of this procedure are analogous to those used in the Manly-Parr method (Seber, 1982) except that the population for each year was obtained from the single-year Petersen estimates. This allows estimates of immigration and emigration between all sample years. The following formulas were used:

$$p_i = n_i/N_i$$
$$R_{i,i+1} = m_{i+1}/(p_{i+1}p_i)$$
$$NR_{i,i+1} = N_i - R_{i,i+1}$$
$$NEW_{i+1} = N_{i+1} - R_{i,i+1}$$

Where:

p_i –proportion of year i population identified in year i

n_i –number identified in year i

m_{i+1} –number identified in year i+1 that had been identified in year i

N_i –total estimated population in study area in year i (from Petersen within-year samples)

$R_{i,i+1}$ –number present in both year i and year i+1

$NR_{i,i+1}$ –number present in year i but not returning in year i+1

NEW_{i+1} –number present in year i+1 that had not been present in year i

Data were tested for evidence of bias resulting from violations of mark-recapture assumptions. Rates at which identified humpback whales were resighted and their tenure (the number of days from the first to last sighting each season) were examined for 1986–8. Field data quantifying the rate of fluking by an individual whale was tested in 1987; these data were gathered during all photographic approaches to humpback whales where we photographed every fluke presented and endeavoured to stay with groups of whales until all in the group fluked and were photographed. We examined the number of fluke photographs per minute of effort (during approaches) among the individuals encountered on multiple occasions. Additionally, differences in the fluke display rate between individuals were examined in relation to the number of days a whale was seen through the study.

We compared a number of characteristics of fluke markings and photograph quality with the number of days that a whale was seen to evaluate the effects of the distinctiveness of marks on the resighting rate. If these qualities had no effect on our ability to identify an individual, there would be no increase in sighting frequency with distinctiveness. The following qualities of 141 whales identified in 1987 were scored from the catalog photographs (the best portrayal of an individual):

Amount of white: 1 = 0–20% to 5 = 80 to 100% white

Fluke trailing edge: 1 = no apparent fringing to 5 = definite distinctive gouges, bites or deep fringing

Scars: 1 = no scars to 5 = distinctive or numerous scars

Catalogue photo quality: 1 = poor to 5 = excellent focus, contrast and lighting

Overall distinctness: 1 = indistinct to 5 = easy to recognize.

The number of days a whale was seen in 1987 was compared among the five possible scores (1–5) for each category above by analysis of variance (ANOVA).

Aerial line-transect surveys

Humpback whale numbers were also examined using line-transect population estimates from aerial survey data. Line-transect surveys were flown in a *Cessna* 172 on 16 September 1986, 21 August 1987 and 26 September 1988; a line-transect calibration survey was flown on 22 August 1987. In 1987 and 1988, surveys were flown along latitude lines every four n.miles, in 1986 lines followed longitudes every 4 minutes (3.2n.miles). The area surveyed was smaller in 1986 than in 1987–8 (Fig. 2) but nevertheless covered the region where humpback whales had been observed in previous vessel and aerial (non-transect) surveys. All surveys were conducted under good or excellent sighting conditions with the exception of the southern portion of the 1988 survey which was aborted due to fog.

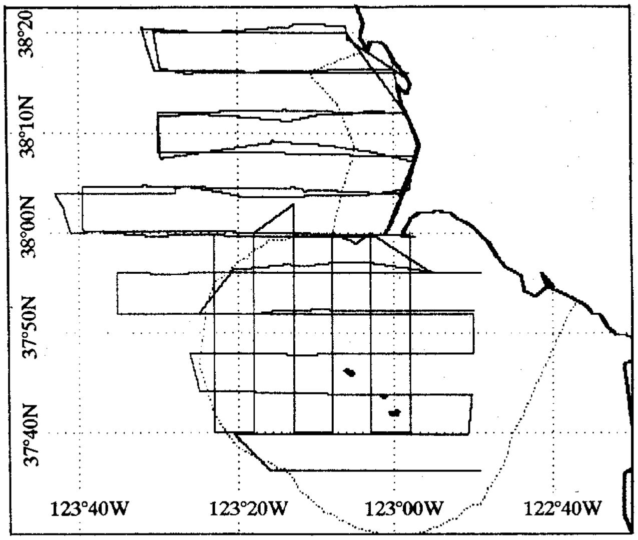

Fig. 2. Tracklines for aerial line-transect surveys in 1986–8. The 1986 survey is represented by north to south transect lines. The 1987 and 1988 surveys covered similar areas with the exception of the southern portion of the study which was not surveyed in 1988 due to heavy fog. Dotted lines shows sanctuary boundary.

Distances to humpback whales from the survey line were measured from aircraft altitude and downward angle to the sighting (measured with an inclinometer) as the aircraft passed abeam of the sighting location. All humpback whale sightings (1986–8) from aerial surveys with distance measurements were used to develop a Fourier Series model of the sighting probability based on distance from the transect line (Fig. 3) as described in Burnham, Anderson and Laake (1980). Methods used for density calculations are described in Burnham *et al.*, (1980). Variances for density estimates were based on the assumption of a binomial distribution for *n* (Burnham *et al.*, 1980).

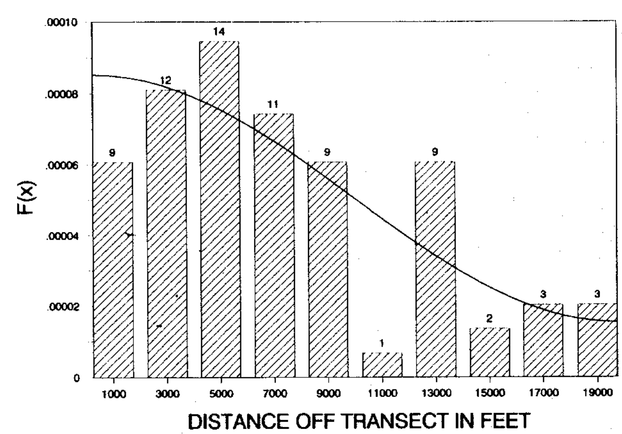

Fig. 3. Fourier series sighting probability curve from aerial line-transect surveys in 1986–8. Bars show the observed distribution of sightings based on distance off transect. The number of sightings is indicated above bars.

We calculated a crude correction factor to estimate the proportion of whales that may have been missed on the transect line because they were underwater. Replicate survey lines and sightings of whales made from adjacent transect lines were used to identify 24 groups of humpback whales known to be within 10,000ft of the transect line (based on a sighting from a different line). Using the sighting curve and the distance off transect, we predicted 18.7 of these 24 groups should have been seen (if whales were at the surface). Only 7 groups (37% of the expected) were seen. The remainder of those expected were presumably out of sight underwater because the sighting function already accounted for the decreasing sighting efficiency due to distance off transect. We therefore used this figure (0.37) to correct for animals missed even if they were on the transect line. This correction is similar to the proportion of time humpback whales spent at the surface (39%) in the Gulf of the Farallones determined from vessel-based behavior observations in 1988 (n=184, T. Kieckhefer, unpubl. data).

RESULTS

Population estimates using individual identification

A minimum estimate of population size is the number of individuals identified each year (Table 1). Each year an increasing proportion of the whales seen through the season had been already identified that year (Fig. 4). Clearly, the number identified is an underestimate because some individuals would have escaped detection. Estimates based on rate of discovery curves were similar to the number of whales identified in 1986 and 1987. In 1988 the estimate was higher than the number of whales identified (Table 2). This is consistent with our failure to identify as high a proportion of the population in 1988 compared to 1986 and 1987, indicated by the fewer times each individual was resighted and the steeper slope of the observed rate of discovery. Observed rates of discovery differed slightly from those expected if the population had been sampled randomly (Fig. 4).

Table 1

Individual humpback whales identified in the Gulf of the Farallones from 1986 to 1988.

	Identified		Times seen		Matches by year		
Year	Number	Unique	mean	SD	86	87	88
1986	466	90	5.2	4.0	-	56	48
1987	793	141	5.6	4.5		-	75
1988	398	135	2.9	2.1			-
1986-8	1,658	225					

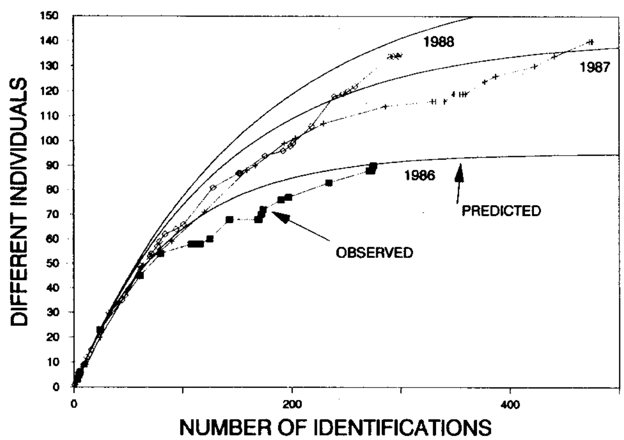

Fig. 4. Rate at which new humpback whales were identified (rate of discovery) in relation to total whales identified each year. Predicted curve shows expected rate of discovery if the estimated population were sampled randomly. Each point is a single day. Multiple sightings of the same whale in a day are counted once.

Table 2

Population estimates based on mark-recapture estimates. All n_1 and n_2 values refer to the number identified in the first and second sample periods. For between-year estimates, values are listed under the second year with n_1 referring to the number identified in the previous year.

	1986					1987					1988					
Samples/method	n_1	n_2	m_2	Est	Var	n_1	n_2	m_2	Est	Var	n_1	n_2	m_2	Est	Var	All yrs
Within-year Petersen without replacement																
Seasonal[1]	58	75	42	103	29	120	75	54	166	75	38	135	24	211	507	
Vessel[2]	75	81	65	93	3	109	125	93	146	8	109	103	62	181	87	
Location[3]	60	83	52	96	8	116	86	61	163	58	113	79	42	211	294	
Within-year Petersen with replacement																
Seasonal	58	160	94	99	41	120	128	95	162	69	38	262	64	157	270	
Vessel	75	170	148	84	3	109	286	236	127	5	109	151	103	156	52	
Location	60	171	105	95	17	116	144	106	149	24	113	89	54	192	204	
Between-year Petersen without replacement						90	141	56	226	198	141	135	75	253	172	
Between-year Petersen with replacement						90	476	229	188	78	141	296	179	233	118	
Total IDs				90					141					135		225
Rate of discovery				95					140					167		261
Jolly-Seber									188	160						

[1] Seasonal division corresponds to period with 1-3 weeks of no effort; 29 August for 1986 and 15 September for 1987 and 1988.
[2] Vessel effort included 3 vessels each year, sample 1 was chosen as vessel with greatest number of IDs, sample 2 based on all other vessels.
[3] Location samples were selected using the 10' latitude division that provided the most similar number of individuals identified in each area; 37°5N in 1986, 38°00'N in 1987, and 38°10'N in 1988.

Population sizes calculated with Petersen estimates using within-year samples divided by date, vessel, or region were higher than the number of individuals identified (Table 2). Estimates using the Chapman modification for sampling without replacement and ignoring multiple recaptures of the same individual were lower than those calculated with the Bailey modification for sampling with replacement (allowing multiple sampling and recaptures of individuals in the second time period). This difference was largest in 1988. Estimates based on sightings divided by date were the highest; estimates based on samples divided by vessel yielded the lowest estimates and may be the most biased because different vessels often worked in the same area and would be more likely to sample the same whales.

Estimates based on samples taken in different years were generally higher than estimates based on within-year samples (Table 2). Even the total number of individuals identified in two years was higher than the estimates from within-year mark-recapture calculations. Using consecutive years as samples, the Petersen estimates ranged from 188 to 253 depending on the year and whether the sampling was with or without replacement. Sampling with replacement again lowered estimates and variances compared to sampling without replacement for the same periods. The between-year estimates exceeded the number of individuals identified in the two years by, at most, 30%.

The Jolly-Seber estimate was the only open-population model employed. Because three years were available, it yielded an estimate for the middle year (1987) only. This estimate (188, Var.=160) was higher than the within-year Petersen estimate for 1987 and lower than the between-year Petersen estimate (without replacement). With the three years of data this method also provided an estimate of survival (which would include permanent emigration) of 0.83 between the first and second year.

Rate of discovery calculations among all three years (Fig. 5) yielded the highest estimates of population size (261). Fig. 5 shows clear changes in the rate of discovery curve with each new season as a result of an apparent change in the individuals returning from year to year. The steeper slope at the start of each year is consistent with either immigration/natality or more complete mixing of whales between years. The predicted curve shows that a different rate of discovery would be expected if a population of 261 were being sampled randomly.

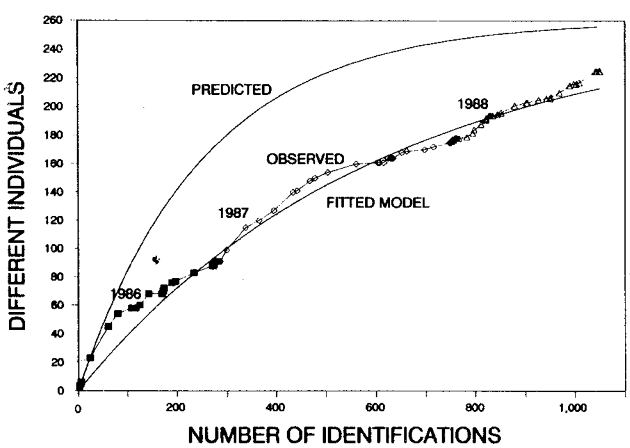

Fig. 5. Rate of discovery of humpback whales across all three years. The modeled curve (based on the rate of discovery calculation) and the predicted curve (if the estimated population were sampled randomly) are shown.

Population closure

Calculations of immigration and emigration indicated the population was not closed between years (Table 3). For 1986 and 1987, 22% and 17% of the whales present each year were estimated not to have returned the following year. Conversely, 54% and 35% of the whales identified in 1987 and 1988 were estimated to have not been present the previous year. These calculations are based on the assumption that the within-year Petersen estimates reflected the true abundance of whales in the study area each year. These changes exceed effects of mortality and natality and therefore reflect substantial immigration and emigration between years to the Gulf of the Farallones feeding group. The higher immigration than emigration rate reflects the increasing estimates of abundance for each of the three years.

Table 3

The estimated number of whales that returned and did not return to the Gulf of the Farallones across years assuming within-year Petersen estimates accurately reflected annual abundance. See Methods for details of calculations. Numbers of whales identified each year and estimated populations sizes are shown in Table 2 under within-year Petersen estimates (without replacement) based on seasonal samples.

	$R_{1,2}$	$NR_{1,2}$	$New_{1,2}$	$\%IM_2$	$\%EM_1$
1986-7	76	27	90	54	26
1987-8	138	28	73	35	17

$R_{1,2}$ = Returning between years; $\%IM_2$ = %new of year 2;
$NR_{1,2}$ = Not returning; $\%EM_1$ = % of year 1 not returning
$New_{1,2}$ = New, not seen the previous year;

Probability of capture

In addition to violations of population closure mentioned above, we found other violations of mark-recapture assumptions, especially the assumptions that all individuals have an equal probability of being identified (captured). Resighting rates and tenure for whales were different for whales seen across years compared with whales seen in only one year (Fig. 6). The number of times and days a whale was seen in each of the three years was significantly different among those whales that had been identified in one, two, or all three years (ANOVA, $p<0.05$ for all six tests). In all cases, whales seen in only one year were seen less often that year than whales that had been seen in other years; whales seen in all three years were seen most often each year. A related pattern was observed with tenure (the number of days from the first to last sighting of an individual each year); tenure in 1987 and 1988 was significantly different depending on other years seen (ANOVA, $p<0.05$ and $p<0.001$, respectively), with whales that had been seen in all three years seen an average of 15 days longer than whales seen in one year only. These data indicate that a subgroup of whales appeared to return annually and remain longer in the Gulf of the Farallones than other whales.

The number of days a whale was seen in 1987 varied significantly by the degree of scarring on the flukes (ANOVA, $n=141$, $p<0.05$) with the most heavily scarred whales being seen most often (Fig. 7, Table 4). Number of days seen did not vary significantly (ANOVA, $p>0.05$) by three other measures of fluke distinctiveness (color, edge and overall distinctiveness). As expected, catalog

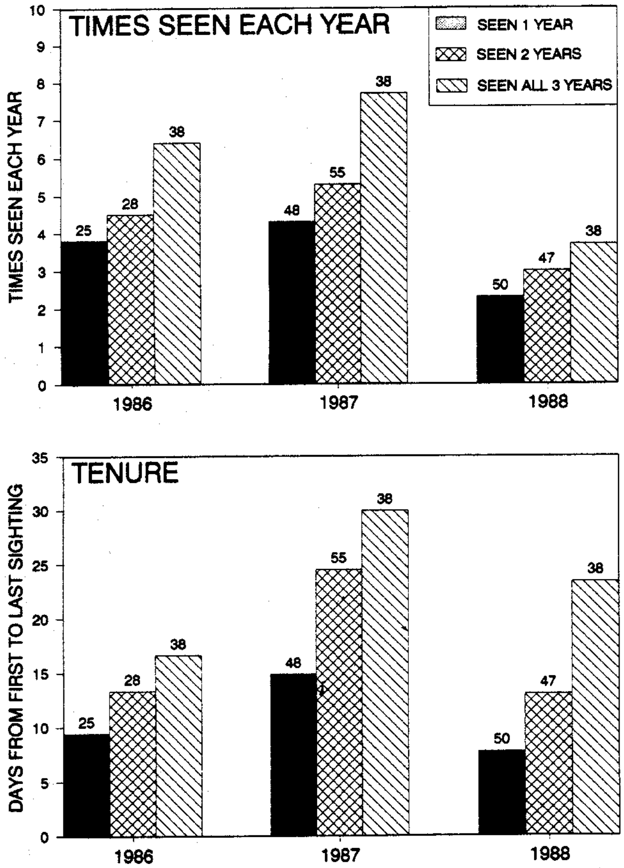

Fig. 6. Number of times individuals were seen each year and tenure (days elapsed from first to last sighting each year) for whales identified in the Gulf of the Farallones. The number of whales is indicated above bars.

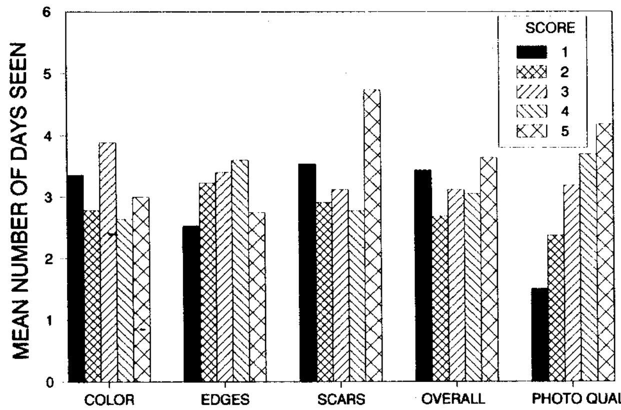

Fig. 7. The mean number of days humpback whales were seen by scored fluke characteristics and photograph quality (scored 1–5, see methods for description) of 141 humpback whales identified in 1987 in the Gulf of the Farallones.

photograph quality tended to increase with number of times an animal was seen and therefore the greater the chance of a good portrait.

Some consistent differences in the behavior of individual whales were found that would make them comparatively more or less 'catchable' with photo-identification. The number of fluke photographs per minute of effort (during approaches) varied significantly among the individuals encountered on multiple occasions (ANOVA, $p<0.05$). Individuals also showed consistent differences in the rate of fluke display expressed as the number of times flukes were photographed in an encounter as a percent (arcsine transformed) of the number of fluke photographs of the whale that fluked most often in the group accompanying the individual (ANOVA, $p<0.05$). These differences in fluke display rate indicated some whales are consistently photographed more or less often than other whales.

These differences in the fluke display rate between individuals, however, did not appear to affect the number of days a whale was seen through the study. There was no correlation between the number of days an individual was photographed and either the average fluke photographs per minute of that whale or the fluke display rate ($n=141$, $p>0.05$). Different fluking rates by individuals illustrate the potential for uneven 'catchability' of individual humpback whales, but this did not bias the recapture rate. The apparent low bias in photographic sampling in this study may reflect the consistent effort to photograph all whales in a group.

Population estimates from aerial line-transects surveys

The line-transect surveys conducted once each year in the Gulf of the Farallones yielded estimates of humpback whale abundance on a single day (Table 5). The yearly estimates, uncorrected for animals missed because they were not at the surface, were about five times lower than those based on individual identifications. When corrected for whales underwater, the line-transect estimates were still consistently lower than those based on individual identification; within-year mark-recapture estimates were about 50% higher than the aerial line-transect estimates in all three years. The area covered by the line-transect surveys was smaller in 1986 than in 1987 and 1988 but

Table 4

Number of days humpback whales were seen in 1987 by degree of distinctiveness in several categories (see Methods for explanation of scoring).

	1			2			3			4			5		
	n	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD
Color	70	3.4	2.4	23	2.8	1.6	18	3.9	1.8	11	2.6	1.6	19	3.0	2.2
Edges	15	2.5	2.0	47	3.2	2.2	47	3.4	2.1	20	3.6	2.5	12	2.8	1.9
Scars	13	3.5	2.5	35	2.9	2.2	34	3.1	2.0	40	2.8	1.5	19	4.7	2.7
Overall	9	3.4	2.2	19	2.7	2.5	24	3.1	2.0	44	3.1	2.0	45	3.6	2.3
Photo quality	6	1.5	0.8	24	2.4	1.8	52	3.2	2.0	48	3.7	2.3	11	4.2	2.2

Table 5

Estimates of humpback whale numbers from aerial line-transect surveys. Group size and f(0) calculated from data for all three years.

Date	Groups seen[1]	Transect km	f(0)	Density per km²	SE density	Area[2] surv.	Est. groups	Group size	Proportion at surface[3]	Estimated number
16 Sept 86	10	222	0.28	0.0062	0.0020	1.646	10.2	2.2	0.37	60
21 Aug 87	11	624	0.28	0.0033	0.00089	4.623	15.2	2.2	0.37	90
26 Sept 88	46	350	0.28	0.0047	0.0014	3.929	18.5	2.2	0.37	109

[1] Number seen likely includes some duplicate animals seen from adjacent survey lines.
[2] Because study area was surveyed systematically. only area (km²) covered by survey lines is used, except for 26 September 1988 where portion of study area where whales were seen in previous day (but could not be surveyed due to fog) is included.
[3] See Methods for calculation.

nevertheless covered the region where humpback whales were being seen from vessel and aerial observations prior to the survey. Additional humpback whales were likely present in areas peripheral to those we surveyed and these individuals would have been included in the mark-recapture estimates if they intermixed and were a part of the same feeding aggregation.

DISCUSSION

The principal problems in our mark-recapture estimates, especially for those based on between-year sampling, are: (1) the lack of a defined, closed population being sampled; and (2) our failure to gather a random sample.

Humpback whales occurred in other areas along the California coast concurrent to our work in the Gulf of the Farallones; there was interchange between these areas that varied as a function of the distance from the region (Calambokidis *et al.*, 1989). Defining the discrete population being sampled in this case is problematic. If we assume we are sampling only the feeding aggregation that uses the Gulf of the Farallones then we have violated the assumption of a closed population because of the mixing (immigration and emigration) with other feeding areas along the California coast. This violation results in an overestimate of the animals in the Gulf of the Farallones. By defining the population sampled as the entire humpback whale aggregation feeding along the California coast, violations of the closed population assumption are reduced but unequal capture probability becomes a problem because: (1) we did not sample all areas of the California coast randomly; and (2) whales do not redistribute randomly between samples (years) to different locations. Sampling at one location increases the probability that animals marked in the first sample will be recaptured in the second sample, resulting in an underestimate of the number of animals present along the entire California coast. These problems are consistent with the higher estimates we obtained from between-year samples compared with within-year samples because the between-year samples were in essence taken from a larger population, albeit in a biased manner.

Hammond (1986) considers accurate definition of the population sampled as an important concern with estimation of cetacean populations. This problem is not unique to our study; between-year estimates of humpback whales on feeding grounds have been reported for West Greenland (Perkins *et al.*, 1984, 1985), Newfoundland-Labrador (Whitehead, 1982; Whitehead and Glass, 1985) and the Gulf of Maine (Katona and Beard, 1990). Humpback whales tend to return to these broad regions consistently (Whitehead, 1982; Balcomb, 1984; Perkins *et al.*, 1985; Katona and Beard, 1990), therefore minimizing the violation of the closed population assumption. Whitehead, Silver and Harcourt (1982) documented the problem of incomplete mixing between years for animals at different sites in the Newfoundland-Labrador region and Hammond (1985; 1986) reported evidence of incomplete mixing off West Greenland. Perkins *et al.* (1984; 1985) considered incomplete mixing to be less of a problem because their annual samples off West Greenland covered a large portion of the region, hopefully reducing the bias caused by incomplete mixing between years. Unless all areas of a region are sampled randomly or sampled in proportion to their contribution to the overall humpback whale population, however, the resulting estimates will still be biased.

Differences in the behavior of humpback whales, that apparently caused unequal catch probability in our samples, have been reported in other cetacean studies. The occurrence of subgroups of whales that tend to be more resident or transient has been reported similarly for southern right whales (Whitehead, Payne and Payne, 1986). Segregation by size class on feeding grounds has been reported for bowhead whales (Cubbage and Calambokidis, 1987) and differential arrival and departure times for humpback whales on feeding grounds by size and reproductive condition has been seen (Pike, 1962; Dawbin, 1966; Whitehead *et al.*, 1982). Whitehead *et al.* (1982) reported that humpback whales with signs of killer whale tooth marks on their flukes tended to arrive later on Newfoundland feeding grounds than those without such scars. Differences in fluking behavior by age class, with calves fluking less often, have been reported by Perkins *et al.* (1985) and Kaufman, Smultea and Forestell (1987).

Two-sample Petersen estimates using data from photo-identified whales can be conducted either with or without replacement. Our estimates were consistently lower when the sampling was with replacement, probably because whales seen (captured) once were more likely to be seen again within the sample period than whales that had not been seen. This unequal capture probability would bias estimates downward. Hammond (1986) recommended use of the Bailey modification of the Petersen estimate for estimates based on photo-identification because it was appropriate for sampling with replacement. Most estimates of humpback whale populations using Petersen estimates, however, have been conducted as if the sampling is without replacement, i.e. resightings of the same individuals within a sample period are ignored. Ignoring resightings is the same as sampling without replacement because it is mathematically equivalent to removing these individuals from the population for the remainder of the sample period. Sampling without replacement is advisable because it appears to be less biased by the unequal capture probability created by repeated sightings of the same individual. The Chapman modification of the Petersen estimate, recommended for sampling without replacement (Seber, 1982), is therefore the more appropriate method for use with photo-identification data.

Whale populations have been estimated extensively with mark-recapture methods in recent years and although most researchers recognize the shortcomings of these techniques, there is little information to quantify the biases. Despite the comprehensive photo-identification effort in our research, our population estimates varied depending on year sampled, estimate procedure, and scheme used to divide samples. A more accurate understanding of stock structure and methods to sample the population randomly is needed because results can be biased substantially. Mark-recapture estimates, especially when employed at a single area across years, should be used in conjunction with other techniques or with improved knowledge of stock structure and other sources of bias.

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REFERENCES

Alvarez, C., Aguayo, A., Rueda, R. and Urbán, J. 1990. Estimates of humpback whale stock size along the mainland coast of the Mexican Pacific. Paper SC/A88/ID27 (published in this volume).

Bailey, N.T.J. 1951. On estimating the size of mobile populations from recapture data. *Biometrika* 38: 293–306.

Baker, C.S. and Herman, L.M. 1987. Alternative population estimates of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. *Can. J. Zool.* 65: 2818–21.

Baker, C.S., Herman, L.M., Perry, A., Lawton, W.S., Straley, J.M., Wolman, A.M., Kaufman, G.D., Winn, H.E., Hall, J.D., Reinke, J.M. and Ostman, J. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Mar. Ecol. Progr. Ser.* 31: 105–19.

Balcomb, K.C. 1984. The stock(s) of humpback whales in the North Atlantic Ocean. *Rep. int. Whal. Commn* 34: 141–3.

Balcomb, K.C. and Breiwick, J.M. 1984. Mark-recapture analysis of western North Atlantic humpback whales using fluke photographs. *Rep. int. Whal. Commn* 34: 141.

Balcomb, K.C., Katona, S.K. and Hammond, P.S. 1986. Population estimates for the North Atlantic humpback whale using capture-recapture methods on photo-identified whales. *Rep. int. Whal. Commn* 36: 110.

Burnham, K.P., Anderson, D.R. and Laake, J.L. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr.* 72: 1–202.

Calambokidis, J., Steiger, G.H., Cubbage, J.C., Balcomb, K.C. and Bloedel, P. 1989. Biology of humpback whales in the Gulf of the Farallones. Report to the Gulf of the Farallones National Marine Sanctuary, NOAA, San Francisco, California (unpublished). 93pp.

Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. *Univ. Calif. Public. Stat.* 1: 131–60.

Cubbage, J.C. and Calambokidis, J. 1986. Size-class segregation of bowhead whales discerned through aerial sterophotogrammetry. *Mar. Mamm. Sci.* 3: 179–85.

Darling, J.D. and Jurasz, C.M. 1983. Migratory destinations of North Pacific humpback whales (*Megaptera novaeangliae*). *In*: R. Payne (ed.) *Communication and Behavior of Whales*. AAAS Selected Symposia Series, Washington, D.C.

Darling, J.D. and McSweeney, D.J. 1985. Observations on the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* 63: 308–14.

Darling, J.D. and Morowitz, H. 1986. Census of 'Hawaiian' humpback whales (*Megaptera novaeangliae*) by individual identification. *Can. J. Zool.* 64: 105–11.

Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. pp. 145–70. *In*: K.S. Norris (ed.) *Whales, Dolphins and Porpoises*. University of California Press, Berkeley, California.

Hammond, P.S. 1985. An analysis of the West Greenland humpback capture-recapture data using log-linear models and the GLIM computer package. Paper SC/37/PS30 presented to the IWC Scientific Committee, June 1985 (unpublished). 4pp.

Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. int. Whal. Commn* (special issue 8): 253–82.

Hammond, P.S. and Larsen, F. 1985. Some notes on estimating populations size of West Greenland humpbacks using mark-recapture. *Rep. int. Whal. Commn* 35: 129.

Katona, S.K. and Beard, J.A. 1990. Population size, migrations and substock structure of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. Paper SC/A88/ID2 (published in this volume).

Kaufman, G.D., Smultea, M.A. and Forestell, P. 1987. Use of lateral body pigmentation patterns for photographic identification of east Australian (Area V) humpback whales. *Cetus* 7: 5–13.

Perkins, J.S., Balcomb III, K.C., Nichols Jr., G. and DeAvilla, M. 1984. Abundance and distribution of humpback whales (*Megaptera novaeangliae*) in West Greenland waters. *Can. J. Fish. Aquat. Sci.* 41: 533–6.

Perkins, J.S., Balcomb III, K.C., Nichols Jr., G., Hall, A.T., Smultea, M. and Thumser, N. 1985. Status of the West Greenland humpback whale feeding aggregation, 1981–83. *Rep. int. Whal. Commn* 35: 379–83.

Perkins, J.S. and Whitehead, H. 1977. Observations on three species of baleen whales off northern Newfoundland and adjacent waters. *J. Fish. Res. Bd Can.* 34: 1436–40.

Pike, G.C. 1962. Canadian whaling off British Columbia, and progress on research, 1948 to 1959. Report to the Fish. Res. Board Can., Nanaimo, British Columbia (unpublished).

Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. Second Edition, MacMillan Publ. Co, New York, NY. 654pp.

Urbán, J., Balcomb, K.C., Alvarez, C., Bloedel, P., Cubbage, J.C., Calambokidis, J., Steiger, G.H. and Aguayo, A. 1987. Photo-identification matches of humpback whales (*Megaptera novaeangliae*) between Mexico and central California. Presented to the Seventh Conference on the Biology of Marine Mammals, Miami, Florida (unpublished).
von Ziegesar, O. and Matkin, C.O. 1986. Humpback whales in Prince William Sound in 1985: a contract report. Contract No. 41USC252, Natl. Mar. Fish. Serv., Natl. Mar. Mamm. Lab., Seattle, Washington (unpublished).
Whitehead, H. 1982. Populations of humpback whales in the northwest Atlantic. *Rep. int. Whal. Commn* 32: 345–53.
Whitehead, H., Chu, K., Perkins, J., Bryant, P. and Nichols, G. 1983. Population size, stock identity, and distribution of the humpback whales off West Greenland-Summer 1981. *Rep. int. Whal. Commn* 33: 497–501.
Whitehead, H. and Glass, C. 1985. The significance of the Southeast Shoal of the Grand Bank to humpback whales and other cetacean species. *Can. J. Zool.* 63: 2617–25.
Whitehead, H., Payne, R. and Payne, M. 1986. Population estimate of the right whales off Peninsula Valdes, Argentina, 1971–76. *Rep. int. Whal. Commn* (special issue 10): 169–71.
Whitehead, H., Silver, R. and Harcourt, P. 1982. The migration of humpback whales along the northeast coast of Newfoundland. *Can. J. Zool.* 60: 2173–9.
Wilkinson, L. 1988. *SYSTAT: The System for Statistics*. SYSTAT, Inc., Evanston, Illinois. 822pp.