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REPRODUCTIVE RATES OF HUMPBACK WHALES OFF CALIFORNIA

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ABSTRACT

From 1986 to 1996 we examined the reproductive rates, calving rates, and reproductive histories of mature females as part of photo-identification studies of humpback whales that feed off California, Oregon, and Washington during summer and fall. Annual reproductive rates were measured by two methods: proportion of all whales that were calves based on sightings (0.6%–5.9% per year, mean = 3.6%, SD = 1.6) and based on individually identified animals (1.1%–8.0% per year, mean = 4.1%, SD = 1.8). The reproductive rate based on sightings varied significantly by year (G test, $P < 0.001$), region (G test, $P < 0.001$), and by month (G test, $P < 0.05$). Seventy-nine sexually mature females were identified with 97 calves out of a total of 844 known individuals over the 11-yr study. Mother-calf separation on the feeding grounds was recorded in several instances. The apparent reproductive rates of this population are considerably lower than rates of 4%–15% reported from other feeding areas for this species. Our estimates are likely biased downward because this population has been increasing at about 5% per year. Calves may have been missed due to early weaning and because of our sampling from small boats late in the season. We also found evidence of geographic segregation of mother-calf pairs within our large study area. Despite these factors, we conclude the reproductive rate of this population appears to be lower than has been reported in other areas.

Key words: reproductive rates, humpback whales, *Megaptera novaeangliae,* photographic identification, North Pacific, California.

Populations of humpback whales (*Megaptera novaeangliae*) were severely depleted by commercial whaling and have been protected in the North Pacific since 1967 (Rice 1974, 1978; Clapham *et al.* 1997). Estimates of abundance have only recently been calculated for most populations and little is known about trends in abundance and reproductive rates. Long-term photo-identification has become a valuable method with which to examine reproduction in

Table 1. Summary of vessel effort off California (includes some surveys off Oregon and Washington)*. Effort of collaborators not included.

Year	Dates	# of surveys	# of hours
1986	23 July–15 Sept	71	513
1987	17 Aug–17 Oct	58	460
1988	19 Aug–2 Nov	66	484
1989	8 Sept–26 Oct	15	111
1990	4 Sept–13 Nov	29	196
1991	16 July–15 Nov	53	368
1992	24 May–16 Nov	73	601
1993	28 July–22 Oct	48	374
1994	15 June–10 Oct	51	432
1995	10 June–3 Dec	60	499
1996	21 Apr–12 Nov	129	761

* Includes surveys off Oregon and Washington 91(1), 92(3), 93(2), 94(2), 95(12), and 96(14).

humpback whales (Baker *et al.* 1987, 1992; Barlow and Clapham 1997; Clapham and Mayo 1987, 1990; Glockner-Ferrari and Ferrari 1984, 1990; Straley 1994; Straley *et al.* 1994).

Humpback whales feed along the California coast throughout summer and fall (Rice 1974, Calambokidis *et al.* 1990*a*). Although some historical accounts suggested that humpback whales migrated only through Californian waters (Kellogg 1929, Tomilin 1957), photographic identification of individual animals (Calambokidis *et al.* 1996) and mtDNA studies (Baker *et al.* 1990) have shown that individuals from this area constitute a separate subpopulation that is resident in the region during the summer and fall. This feeding group ranges between southern California and northern Washington (Calambokidis *et al.* 1996), although numbers off Oregon and Washington appear to be relatively small (Green *et al.* 1992). Recent estimates of abundance for this population were 597 (CV = 0.07) from photographic identification (Calambokidis and Steiger 1995) and 626 (CV = 0.41) from line-transect ship surveys (Barlow 1995). Evaluations of trends in abundance have suggested that this subpopulation may be increasing (Barlow 1994, Calambokidis and Steiger 1995).

We report here on reproductive rates, calving rates, and reproductive histories of mature females observed during boat surveys and photographic identification of individual whales conducted primarily off California from 1986 to 1996.

Methods

Data were collected as part of humpback and blue whale (*Balaenoptera musculus*) studies (Calambokidis *et al.* 1990*a, b*; Calambokidis and Steiger 1995). Research was conducted between April and December (Table 1) in the waters primarily within 50 nmi of California (Fig. 1). Surveys were limited to central

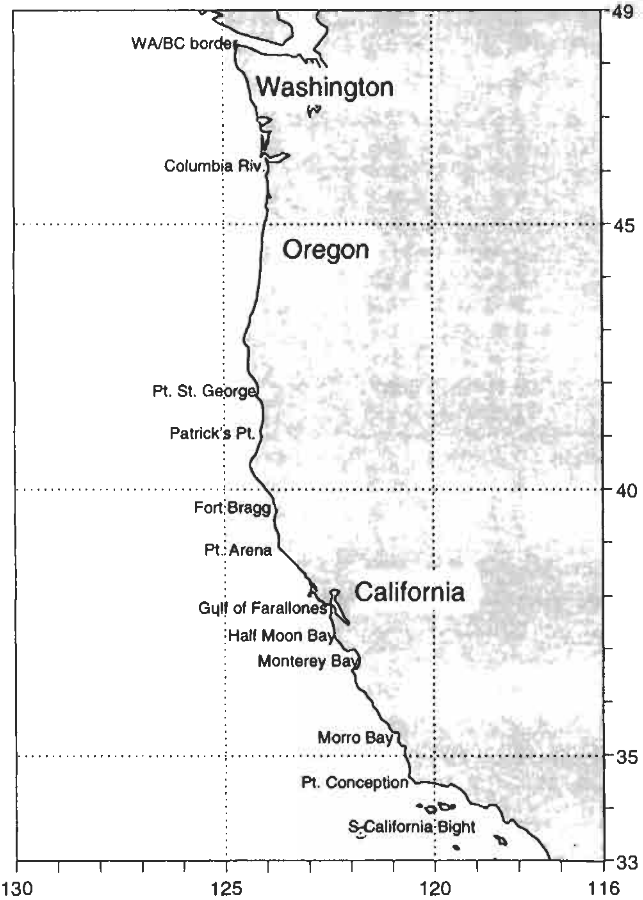

Figure 1. Study area of humpback whales. Most effort was between Pt. St. George and Southern California Bight.

California in 1986, 1987, and 1989. Geographic coverage was most extensive starting in 1991 when whales were sampled along most of the California coast. Several surveys between 1991 and 1996 also included regions off Oregon and northern Washington (Table 1).

Most surveys were conducted using 4–6-m inflatable boats; a 14-m motor sailer and a 6-m fiberglass motor boat were used for some surveys. Additionally, some of the surveys starting in 1993 were conducted in conjunction with Southwest Fisheries Science Center (SWFSC) surveys using the NOAA ship *McArthur.* During transect surveys out to 350 nmi off California, a 5–7-m inflatable boat was launched for photo-identification when possible, and those data are included here. All other surveys were non-systematic; effort was targeted at areas where whales were concentrated with an emphasis on photographing flukes of as many whales as possible. We attempted to approach all observed humpback whales for photo-identification. Photographs of the ventral side of the flukes were taken by one or two photographers. Whales were followed through several dive sequences until suitable photographs were obtained or until we determined that it was unlikely that an animal was going to fluke. Photographs were taken with *Nikon* motor-advance 35-mm SLR cameras with 300-mm f4.5 lenses and *Ilford* HP-5 black-and-white negative film. Whales were identified photographically by natural markings on their flukes (Katona and Whitehead 1981). A total of 844 individual whales was identified between 1986 and 1996 in the study area.

The following terms are used in this study:

Calf—A small whale in its first year of life that is in close and consistent association with a larger whale (presumed to be the mother); a calf on the feeding grounds is at least half the size of the mother. These animals were probably born between January and March (Johnson and Wolman 1984) and would therefore be approximately 4–11 mo old during our study.

Mother—A large whale in close association with a calf in that year. Tentative identifications of mothers were assigned when the field notes on whether animals were accompanied by calves were inconsistent (*i.e.,* they were not recorded as mothers with calves in all encounters).

Mature female—A female that has been seen with a calf in any year. Females were considered to be sexually mature from the year prior to which they were first recorded with a calf (the year they became pregnant). For analyses of sighting histories of whales of known age or sex, we also included an assumption that whales that were at least 5 yr old were sexually mature based on other research that demonstrated that most females attain sexual maturity at an average of 5 yr (Clapham 1992). Whales that had not been seen as calves were considered at least 5 yr old in the fourth year after they were first seen.

Reproductive rate—Two different methods were used to estimate reproductive rates. The first, which is termed the *reproductive rate based on sightings,* is the proportion of all humpback whales approached (including calves) that were determined to be calves, per year. The second method, the *reproductive rate based on photo-identification,* is the number of mothers identified photographically as a percentage of the total number of all whales identified (including mothers and calves) calculated annually. We used identified mothers instead of calves because calves tended to raise their flukes less often and therefore were sometimes not identified. In 1989, however, the number of calves was used because more were identified than mothers. Although we refer to these as reproductive rates, they also include any neonatal mortality that occurred before the whales were observed on the feeding grounds.

Calving rate—For our primary estimates, the calving rates were calculated as *calves per mature female per year,* using all sighting histories of females starting with the year of their first known pregnancy (the year prior to being seen with a calf). This method is described by Clapham and Mayo (1990) as the maximum calving rate. Because of the potential for an upward bias introduced by including the first reproductive year (Barlow and Clapham 1997), we also calculated an *alternate minimum calving rate* starting with the year after the

Table 2. Observed reproductive rates based on sightings and photoidentification and estimates of calving rate (see text). Tentative identifications of mothers and calves included but sightings by collaborators not included.

	Repro. rates based on sightings			Repro. rates based on photo-ID				Calving rate	
Year	# calves	# whales	Rate	# calves	Moth-ers	Total IDs	Rate	# mature females	Rate
86	4	711	0.6%	1	1	88	1.1%	3	0.33
87	17	845	2.0%	4	4	143	2.8%	11	0.36
88	26	439	5.9%	4	8	170	4.7%	11	0.73
89	6	135	4.4%	3	1	62	4.8%*	7	0.14
90	7	269	2.6%	2	4	126	3.2%	9	0.44
91	26	659	3.9%	8	11	225	4.9%	18	0.61
92	24	1,039	2.3%	4	11	350	3.1%	32	0.34
93	23	524	4.4%	11	11	214	5.1%	24	0.46
94	13	389	3.3%	5	5	205	2.4%	23	0.22
95	43	758	5.7%	19	25	314	8.0%	39	0.64
96	34	726	4.7%	10	16	306	5.2%	31	0.52
Total	223	6,494	3.4%	71	97	2,203	4.4%	208	0.47
Mean			3.6%				4.1%		0.44
SD			1.6%				1.8%		0.18

* Based on calf identifications, due to lower number of cows identified.

first year that a mother was seen with a calf. This estimated a rate for females after their first observed birth.

Rake marks—A series of parallel indentations or scars on the body of a whale that are evidence of non-fatal attacks on these animals. In this study the photographs of flukes were examined for these scars. We looked for signs of predatory pressures on these humpback whales by examining flukes for rake marks. Fluke photographs of the 79 mature females (including the four whales photographed by collaborators) and 33 first-year calves were examined and scored as: (1) no rake marks, (2) possible marks, (3) distinctive marks, and (4) severe marks (with three or more separate rake marks or bites that resulted in damage to the fluke). Only those with distinctive and severe marks are reported here.

Additional data provided by collaborators were included in the sighting histories of known mature females (and photographs were examined for scarring) but were not included with the data that were used to calculate all rates reported here. Only data collected by the primary research personnel were included in these calculations. The arcsine transformation (Zar 1984) was used when we tested percentages statistically.

Results

Reproductive Rates

Between 1986 and 1996, reproductive rates based on sightings ranged from 0.6% to 5.9% (mean = 3.6%, SD = 1.6) (Table 2). These were not significantly different (paired t-test by yr, $P > 0.05$) from the reproductive rates based on photo-identification, which ranged from 1.1% to 8.0% (mean = 4.1%, SD = 1.8) (Table 2). These two annual rates were closely correlated ($r = 0.86$, $P = 0.001$). Reproductive rates based on sightings varied significantly among years (G test, $P < 0.001$); however, annual differences based on photo-identification fell short of significance (G test, $P < 0.10$), probably because of the smaller sample size. Although reproductive rates showed a general tendency to increase over the years, for both methods this trend fell short of statistical significance ($P = 0.12$ based on sightings and $P = 0.07$ based on photo-identification). Annual differences could have been partly influenced by geographic coverage, which became more extensive beginning in 1991 (see section on temporal and spatial occurrence of calves).

Calving Rates and Intervals

The estimated annual calving rate ranged between 0.14 and 0.73 calves per mature female per yr (mean = 0.44, SD = 0.18) (Table 2). Similar to the reproductive rates, these varied significantly by year (G test, $P < 0.05$). Only limited information was available on calving intervals because only 16 (20%) of the 79 mothers were seen with calves in multiple years (14 were seen with two calves and 2 with three calves). Most of the intervals were unbounded (with years when animals were not seen); of those that were bounded, one-year ($n = 2$), two-year ($n = 2$) and three-year ($n = 2$) calving intervals were observed. These bounded calving intervals are biased towards short intervals because mothers in our study were seen on an average of only 4.0 yr (SD = 2.1) out of the 11 yr of the study. The sparse sighting histories make it unlikely for a female to be seen in many consecutive years to provide evidence of longer bounded calving intervals.

Our estimates of the calving rate appeared to be biased by the sparse sighting histories of many of the animals. Calving rate estimates (for all years) were lowest (0.34) for females that were known to have been sexually mature for eight or more years in our study and highest (0.65) for females that were known to have become sexually mature only in the last three years of the study. The low estimate of the calving rate in this latter group is partly the result of the 20 females that had been seen only once (with a calf) in the two-to-three-year period for which they were known to have been sexually mature. The alternate minimum calving rate for the years after the sighting of the first calf was 0.18, substantially lower than our primary estimate. This estimate is probably biased downwards because it excluded the first observed year of reproduction. It may be more accurate than our primary estimate, however, which has a substantial upward bias when sighting histories are sparse.

Temporal and Spatial Occurrence of Calves

Although calves were seen in all areas sampled, reproductive rates based on sightings between 1986 and 1996 varied significantly by region (G test, $P <$

Table 3. Percentage of whales that were calves by month and region between 1986 and 1996.

Month/Region	Calves	Total	% calves
Months			
April–May	3	75	4.0%
June	9	177	5.1%
July	16	370	4.3%
August	41	1,648	2.5%
September	77	1,949	4.0%
October	63	1,651	3.8%
Nov–Dec	14	624	2.2%
Regions			
S. Calif. Bight	24	475	5.1%
Pt. Conception–Morro Bay	6	220	2.7%
Monterey Bay	3	95	3.2%
Half Moon Bay	21	312	6.7%
Gulf of Farallones/Cordell	133	4,437	3.0%
Pt. Arena	1	158	0.6%
Ft. Bragg–Patricks Pt.	2	196	1.0%
Pt. St. George	21	405	5.2%
Oregon	2	30	6.7%
Washington–B.C. border	10	166	6.0%

0.001) and ranged from 0.6% to 6.7% (Table 3). The highest proportions seen were in northern waters (6.7% off Oregon and 6.0% near the Washington/British Columbia border), as well as in one location off central California (6.7% off Half Moon Bay). Lowest rates were seen in several areas off northern California (0.6% off Pt. Arena and 1.0% off Ft. Bragg). The largest portion of our sample (68% of sightings) was from the Gulf of the Farallones/Cordell Bank area, where the reproductive rate was 3.0%, compared to 4.4% for all other areas.

Reproductive rates based on sightings from 1986 to 1996 also differed significantly by month (G test, $P < 0.05$) with highest proportions in June (5.1% of 177 whales seen) and lowest in November–December (2.2% of 624 whales seen, Table 3). Despite the lower rate at the end of the season, the association between reproductive rate and month fell short of statistical significance ($n = 7$, $r^2 = 0.34$, $P = 0.17$).

We did see several cases that indicated early weaning or neonatal mortality between sightings (*i.e.,* mothers that had been seen with calves earlier in the season were observed later without them) which could affect the observed reproductive rates by month. One mother (10410) was observed with a calf on 22 September 1992 and was resighted on 13 and 14 Nov 1992 without a calf. Another (10230) was documented with a calf through 26 August but without one during two observations on 26 Sept. A third (10107) was observed with a calf off Mexico in the winter of 1990[1] and was resighted by us off

[1] Personal communication from K. C. Balcomb, Center for Whale Research, 1359 Smuggler's

California without a calf on 31 October of that year. On two occasions in 1995, mothers and calves were observed to be loosely associated on 1 December. One mother (10083) was first photographed without its calf (10860), then was seen with it 35 min later. In the second case, a calf (10840) was first observed rolling in kelp alone, then shortly thereafter was joined by the mother (10801).

Because sighting effort varied by year, region, and month, some of the significant differences seen could be artifacts of one of the other factors or of uneven sampling effort. Sample sizes were too small to allow a multivariate analysis of the interaction of year, region, and monthly patterns.

There were also significant differences in the average distance from shore of mothers with calves compared to other whales. Distance from shore of all whales varied significantly by region (ANOVA, $P < 0.001$). Within the Gulf of the Farallones region (representing over two thirds of our total sample), mothers with calves were seen an average of 22 km from shore *versus* 25 km for other whales (ANOVA, $P < 0.001$).

Sighting Histories of Whales

Over the 11-yr study 844 humpback whales were individually identified. Of these, 79 were mature females (including tentative identifications) that were accompanied by 97 calves (Fig. 2). The number of times an identified whale was seen in a year was significantly different (ANOVA, $P < 0.01$) among the four groups (females with calves, mature females without calves, females of unknown maturity, and males). Known mature females (both with and without calves) were seen fewer times (2.51 and 2.34 times/yr, respectively) than females of unknown maturity or males (3.12 and 3.25 times/yr, respectively), although these differences were small. There were no significant differences in the dates of initial and final sightings or the minimum tenure among the four groups.

Some of the reproductive females identified in this study have demonstrated interesting long-range movements between California and wintering areas. One female (10144) was one of only four whales documented to move between California and Hawaii; it was photographed off Hawaii in 1980 by the Kewalo Basin Marine Laboratory, University of Hawaii (Perry *et al.* 1988) and resighted with a calf in 1988 off California. Four of these mature females have been seen at a wintering area off Costa Rica (Steiger *et al.* 1991; Cascadia Research, unpublished data); in one case, a female (10233) was seen without a calf there on 10 February 1996 and then observed with a calf later that year (23 September) in the Gulf of the Farallones, California.

Cove Road, Friday Harbor, WA 98250, U.S.A. and J. Urbán R., Departamento de Biología Marina, Universidad Autonoma de Baja California, Ap. Post. 19-B, B.C.S. 23081, Mexico, May 1998.

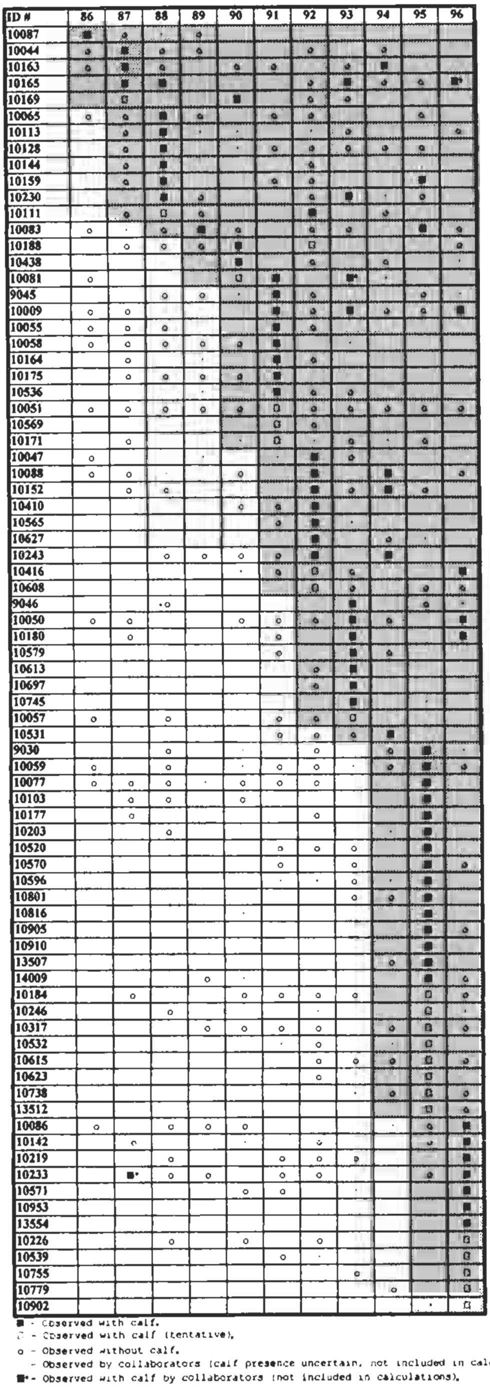

Figure 2. Sighting histories of 79 female humpback whales seen with calves between 1986 and 1996. Shaded areas show years in which females known to be sexually mature based on first known pregancy (used to calculate pregnancy rate). ■ = observed with calf, □ = observed with calf (tentative), ○ = observed without calf, ● = observed by collaborators (calf presence uncertain, not included in calculations), ■* = observed with calf by collaborators (not included in calculations).

ID #	86	87	88	89	90	91	92	93	94	95	96
10090	C		·								
10135		C				o	o	o	·	·	o
10138		C			o		o	o			
10105		C			o		o		o		
10120		C	o				o	o		o	
10181		C					o	o		o	
9503			C								
10211			C		o	o	o		o		o
10216			C		o	o	o		o	o	o
10253			C								
10308				C	o		o				
10315				C		·	o				
10318				C		o	o	o			o
10426					C		o				o
10437					C		o				
10511						C				o	o
10528						C		o		o	o
10538						C					
10548						C					
10550						C	o			o	o
10589						C				o	
10736						C		o	o		

C - Year seen as a calf.
o - Observed without calf.
· - Observed by collaborators (calf presence uncertain, not incl. in calculations).

Figure 3. Sighting histories of humpback whales that were initially identified as calves in 1991 or earlier. Shaded area represents sightings of five or more years after birth, when we consider most whales to be sexually mature. C = year seen as calf, ○ = observed without a calf, ● = observed by collaborators (calf presence uncertain, not included in calculations).

Reproductive Histories of Known-Age or Known-Sex Whales

Although data on reproductive histories of known-age or -sex individuals were limited, it provided evidence that females were reproducing at a low rate. Seventy-one calves were identified during the 11-yr study. Of these, 22 had been identified in 1991 or earlier and probably became sexually mature during our study. Of these 22 calves, 12 were resighted in a total of 23 yr after they were assumed to be sexually mature (Fig. 3). None were observed with calves in any year. Assuming a sex ratio of 1:1 and a calving interval of 2.38 (Barlow and Clapham 1997), five of these whales would have been expected to have had a calf.

Additionally, 13 identified whales were known to be females from skin biopsies taken in 1988 and 1991 (Fig. 4). All of these would have been reproductively mature no later than 1995. Only 6 of these 13 individuals have been seen with calves in this study (7 calves in 23 female-years) and seven females had not been seen with calves in eight female-years after they were judged to be sexually mature (Fig. 4).

ID #	86	87	88	89	90	91	92	93	94	95	96
Biopsied females seen with calves											
10111		o		o			■		o		
10051	o	o	o	o	o		o	o	o	o	o
9045			o	o	·	■	o			o	·
10184		o			o	o	o	o			o
10410					o	o	■				
10571					o	o		·			■
Bopsied females not seen with calves											
10115	·	o	o		o		o	o	·		
10201			o	o		o	·			o	
10223			o		o						
10234			o	o					o	·	
10237			o	o		·	o				o
10519						o			o	o	
10548						o					

■ - Observed with calf.
o - Observed without calf.
· - Observed by collaborators (calf presence uncertain).

Figure 4. Sighting histories of know females based on skin biopsies collected in 1988 and 1991. Shaded area shows period animal presumed to be sexually mature based on either sighting with calf in previous year or interval of four years since whale was first see (in all cases, the whale was not calf when first seen. ■ = observed with calf, ○ = observed without calf, ● = observed by collaborators (calf presence uncertain).

Signs of Predatory Attacks

Because we were interested in the neonatal mortality that occurred before whales arrive at the feeding grounds, we examined the prevalence of rake marks on the flukes of mothers and calves as evidence of predatory attempts on these animals, presumably by killer whales (*Orcinus orca*). Of the 79 known mature females, 24 (30%) had distinctive rake marks on their flukes. The marks were severe on the flukes of eight of these whales.

Discussion

The reproductive rates that we have estimated for humpback whales off California are unusually low compared to those reported elsewhere (Table 4). Reproductive rates determined on other feeding grounds through photo-identification studies averaged 7.9% (range = 4.5%–10.3%) in the Gulf of Maine from 1979 to 1987 (Clapham and Mayo 1987, 1990), 9.5% (range = 3.6%–14.6%) from 1980 to 1988 in Prince William Sound, Alaska (von Ziegesar *et al.* 1994), and 12.5% in 1986 in southeastern Alaska (Baker *et al.* 1992). The average of the reproductive rates based on photo-identification off California was significantly lower than those reported for the Gulf of Maine and Prince William Sound (t-test, $P < 0.001$ in both cases). The methods used to cal-

Table 4. Comparison of reproductive rates based on photo-identification and calving rates to those from other photo-identification studies.

Study	Region	Years	Reproductive rate		Calving rate	
			Mean	Range	Mean	Range
This study	California–Washington	86–96	4.0%*	1.1–8.0	0.47**	0.14–0.64
Clapham and Mayo (1990)	Gulf of Maine	79–87	7.9%	4.5–10.3	0.41	0.24–0.50
Baker *et al.* (1992)	SE Alaska	86	12.5%		0.38	
Straley (1994)	SE Alaska	80–92	—		0.50**	0.25–0.59
von Ziegesar (1992)	Prince Wm. Sound, Alaska	80–88	9.5%	3.6–14.6	—	

* Based on identification of mothers with calves (all other studies used calf IDs).
** Weighted mean.

culate these rates were similar, except that Clapham and Mayo (1987, 1990) and von Ziegesar *et al.* (1994) used the number of calves photographed (instead of mothers) as a proportion of all whales identified. This discrepancy would not make a difference if most calves were identified in their studies. Other studies based upon whaling data and sighting surveys have estimated reproductive rates between 4% and 13% for humpbacks in other regions (Chittleborough 1965, Herman and Antinoja 1977, Whitehead 1982).

The primary calving rate calculated in our study was similar to those reported elsewhere (Table 4). This rate is high relative to our reproductive rate and may be affected by the upward bias in this calculation when applied to the sparse sighting histories of animals in our study. The calculation of calving rate using (1) only animals known to have been sexually mature for eight or more years, (2) the calving rate for biopsied females, and (3) the use of an alternate minimum calculation using only years after the sighting of the first calf, all yielded far lower estimates of the calving rate. Calculation of this alternate minimum calving rate using data reported by Clapham and Mayo (1990) yielded an estimate of 0.32 compared to 0.18 for our data. This estimate would make our calving rate just over half of that for the Gulf of Maine, comparable to the difference we found in the estimates of reproductive rates.

The calving rate of the biopsied females (0.23 calves per mature female per year) is about half the value reported for the Gulf of Maine (Clapham and Mayo 1990, Barlow and Clapham 1997) which is consistent with the lower observed reproductive rate. Once a larger set of sighting histories of known females is available, data should be adequate to compute calving rates using the more recently developed unbiased methods suggested by Barlow and Clapham (1997).

It is unclear whether the low reproductive rates that we observed reflect biases in our sampling methods or if they are genuinely low. We report these values cautiously because a low rate of recruitment would not be expected in a population recovering from exploitation. Humpback whale populations in the eastern North Pacific were severely depleted between 1905 and 1965; 23,000 were killed, including whales off California (Rice 1978, Johnson and Wolman 1984). Also, whaling data suggest that the present size is well below that of this population in the 1920s (Clapham *et al.* 1997). Best (1993) concluded that most depleted stocks of baleen whales for which there are suitable data are increasing. Studies examining trends in abundance have suggested that humpback whale numbers off California may be increasing. Barlow (1994) reported an increase in humpback whale sightings during vessel transect surveys in 1991 compared to similar surveys in 1980, although the abundance estimates did not differ significantly between surveys. An increase of about 5% a year has also been detected using capture-recapture abundance estimates from photo-identification studies since 1986 (Calambokidis and Steiger 1995). We cannot reconcile the low reproductive rates with these results.

Possible sampling biases could include (1) geographic variation in the distribution of calves that resulted in an underrepresentation in our sample, (2) differences in arrival and departure times by gender or age class, that resulted in fewer mothers with calves being present during our effort, or (3) early weaning and separation of mothers and calves that caused us to misclassify weaned animals as yearlings instead of first-year calves. All of these factors could bias our estimates of reproductive rates downward and are examined in more detail below.

Although we saw geographic variation in reproductive rates based on sightings and photo-identification, these differences did not appear to account for the overall low rates, because none of the areas sampled had a high proportion of mother-calf pairs. Geographic segregation, while not apparent in most humpback populations, has been suspected to occur in the Arabian Sea (Mikhalev 1997). Reproductive rates from sightings were slightly higher off Oregon and Washington, areas that we did not sample heavily, but were still lower than in other studies. In aerial surveys for marine mammals off Oregon and Washington in 1989 and 1990, of 68 humpback whales seen, none were calves (Green *et al.* 1992).

An offshore-inshore segregation of humpback whales by reproductive condition could also influence observed reproductive rates, although such an effect appears small. We found evidence for mothers and calves being significantly closer to shore than other whales in the Gulf of Farallones, although the difference was small. It also did not appear that we were missing calves in waters far offshore outside our normal operating area. Vessel surveys to 350 nmi offshore of California showed few humpback whales far offshore; most were distributed near the edge of the Continental Shelf (Hill and Barlow 1992), which is within our study area. There is conflicting information from previous studies regarding whether mothers with calves prefer coastal or offshore waters compared with other animals. Kellogg (1929) reported that humpback whale mothers and calves kept well out to sea during the southbound migration past southern California but did not mention the whales that used this area to feed. North Atlantic humpback whale mothers with calves were seen in shallower water than other animals on the feeding grounds (Perkins *et al.* 1985).

Differences in arrival and departure times on the feeding grounds by age class probably did not bias our findings, because the number of days an identified whale was seen, the first and last sightings, and tenure were not significantly different for mothers with calves than for other subgroups. Studies show that temporal segregation by age class occurs during humpback whale migrations (Dawbin 1966, 1997). On the wintering grounds, mothers with calves tend to arrive later and leave later than other whales (Chittleborough 1958; Nishiwaki 1959; Dawbin 1966, 1997; Herman and Antinoja 1977; Gabriele 1992). Studies on feeding grounds have reported conflicting observations. Dawbin (1966, 1997) reported that lactating females left antarctic feeding grounds earlier than other whales. In other regions some exceptions have been reported: Straley (1990) reported mothers with first-year calves present as late as January in southeastern Alaska, and Clapham and Mayo (1987) observed early-season sightings of lactating females in the Gulf of Maine.

It is possible that because most of our sampling effort was conducted in late summer and fall, calves were not recognized (due to early weaning or their larger size and looser association with their mothers). This is supported by the lower rates based on sightings (lower proportion of whales that were calves) late in the season and by our observations of mothers with calves seen first with and later without calves. A contributing factor to a failure to recognize calves late in the season could be our use of small boats (inflatables), often in rough seas, making it harder to recognize more subtle size differences. Although most humpback whale calves separate from their mothers on the wintering grounds when they are 1 yr old (Chittleborough 1965, Johnson and Wolman 1984, Clapham and Mayo 1987, Baker *et al.* 1987), there have been two documented cases where calves separated from their mothers by October of their first year on the feeding grounds in the Gulf of Maine (Baraff and Weinrich 1993). Clapham and Mayo (1987) observed calves feeding on fish when they were 5–6 mo old, although the calves remained with their mothers for at least a year. Even if late-season sampling biased our estimates downward, the early-season data still show low reproductive rates.

The close agreement between the values obtained from the two different methods used to estimate reproductive rates also helps to eliminate other biases. Estimates of reproductive rates based on sightings could be biased if resighting rates of mother-calf pairs were different from resightings of animals in other age classes. Reproductive rates based on photo-identification could be biased downwards because calves tend to fluke less often than other whales (Perkins *et al.* 1985). We lowered this bias by using the identification of mothers instead of calves, because we clearly were able to identify mothers more often. The close agreement between the two methods leads us to conclude that these biases in this study were small.

Although a number of factors could have biased our results, we cannot find evidence that any would be large enough to cause our estimates of reproductive rates to be so low. Low rates could also be the result of low pregnancy rates or high neonatal mortality. In one of the primary wintering areas for these whales, reproductive rates that are similar to those we found have been reported. Most humpback whales off California migrate to areas off Baja California, mainland Mexico (Calambokidis *et al.*, in press) and some to Costa Rica (Steiger *et al.* 1991). Between 1986 and 1991, calves comprised an average of 5.8% of the whales identified in Bahia de Banderas off mainland Mexico (Salas 1993).

A possible cause of low reproductive success is scarcity of prey. There are several indications of changes in the prey base of humpback whales off California. Although the primary prey of humpback whales off central California during whaling was northern anchovy (*Engraulis mordax*) (Rice 1963), direct observations and examination of fecal samples in the same areas in the late 1980s indicated that whales fed almost exclusively on euphausiids (Kieckhefer 1992). This shift could have been the result of dramatically smaller anchovy populations in the 1980s compared to 1950 through the mid-1970s (Lluch-Belda *et al.* 1989). More recently, dramatic declines in overall plankton abundance have also been documented off southern California since the 1970s due to increased surface water temperature (Roemmich and McGowan 1995). Additionally, a shift of blue whale distribution to more coastal waters since the early 1980s (Calambokidis *et al.* 1990*b*) could result in competition for euphausiid prey, although there is no evidence for such interspecific competition. Over 2,000 blue whales feed in the coastal waters off California during the same time of year (Calambokidis *et al.* 1990*b*).

Although chemical contaminants have been linked to reproductive dysfunctions in other marine mammal species (Reijnders 1986, Addison 1989, DeLong *et al.* 1973, Gilmartin *et al.* 1976), mysticetes have lower exposure to chlorinated hydrocarbons than pinnipeds and odontocetes (O'Shea and Brownell 1994). Surprisingly high concentrations of PCBs and DDT were reported, however, in an adult minke whale (*Balaenoptera acutorostrata*) that stranded in southern California in 1977 (Schafer *et al.* 1984). Tissues from humpback whales from this area have not been tested. Contaminant levels in humpback whales from other areas have been relatively low (Peard and Calambokidis 1981, Taruski *et al.* 1975).

One possible cause of neonatal mortality is predation, presumably by killer whales. Many of the mothers and calves in our sample showed evidence of attacks based on the presence of rake-mark scars on their flukes and, although these attacks were not fatal, we assume that others were. It is thought that killer whale attacks may target the young and the weak in humpback whales (Whitehead and Glass 1985, Clapham 1996) as well as in other marine mammal species (Jefferson *et al.* 1991). Clapham (1996) suggests that most of these attacks occur during the migration, because few have been witnessed in areas where humpbacks have been studied and very few whales appear with scars after their calf year.

We conclude that our estimates of low reproductive rates for humpback whales off California cannot be explained by any single factor. Our estimates are likely biased downward somewhat by our effort from small boats often operating late in the season and possibly by geographic segregation within this large study area; although these do not appear to fully account for the low rates, they may be biasing our estimates downward somewhat. If the indications of increasing population size are accurate, these could only be reconciled with our findings if there was an extremely low mortality rate or immigration was occurring from other areas. Calambokidis *et al.* (1996) found little evidence of interchange of humpback whales between California-Washington and other feeding areas. Although there are a number of possible causes for the low reproductive rates we report, we cannot conclude which is responsible.

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