BIOLOGY OF HUMPBACK WHALES IN THE GULF OF THE FARALLONES

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To:

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EXECUTIVE SUMMARY

Under a research contract to the Gulf of the Farallones National Marine Sanctuary and the National Park Service, we studied the abundance, distribution, and behavior of humpback whales in central California from 1986 to 1988. The goal of the research was to gain information helpful to management and protection of humpback whales and other marine mammals present in the Gulf of the Farallones National Marine Sanctuary and the proposed sanctuary around Cordell Bank. In addition, other marine mammals were studied and research on blue whales was conducted concurrently to this study (see Calambokidis et al. 1989).

We conducted 1,457 hours of vessel surveys over the three year period primarily in August through October of each year. The purpose of the surveys was to photographically identify individual humpback whales and gather sighting information on marine mammals. We also flew over 88 hours of aerial surveys to examine the distribution of marine mammals, provide information on whale distribution to vessels, measure the length of whales through photogrammetry, and conduct line-transect estimates of abundance. Additionally, cooperating researchers and naturalists aboard nature trips in the region provided photographs of individual humpback whales and information on sightings.

Over 1,000 sightings of humpback whales were made during the vessel and aerial surveys in the study area. The sighting rates were highest in 1987 compared to 1986 and 1988. An influx of humpback whales occurred in August in all three years. Maximum numbers were seen from the middle of August to the middle of September in 1986 and 1987 and in September and October in 1988. The distribution of sightings in the study area varied both by season and by year. The areas around the Farallon Islands and to north of Fanny Shoal were some of the most consistent areas to find humpback whales. They were episodically abundant at other areas, including near Cordell Bank and north of Bodega Canyon (west of Bodega Bay), during some years and months. Humpback whales were significantly associated with water depths of 200 to 500 feet, though the depth varied significantly among years.

The changes in distribution we observed are likely the result of variations in the distribution and availability of prey, predominantly euphausiids and anchovies (Rice 1977). We examined raw data made available to us by D. Rice (pers. comm.) from humpback whales taken during commercial whaling in the Gulf of the Farallones from 1956 to 1965. In those catches there were dramatic annual and seasonal variation in the locations of capture, as well as annual variations in prey species.

Through fluke markings, we identified 225 different individual humpback whales from 1986 to 1988, with the most seen in 1987 when 141 were identified. Just over half the identified whales were seen in only one year (122), 65 were seen in two years, and 38 were seen across all three years. Three whales first identified by other researchers in 1981 were seen in our study, up to seven years later. On average, identified whales were seen more than five times each year. A "resident" subgroup of whales tended to be seen more often each year and across years. One of the humpback whales identified all three years was Humphrey, the whale that attracted public attention when it swam up the Sacramento River in 1985. During our study in 1986 and 1987, Humphrey was seen in consort with other humpback whales. However, in 1988 it was seen alone on three separate days in the shallow waters of Drakes Bay, Bodega Bay, and Bodega Harbor; all areas where we had not seen humpback whales previously.

Comparison of humpback whale photographs from the Gulf of the Farallones to those in other areas revealed movements of whales to other areas. Along the California coast, a majority of the humpback whales seen from Pt. Sur to Pt. Arena matched with whales in the Gulf of the Farallones, whereas a smaller proportion seen north and south of these points matched with the Farallones group (implying the existence of a central California feeding aggregation). The wintering grounds of central California humpback whales are preponderantly along the coast of Mexico and Central America. Twenty-three humpback whales seen in the Gulf of the Farallones (almost 10%) matched with Mexico and two matched with Costa Rica (provided by Richard Sears and the only two identified from this area). A few individuals (3) from the Farallones also occurred in Hawaii.

Few calves were seen during the study, though sightings increased over the three years. Calves were seen as 0.4%, 1.7%, and 5.3% of the whales sighted in 1986, 1987, and 1988, respectively. The proportion of identified cows with calves was low compared to other areas. The lengths of humpback whales measured from aerial surveys ranged from 10.5 to 13.6 m ($n=24$, mean=12.0, s.d.=0.76) and were generally smaller than lengths reported from whaling data.

Estimates of the abundance of humpback whales were calculated from line-transect aerial surveys and individual identification data. One aerial survey each year was flown using line-transect methods to provide a single-day abundance estimate. These estimates ranged from 60 humpback whales on 16 October 1986 to 109 on 25 September 1988. The number of individuals identified each year were higher than the line-transect estimates, probably reflecting individuals moving in and out of the study area. Within-year estimates based on mark-recapture yielded from 109

whales in 1986 to 211 in 1988 while between year estimates tended to be slightly higher, 226 for 1986 to 1987 and 253 for 1987 to 1988. However, we found violations of some assumptions of mark-recapture estimates based on the Gulf of the Farallones data.

Our estimates of population size are all lower than those reported for September 1982 by Dohl et al. (1983). The population at that time was thought to be increasing based on the survey results from 1980 to 1982 and the reoccurrence of spring sightings of humpback whales near the Farallon Islands (Huber et al. 1980). Our data and that from other sources do not reveal an increase in humpback whale abundance. Instead there appears to be large annual variations in numbers, timing, and distribution of humpback whales in this area. Variations in timing and distribution also were apparent in the whaling data.

Sixteen other species of marine mammals were seen. The most frequently seen marine mammals included three pinniped species (harbor seals, California sea lion, and northern sea lions), three small cetaceans (Dall's porpoise, harbor porpoise, and Pacific white-sided dolphin), and two whales (minke whale and blue whale). Blue whale occurrence in the study area increased dramatically during the three years consistent with an increased abundance that began in the late 1970s (Calambokidis et al. 1989).

INTRODUCTION

Humpback whales (Megaptera novaeangliae) are listed as endangered due to heavy exploitation by commercial whaling throughout their range including along the California coast through 1965. Commercial whaling in the North Pacific Ocean in this century killed about 28,000 humpback whales (Rice 1978). Whaling in the Gulf of the Farallones from 1956 to 1965 caught 842 humpback whales (Rice 1963a, Rice unpubl. data). The U.S. National Marine Fisheries Service lists the North Pacific humpback population at 1,200 (NMFS 1987), though this is probably an underestimate; the portion of the North Pacific population that breeds in Hawaii appears to number at least 1,200 based on photoidentification research (Darling and Morowitz 1986, Baker et al. 1986).

Sightings of humpback whales in the Gulf of the Farallones, California, since whaling ceased, have been reported by a number of researchers. Incidental sightings from the Farallon Islands from 1970 to 1985 have been reported by the Point Reyes Bird Observatory (Ainley et al. 1977, 1978, Huber et al. 1979, 1980, 1981, 1982, 1983, 1985, 1986). They reported an increase in spring sightings of humpback whales in 1979 and speculated this may reflect the return of a resident population to the region (Huber et al. 1980). This increase in spring sightings, however, did not persist past 1982. Large aggregations of humpback whales in the Gulf of the Farallones were noted during aerial surveys conducted along the central and northern California coast from 1980 to 1983 (Dohl et al. 1983, Dohl 1984). The number of humpback whales in the Gulf of the Farallones increased from 1980 to 1982 and in 1982, most of the California humpback whale population appeared to be concentrated in this area in the late summer and early fall (Dohl et al. 1983). Incidental sightings of humpback whales from nature trips in the early 1980s in the Gulf of the Farallones and Cordell Bank were reported by Webber and Cooper (1983), Szczepaniak and Webber (1985), and Rondeau (1987).

The photoidentification of individual whales using natural markings is a valuable tool for determining the movements and population structure of humpback whales (Katona et al. 1979). Mark-recapture calculations based on naturally marked cetaceans have provided an alternate method for assessing population size (Hammond 1986). Photoidentification of humpback whales in other regions of the North Pacific provided a basis for comparison to individuals seen in an area (Perry et al. 1988, Baker et al. 1986, Alvarez 1987). Migration of humpback whales between breeding areas in Hawaii and feeding areas in Alaska has been well established (Baker et al. 1986, Darling and Jurasz 1983, Darling and McSweeney 1985). Movements of a few whales between Hawaii and Mexico and between Mexico and Alaska have also

been found (Baker et al. 1986, Darling and McSweeney 1985). Prior to the research reported here, only a small sample of humpback whales from the Gulf of the Farallones (18) had been compared to other regions resulting in a single match to Hawaii and a single match to Mexico (Baker et al. 1986, Perry et al. 1988).

Partly because of its significance to marine mammals, the Gulf of the Farallones National Marine Sanctuary was designated in 1981. The sanctuary covers 948 square nautical miles, including waters surrounding the Farallon Islands, off Pt. Reyes, and Bodega Bay, California (NOAA 1987). National marine sanctuaries are areas designated by the federal government for protection because of their significant natural and cultural resources. Goals for marine sanctuaries include promoting resource protection, education, and research.

We examined the distribution, abundance, behavior, and movements of humpback whales in the Gulf of the Farallones region from 1986 to 1988. Our research was funded by the National Marine Sanctuary Program of NOAA and the National Park Service to provide baseline information on humpback whales that will assist in their management and protection in the marine sanctuary. This report summarizes the three years of research we conducted from 1986 to 1988 and incorporates the information contained in two previous annual reports (Cubbage et al. 1987, Calambokidis et al. 1988).

METHODS

Aerial and vessel surveys were conducted in the vicinity of the Gulf of the Farallones from July to October 1986 to 1988 (Figure 1). The study area included all of the Gulf of the Farallones National Marine Sanctuary plus the area surrounding Cordell Bank and offshore from Bodega Bay. This area encompassed the waters from the shore to the continental shelf edge from 37° 30' N to 38° 30' N.

Vessel Surveys

Vessels were used to examine humpback whale distribution and relative abundance and to photograph individual whales. Vessel effort was concentrated in areas of highest humpback whale concentrations. Vessels generally operated out of Bodega Bay. Vessel coverage by year is shown in Figure 2.

Three types of vessels were used in the study: 1) Noctilio, a 44' motor sailer, 2) Shachi, a 19' Boston Whaler, and 3) 14-16' inflatable boats. Tracks of all dedicated surveys are shown in Figure 2; effort is summarized in Table 1. Total vessel effort was 513 hr in 1986, 460 hr in 1987, and 484 hr in 1988. In 1986, our effort was conducted in a 7-week period from 23 July to 15 Sept; the 1987 surveys were conducted in two three-week sessions between 17 Aug-4 Sept and 25 Sept-17 Oct; the 1988 surveys were conducted in two three-week sessions 19 Aug-5 Sept and 21 Sept-17 Oct, as well as a short late season effort from 27 Oct-2 Nov. Data collected on other vessels included one dedicated survey conducted by Farallon Research Associates under sub-contract and six surveys on larger vessels with Cascadia personnel.

Other researchers, naturalists, and nature trip operators provided information used in our study (see Acknowledgments) and photographs for use in our catalog (Table 2). Under a subcontract, Farallon Research Associates photographed and recorded sightings of marine mammals during Oceanic Society nature trips to the Farallon Islands in 1986 and 1987 (not in 1988). Cruises were conducted on 34 days between 7 June and 26 Oct 1986 and 53 days between 6 June and 8 November 1987. Their usual route covered the Farallon Island vicinity and between the islands and San Francisco Bay.

Data collection

Movement of each vessel and environmental conditions were recorded as effort data. Time, position, depth, and presence of ships, boats, and birds in the area were recorded every 15 or 30 minutes, depending on vessel;

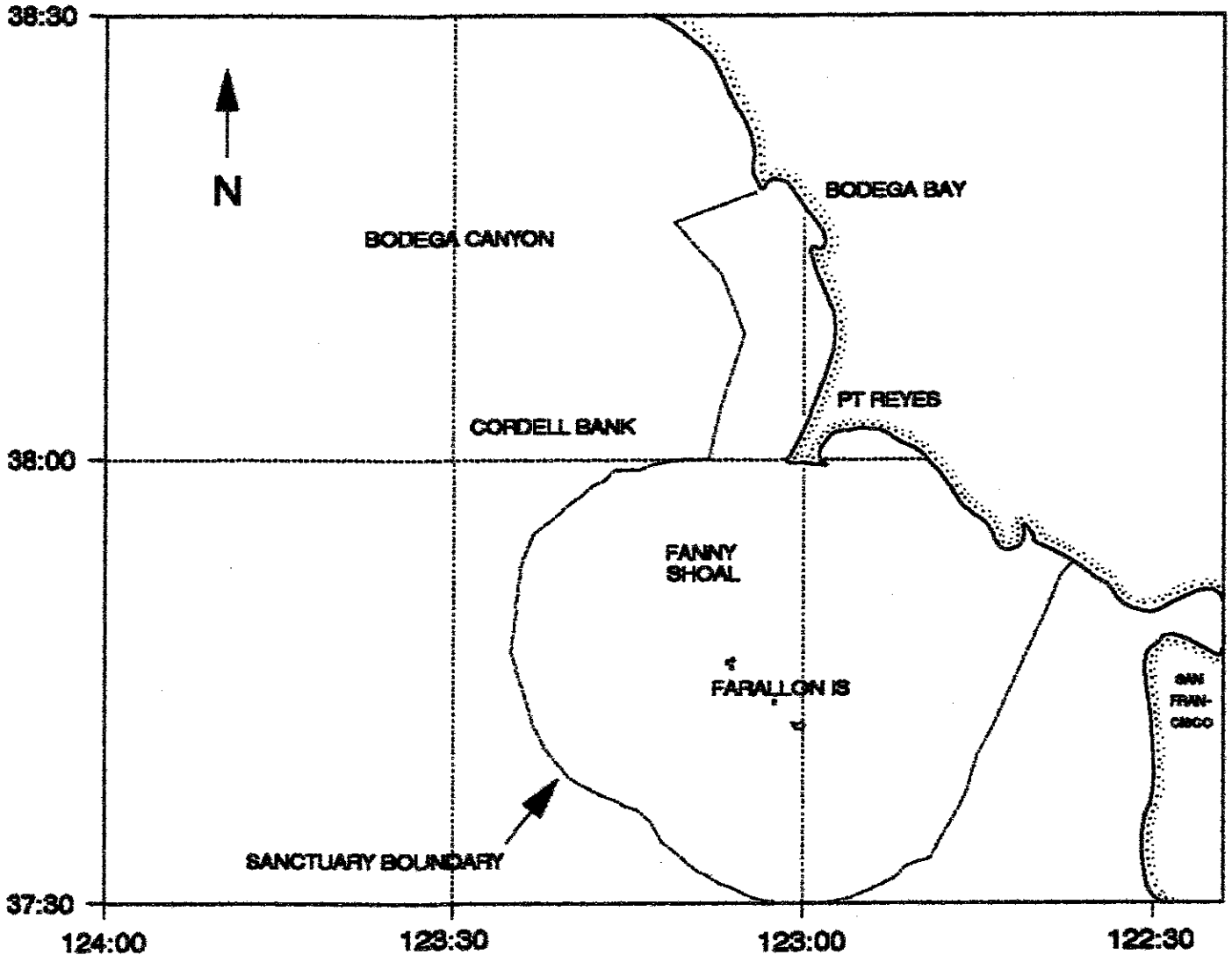
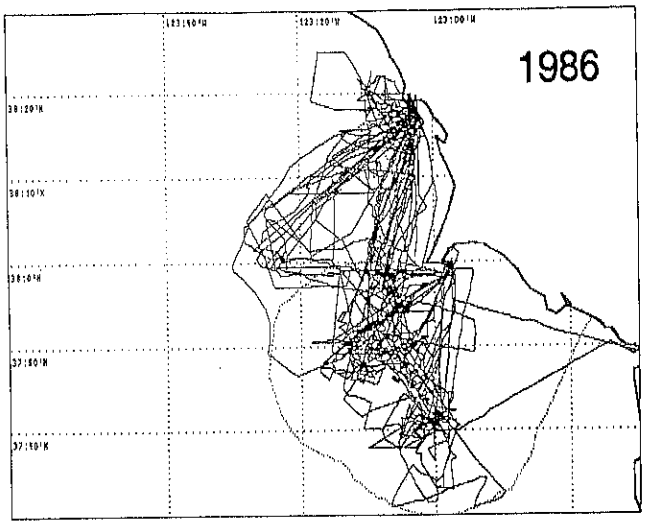
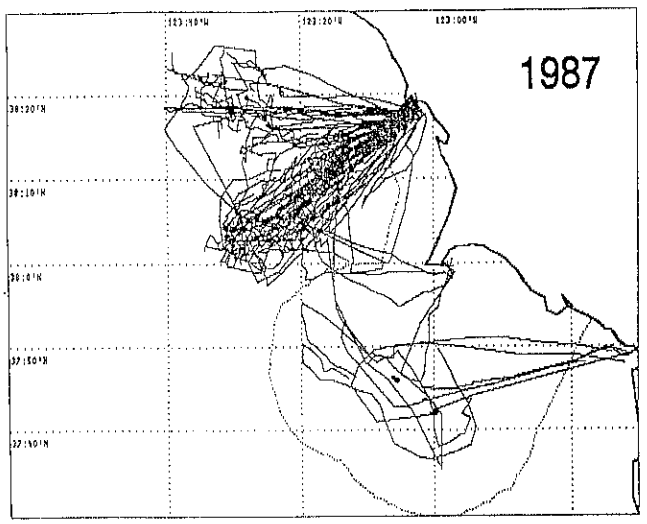


Figure 1. Study area off central California showing the Gulf of the Farallones National Marine Sanctuary and surrounding areas.





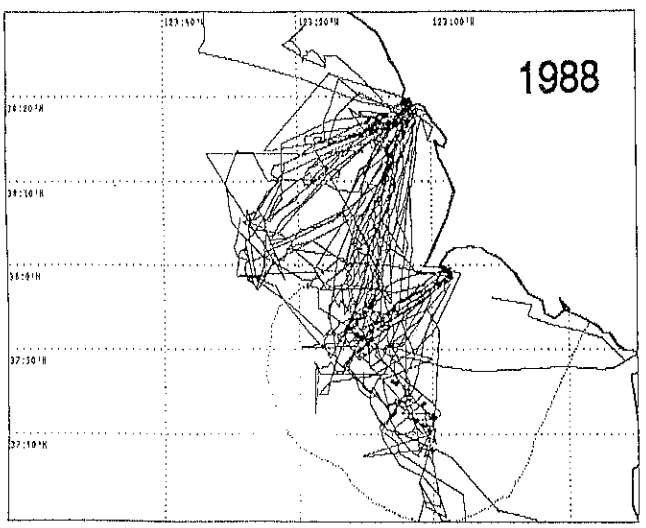


Figure 2. Tracklines of vessel surveys in 1986-1988.

Table 1. Summary of dedicated vessel effort in 1986-1988 in the Gulf of the Farallones.

Vessel	Operating dates Start	End	Effort Days	Hours	Description
1986					
Zodiac	27 July	15 Sept	24	114	14' inflatable
Shachi	23 July	2 Sept	15	69	19' Boston Whaler
Noctilio	23 July	15 Sept	32	330	44' motor sailer
Total	23 July	15 Sept	-	513	
1987					
Zodiac	17 Aug	17 Oct	20	145	
Shachi	18 Aug	11 Oct	15	100	
Noctilio	18 Aug	14 Oct	19	184	
Other*	23 Jul	10 Oct	4	31	
Total	17 Aug	17 Oct	-	460	
1988					
Achilles	20 Aug	2 Nov	28	174	16' inflatable
Kupe	22 Aug	12 Oct	13	79	16' inflatable
Noctilio	19 Aug	6 Oct	22	208	
Other*	11 Oct	13 Oct	3	23	
Total	19 Aug	2 Nov	-	484	

* Data collected by Cascadia personnel on board other research or charter vessels.

Table 2. Names of researchers/naturalists/photographers, including those who worked on this study, who contributed photographs that have been incorporated into the humpback whale catalogue.

Affiliation	Photographer	
Cascadia Research Collective and Center for Whale Research	K. Balcomb	J. Calambokidis
	L. Barry	D. Claridge
	S. Bartok	J. Cubbage
	L. Bloedel	J. Smith
	P. Bloedel	G. Steiger
	D. Bockus	N. Wadsworth
Farallon Research Associates	C. Ewald	B. Keener
	P. Ewald	I. Szczepaniak
	P. Jones	M. Webber
Long Marine Laboratory	D. Goley	J. Ostman
	S. Kruse	R. Wells
Moss Landing Marine Laboratory	N. Black	T. Kieckhefer
	T. Jefferson	C. Tanner
Other contributors:	R. Baird	J.E. Scarff
	B. Elliot	R. Sears
	M. Ezikial	D. Shearwater
	P. Folkens	R. Stallcup
	C. Gottlund	J. Stern
	R.D. Harris	R. Storro-Patterson
	T. Johnson	S. Swartz
	R. Levalley	N. and L. Walsh
	H. Rondeau	M. Weinrich

weather conditions (visibility, cloud cover, Beaufort, swell height, and overall observation quality) were recorded every hour. These data allowed tests of trends in water depth of sightings, association with birds (examined in 1986 and 1987), and relative density of sightings by area. All sightings of marine mammals were recorded. Additional data were collected in 1987 and 1988 during each closing (when whales were approached and followed to photograph). Closing data included: start and end times of closing effort, position, depth, number of whales, number and species of birds within 300 m of the whales at the beginning of the closing, photographs taken, and behavior of the whales.

To test for association between humpback whales and ships, boats, birds, or water depth, we compared data gathered during all vessel effort to data gathered when humpback whales were sighted. Two tests were used to determine the statistical significance of associations between humpback whale distribution and birds or depth. Analysis of Variance (ANOVA) was used to test for differences among years in numbers of birds and water depth when humpback whales were seen. Chi-square tests were used to compare the frequency distribution of values (depth or birds within 300 m) during humpback sightings to those expected from the effort data within a year.

Photographic Identification

Photographic techniques

To identify individual humpback whales, ventral sides of flukes were photographed. 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. Shutter speeds were 1/1000 or faster when lighting conditions permitted. The black and white film was exposed for ISO rating 1000 and development times were adjusted accordingly. Individual prints were custom enlarged on RC paper 2 1/4" x 3 1/2" for comparison matching. Most of the photographs received from other researchers were color slides. Slides were copied with a duplicator onto black and white negative film and custom printed onto Kodak or Ilford RC paper.

Humpback whales were approached slowly from behind, to within 100 feet whenever possible. They were followed through several dive sequences until flukes were raised. Several identifying photographs of the ventral side of the flukes were then taken. Usually, the whales were approached without signs of disturbance such as changes in behavior. In the few cases were whale behavior suggested possible disturbance, vessels increased the distance between the boat and whales.

Catalog development

Catalogs of identifiable whales encountered during each field season were developed by comparing all photographs taken of individual whales. From 150 to 200 rolls of 36-exposure film taken each season, the collection was merged and purged until distinct individual whales remained. For each year, a separate photographic catalog of all whales not identified previously was compiled. Copies of these catalogs for each year were submitted to the Gulf of the Farallones National Marine Sanctuary and the National Marine Mammal Laboratory's North Pacific humpback whale database. Copies were also retained by Cascadia research and the Center for Whale Research for future comparison and continued collaboration with other researchers.

Comparison to other regions and time periods

Humpback whale fluke photographs in the Gulf of the Farallones 1986-1988 catalogs were compared to photographs taken in a number of different regions of California, Washington, British Columbia, Alaska, Hawaii, Mexico, and Costa Rica (see Table 3). Results of these comparisons are part of ongoing collaborative efforts with other researchers and will be the subject of future joint authored manuscripts. Comparison to the University of Hawaii catalog for Hawaii, Alaska, and portions of Mexico was conducted at Cascadia using photographs from their published catalog (Perry et al. 1988). Matches were confirmed using photographic prints from the published catalog (C.S. Baker, A. Perry, and L. Herman Pers. Comm.). Comparison of our catalog to the collection of humpback whales maintained by the Universidad Nacional Autonoma de Mexico (UNAM) was conducted in several stages in collaboration with researchers from UNAM. Comparison of humpback whales first identified in the Gulf of the Farallones in 1988 with the UNAM catalog has not been completed. Details of the sources of photographs and regions compared are provided in Table 3.

Computer databases and plotting

A computerized database was developed of all humpback whales identified in this study or from photographs provided by others. Each database record summarized the information for each sighting of an identified individual including: date, time, location, identification number, vessel, sighting number, other individuals in group, geographic region, and photographer.

Table 3. Number of humpback whales from different regions (not including Gulf of Farallones) compared to humpback whales photoidentified in the Gulf of the Farallones. Full list of contributors of photographs to this study are given in Table 2. Comparisons to whales identified outside of California were conducted in collaboration with the researchers in the regions listed here and will be the subject of a future collaborative manuscript.

Region	Years	Number of IDs	Primary source or photographers
California			
Northern California	80, 88	11	P. Bloedel, R. LeValley
Pt. Arena	86, 88	6	J. Calambokidis, K. Balcomb, D. Claridge
Pillar Pt. and Monterey	86-88	23	J. Stern, N. Black, J. Calambokidis, G. Steiger
Pt. Sur to Pt. Arguello	87-88	63	P. Bloedel, D. Bockus, J. Calambokidis, G. Steiger
Mexico			
Mainland Mexico and Revillagigedo Archipelago	83-87*	>250	Universidad Nacional Autonoma de Mexico, A. Aguayo, C. Alvarez, J. Urban, M. Salinas
Mainland Mexico and Revillagigedo Archipelago	78-85	36	From Perry et al. (1988) University of Hawaii
Baja, Mexico	87-89	111	K. Balcomb and J. Urban (Univ. Auton. Baja Cal. Sur)
Costa Rica	88	2	R. Sears, Mingan Island Cetacean Study
Hawaii	77-85	634	From Perry et al. (1988) University of Hawaii
Southeastern Alaska	79-85	464	From Perry et al. (1988) University of Hawaii
Western Gulf of Alaska	77-85	95	From Perry et al. (1988) University of Hawaii
Washington	88	2	J. Calambokidis, G. Steiger
Vancouver Is., B.C.	88	1	N. and L. Walsh (provided by R. Baird)

* Compared to humpback whales identified in 1986 and 1987 (not 1988) in the Gulf of the Farallones.

Mark-Recapture Analysis

Mark-recapture population estimates were based on individually identified whales and conducted as described in Hammond (1986) and Seber (1982). Estimates from within-year and between-year sample periods were both calculated. Assumptions and potential biases for these calculations are presented in Results. Identifications based on all photographs were used in the calculations. During the first year of analyses, estimates were also based on selected photographs that fit image-quality criteria independent of whether the whale was identified (Cubbage et al. 1987). The estimate based on selection criteria was used to reduce potential biases in recapture probability of individual whales based on the distinctness of their fluke markings. However, no evidence of this bias appeared; estimates made using the two data sets were similar (Cubbage et al. 1987). Mark-recapture analyses reported here include all photographs with identifiable whales.

Mark-recapture estimates of the humpback whales present each year in the Gulf of the Farallones were made using the Chapman modification of the Petersen estimate (Seber 1982). This modification was used because it was appropriate for sampling without replacement (Hammond 1986). For the second sample period we did not count multiple samples or recaptures of the same individual, effectively making the sampling without replacement.

Formulae were as follows:

$$N = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1$$

where n_1 is the number of different (unique) whales identified in the first sample, n_2 is the number of different whales identified in the second sample, and m_2 is the number of different whales identified in the second sample that had also been seen in the first sample.

Variance of these samples was measured according to the following formula (as described in Seber 1982):

$$Var = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)}$$

Confidence limits were calculated as described in Seber (1982). The formula used was as follows:

$$95\%\ \text{C.I. for } p = \pm\ (1.96[p(1-p)/(n_2-1)]^{\frac{1}{2}} + 1/(2n_2))$$

Where $p = m_2/n_2$, the confidence limit for p was then used to calculate lower and upper bounds for N. The unknown sampling fraction (f) was neglected as recommended by Seber (1982) resulting in overly wide confidence limits.

Aerial Surveys

Aerial surveys were conducted primarily to search large portions of the study area to direct vessels to concentrations of humpback and blue whales for vessel-based photo-identification work. At least one line-transect survey was conducted per year to provide an estimate of humpback whale abundance in the study area. In addition, whales were measured with photogrammetry techniques to determine the approximate age-class of animals found in the Farallones area.

Surveys were generally flown in a Cessna 172, a single-engine high-winged aircraft. A crew of three (1 pilot, 2 observers) flew most surveys. The left aft observer searched for whales and recorded data; right front observer searched for whales and directed the flight. The pilot/biologist also searched for whales. A portable LORAN was used to determine positions during surveys in 1987 and 1988; VOR radial intersections were used for positions in 1986.

Flight time for aerial survey effort was 37 hr in 1986, 26 hr in 1987, and 24 hr in 1988; surveys were conducted from July through Oct in 1986 and Aug through Oct in 1987-88 (Table 4). One survey was conducted before the study season on 13 May 1986. Survey tracklines flown by year are shown in Figure 3.

Line-transect population estimates

Humpback whale population sizes were examined using line-transect population estimates from aerial survey data. In 1987 and 1988, line-transect surveys were flown along latitude lines every four nm. Distances of humpback whales from the transect line were determined based on aircraft altitude and downward angle to the sighting (measured with an inclinometer) as the aircraft passed abeam of the sighting location. All humpback sightings (1986-1988) from aerial surveys with distance measurements were used to model a sighting probability curve based on distance from the transect line (Figure 4). The equations used for the density calculations were reported in Burnham et al. (1980). Variances and confidence limits

Table 4. Aerial surveys flown 1986-1988.

Date	Start time	Landing time	Elapsed time	Completed?	Survey description
1986					
05/13	0855	0934	0:39	No	Severe fog and high winds
07/22	1302	1349	0:47	No	Fog and low ceiling
08/01	1418	1733	3:15	Yes	Survey of south study area
08/14	1303	1649	3:46	Yes	Survey of north study area
08/28	1209	1553	3:44	Yes	Survey of north study area
09/06	1440	1524	0:44	No	Fog and high wind
09/09	1037	1427	3:50	Yes	Reconnaissance and photogrammetry
09/10	1140	1753	5:29	Yes	Reconnaissance and photogrammetry
09/11	1052	1126	0:34	No	Heavy fog
09/12	1600	1905	3:05	Yes	Survey of north study area
09/16	1525	1839	3:14	Yes	Line-transect survey
10/21	1339	1432	0:53	No	Fog, low ceiling
10/23	1147	1639	4:52	Yes	Survey - fair conditions
10/24	1230	1443	2:13	Yes	Survey of south study area
Total			37:05		
1987					
08/21	1217	1830	6:13	Yes	Line-transect survey
08/22	1332	1628	2:56	Yes	Line-transect calibration
08/31	1353	1655	3:02	Yes	Reconnaissance and photogrammetry
09/07	1122	1506	3:44	Yes	Reconnaissance and photogrammetry
09/27	1205	1250	0:45	No	Mechanical problems
10/05	1445	1818	3:33	Yes	Reconnaissance and photogrammetry
10/09	1154	1517	3:23	Yes	Survey of south study area
10/13	1433	1704	2:31	Yes	Reconnaissance and photogrammetry
Total			26:07		
1988					
08/19	1301	1355	0:54	No	Heavy fog
08/23	1205	1303	0:58	No	Heavy fog
08/24	1238	1544	3:06	Yes	Reconnaissance and photogrammetry
09/25	1218	1633	4:15	Yes	Reconnaissance and photogrammetry
09/26	1108	1610	4:39	No	Line-transect survey
09/29	1000	1300	3:00	Yes	Reconnaissance
10/08	0946	1256	3:10	Yes	Reconnaissance
10/14	1028	1608	4:36	Yes	Reconnaissance and porpoise research
Total			24:38		

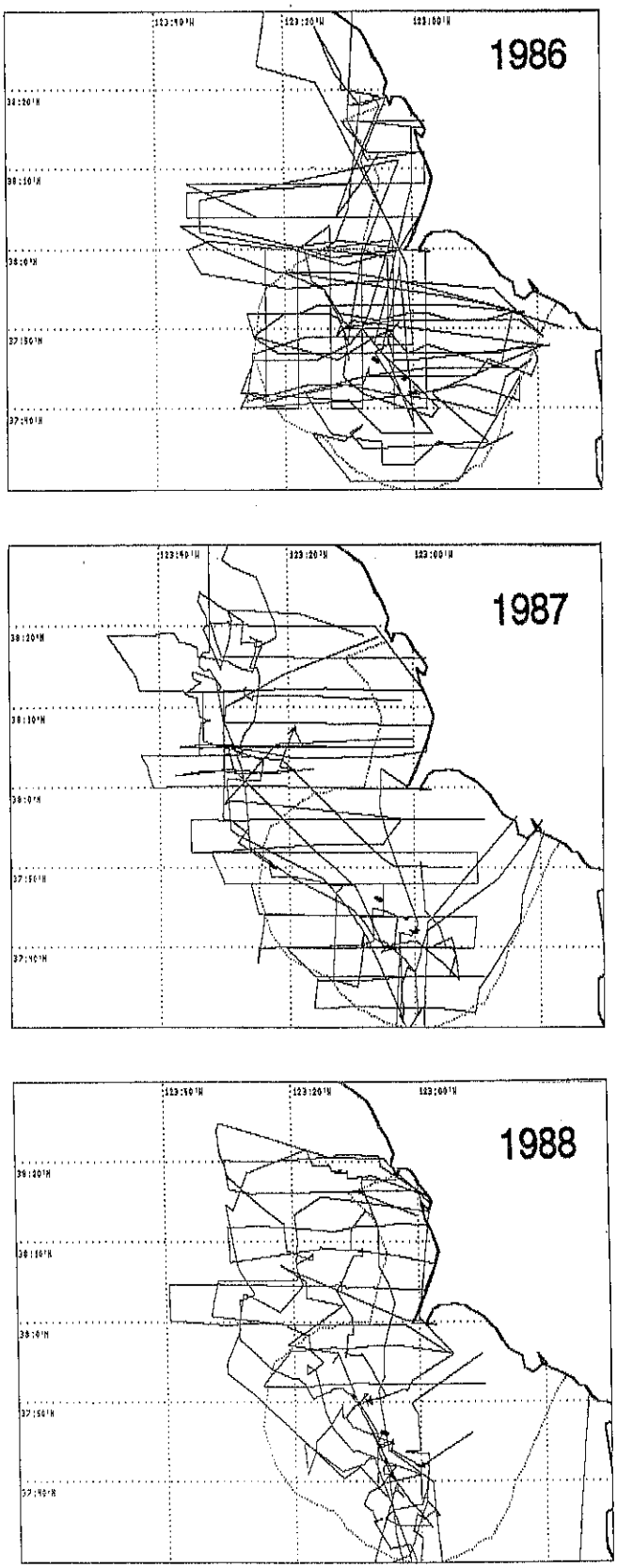


Figure 3. Tracklines of aerial surveys in 1986-1988.

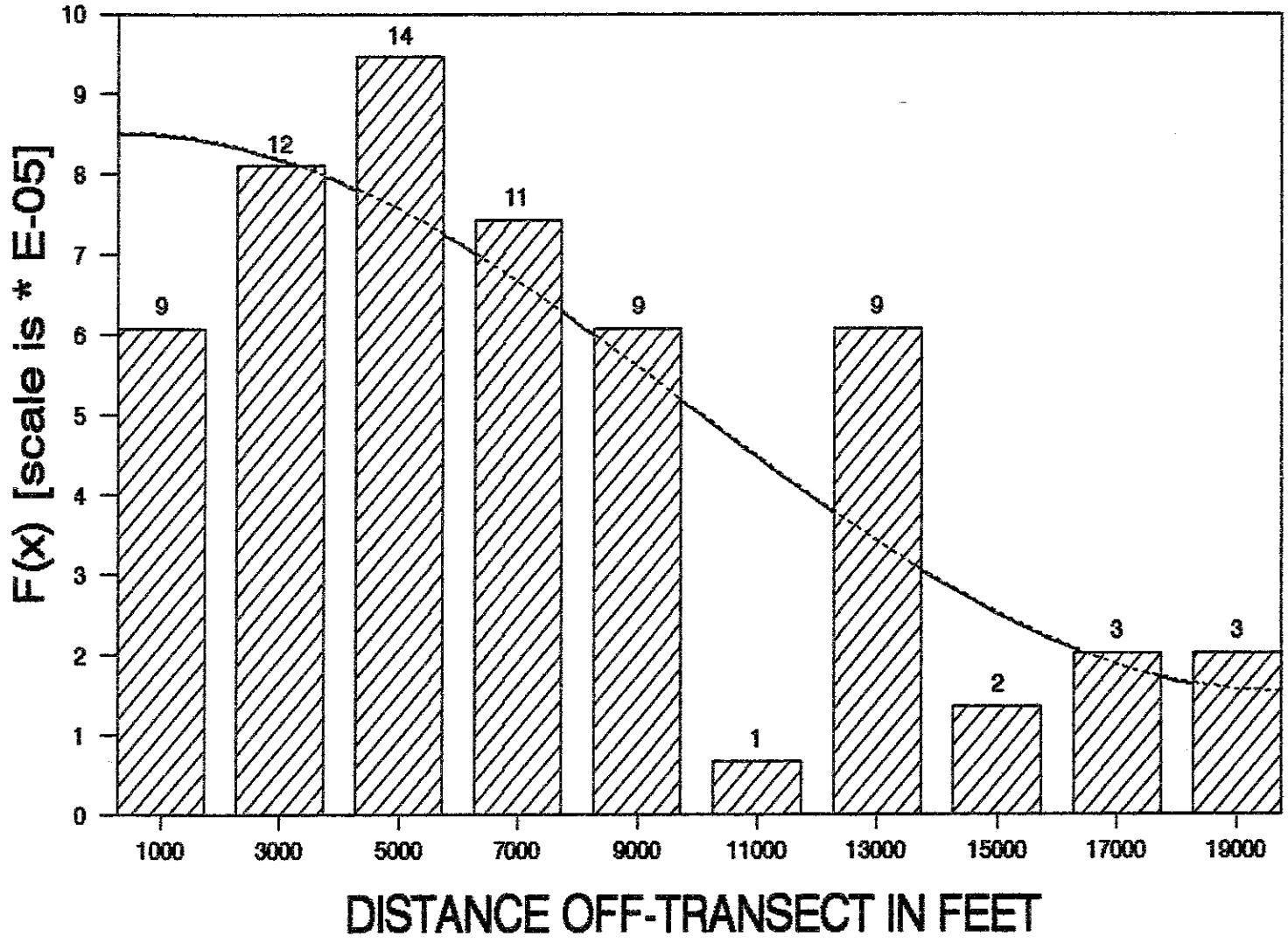


Figure 4. Fourier series sighting probability curve for aerial line-transect surveys in 1986-1988. Bars show the observed distribution of sightings based on distance off transect.

were calculated for the estimates of density of whales as described by Burnham et al. (1980) based on the assumption of a binomial distribution for n. These calculations are discussed in more detail in Burnham et al. (1980, p. 63).

Replicate survey lines flown on 22 August 1987 were used to estimate the proportion of whales missed because they were below the surface. We identified 24 groups of humpback whales known to be within 10,000 feet of the transect, from previous or subsequent passes along the 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 sighting function already accounted for the decreasing sighting efficiency due to distance off-transect. The primary factor responsible for the 37% sighting rate is animals missed because they were underwater. We therefore employed this figure as our correction factor for animals missed even if on the transect line. This figure is similar to the proportion of time humpback whales spent at the surface (39%) in the Gulf of the Farallones based on vessel-based behavioral observations in 1988 (n=184 dive series, T. Kieckhefer unpubl. data).

Photogrammetry

Whales were photographed from the air and measured with photogrammetric techniques to discern length and general age-class of animals residing in the study area. Vertical photographs were taken with a hand-held 35mm Nikon FE camera equipped with a 105mm or 200mm fixed focal length lens and color slide film. Photo scale was derived from focal length of the lens and barometric altitude.

Images of whales were measured with a stereo dissecting microscope (15x and 25x) equipped with an ocular reticle calibrated with a stage micrometer that allowed measurements to the nearest 0.04mm.

The equation used to measure whales was:

$$\text{whale size} = \text{image size (calibrated scale)}$$

$$\text{calibrated scale} = (\text{altitude}/\text{NFL})(C1)+C2$$

where NFL is the nominal focal length of the lens and C1 and C2 are correction factors based on a regression of true scale to altimeter-based scale. True scale was determined using vertical photographs of known-sized objects near the whales. The precision of whale length measurements was

evaluated using five blue whales that were photographed using the same methods and measured more than once; repeat measurements averaged 0.8% difference and the mean difference in whale length was 17 cm (n=5, s.d.=15)(Calambokidis et al. 1989).

Twenty-four acceptable quality images of 24 whales were measured, 10 measured on three days in 1986, 14 measured on 22 Aug 1987, and none in 1988. Whale images were graded according to observed whale flex and resolution of the image. Flex was graded from 1 to 5 with 1 being straight and 5 unacceptable. Clarity and resolution of the snout and flukes were also graded from 1 to 5 with 1 being clear and 5 being unusable.

Analysis of Historical Whaling Data

We analyzed historical data from commercial whaling operations in the Gulf of the Farallones to compare to contemporary distribution and sizes of humpback whales. Unpublished data of 842 humpback whales killed between 1 May 1956 and 4 July 1965 in the Gulf of the Farallones region were provided by Dale Rice, National Marine Mammal Laboratory. Data included whale capture date, location, length, sex, prey, and presence fetuses, as reported by the whaling stations to the government. There were no precise location data for just over 200 whales.

RESULTS

Distribution and Relative Abundance

Humpback whales were sighted on 905 occasions during vessels surveys and 231 times during aerial surveys from 1986 to 1988 (Table 5). Overall hours of vessel coverage were similar among years, though aerial survey hours declined slightly from 1986 to 1988.

Both the number and rate of sightings varied among years. The number of sightings and sighting rate was highest in 1987 for both vessel and aerial surveys. In 1988, vessel sighting rates were low, though this decrease was not apparent in the aerial sighting rates. The changes in the relative abundance of whales seen in vessel sightings, however, are biased by changes in the distribution of whales. In 1987, humpback whales were closest to our base in Bodega Bay, making access more frequent and efficient. In 1988, the opposite pattern occurred, with humpback whales less accessible by vessel surveys.

Seasonal patterns of relative abundance

Seasonal differences in the relative abundance of humpback whales were noted from vessel and aerial surveys in the Gulf of the Farallones (Figure 5). In all three years the relative abundance was low in July and early August with a dramatic increase occurring in middle to late August. The peak abundance of whales in 1986 and 1987 was from mid-August to mid-September. The peak abundance in 1988, however, occurred somewhat later, in September and October. Humpback whales remained abundant through the end of our observations in October and early November.

The seasonal occurrence of humpback whales, as seen from Oceanic Society nature trips, was similar to that observed in our study (Figure 6). These trips primarily covered the area in the vicinity of the Farallon Islands and only reflect the relative abundance of whales in that area. For observations from 1983 to 1987, peak numbers of humpback whales were seen in August to October with the highest sighting frequency in October.

General distribution of sightings

The distribution of humpback whales seen from vessels in the study area varied by year (Figure 7). Because vessel effort was not randomly distributed in the study area, the locations of humpback whales shown reflects higher vessel effort as well as whale concentration. To examine areas of overall humpback whale concentrations, we determined an effort-

Table 5. Summary of effort and humpback whale sightings in 1986-1988 in the Gulf of the Farallones.

Year	Effort		Humpback whale sightings		
	Days	Hours	Sightings	Whales	Num./hr.
Dedicated vessels					
1986	71	513	256	711	1.4
1987	58	460	451	1,129	2.5
1988	76	484	198	435	0.90
Total	205	1457	905	2,275	1.6
Aerial surveys					
1986	9[a]	33.5[a]	35[b]	155	4.6
1987	7	25.4	103	264	10.4
1988	6	22.8	93	220	9.6
Total	22	81.7	231	639	7.8

[a]Number and hours of aerial surveys includes only flights of greater than 1 hour. Hours includes transit time.
[b]Several sightings of large aggregations of humpback whales were treated as single sightings in 1986; in 1987 and 1988 each subgroup was treated as separate sightings.

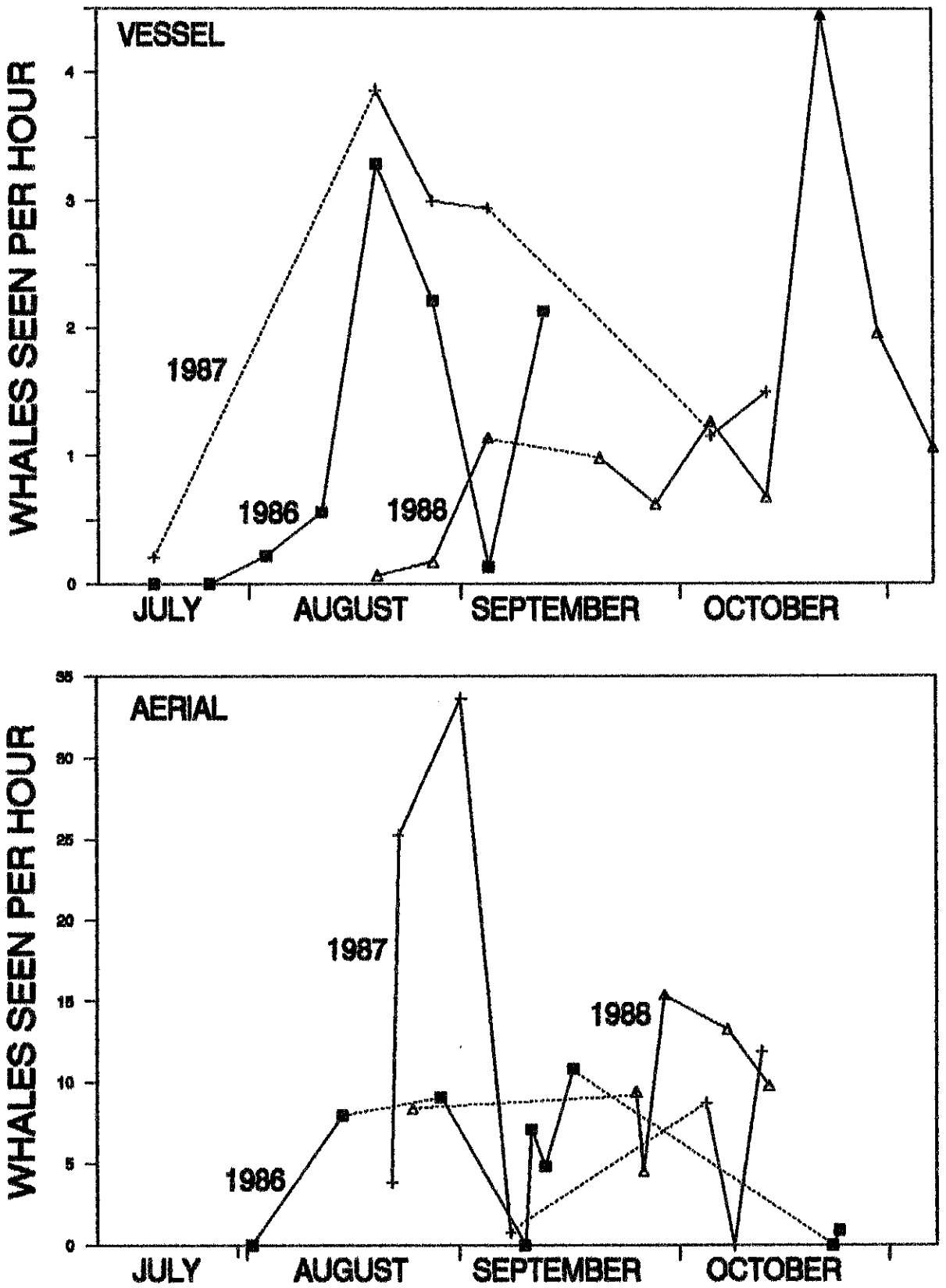


Figure 5. The number of humpback whales seen per hour of effort in 1986-1988. Vessel data show sighting rates by week; aerial survey data show sighting rates by survey. Dotted lines connect surveys or time periods more than 2 weeks apart.

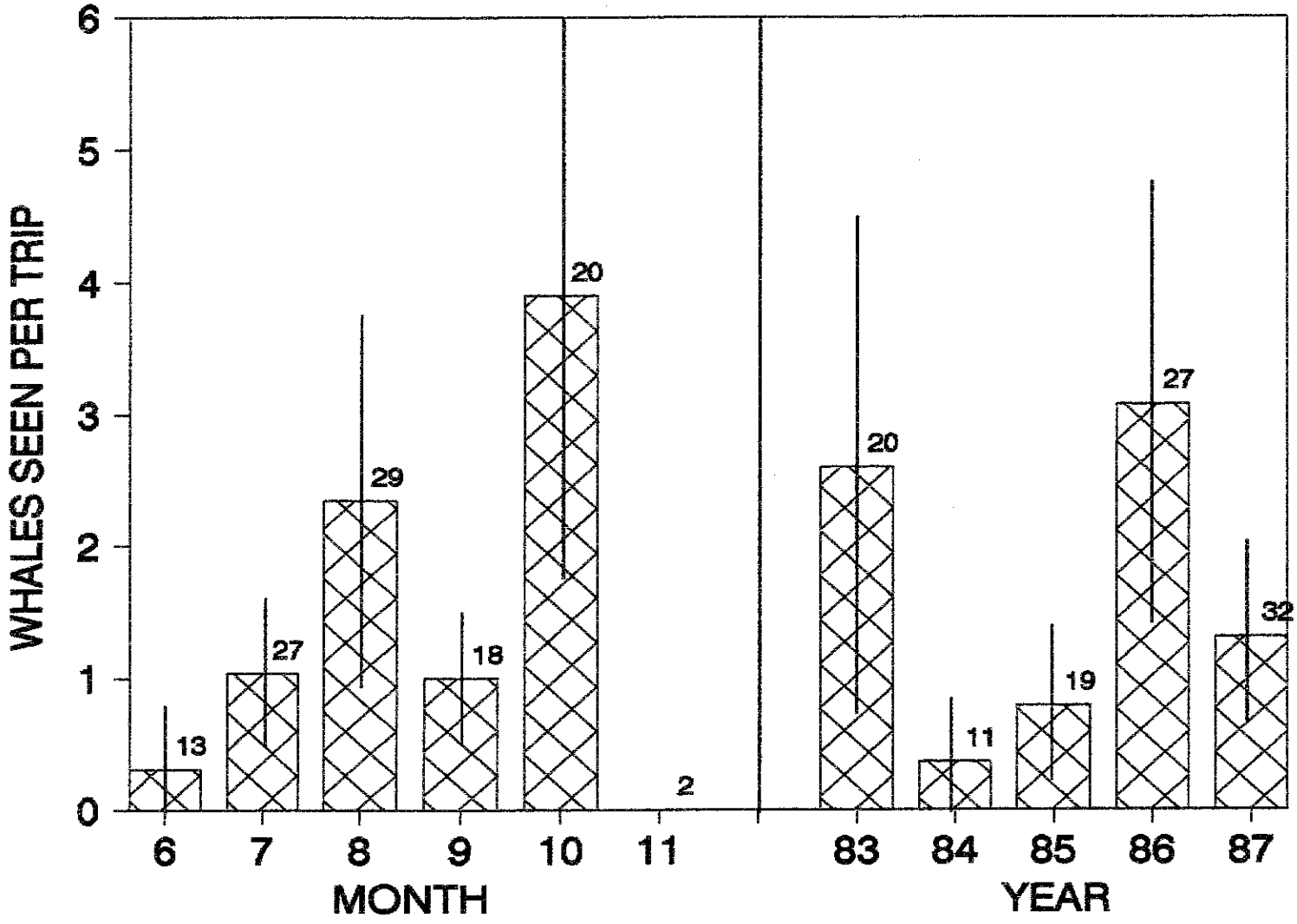
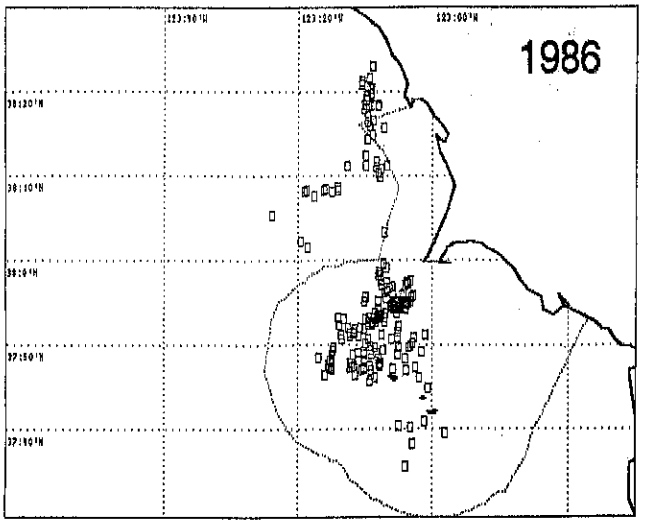
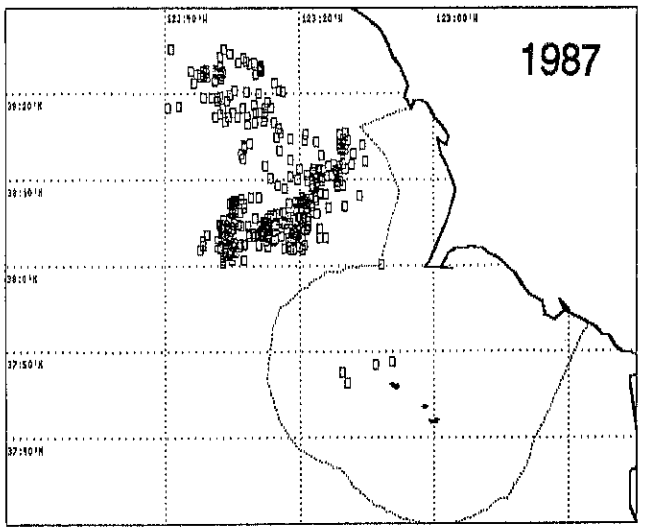


Figure 6. Average number of whales seen per trip from Oceanic Society nature trips to the Farallon Islands by month and year between 1983 and 1987. Data were provided by Farallon Research Associates. Numbers above bars are number of trips; lines show 95% confidence limits.





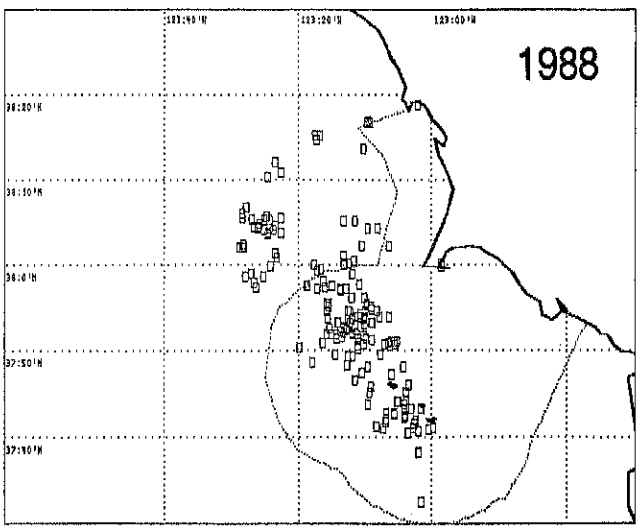


Figure 7. Locations of humpback whale sightings made from dedicated vessels, 1986 to 1988.

corrected sighting rate (all three years) by location in the study area (Figure 8). Areas of high whale density (measured by whales seen per hour of effort) included Cordell Bank and surrounding waters, off Bodega Head, and the area between Fanny Shoal and Point Reyes.

Seasonal and annual changes in distribution

The distribution of humpback whales in the study area shifted by season and year (Figure 9). The sighting locations from aerial surveys provide an unbiased representation of the locations of sightings. No two years were similar in distribution of sightings from August to October. In 1986, sightings were concentrated northwest of the Farallon Islands in mid-August and off Bodega Head in late August; sightings in September were more broadly scattered around the Farallon Islands. In 1987, humpback whales were primarily seen farther north and offshore in the vicinity of Cordell Bank in August and September and near Bodega Canyon in October. In 1988, sightings from August to October were distributed from south of the Farallon Islands to Cordell Bank.

Association with depth

Sightings of humpback whales occurred at significantly different water depths among years (ANOVA, $p<0.001$). The average water depth ranged from 300 feet in 1986 to 508 in 1988. Whales were not seen in water depths of less than 200 feet (Figure 10), except for one whale. On three occasions in 1988, "Humphrey" (the humpback whale that swam up the Sacramento River in 1985) was seen in Drakes Bay, Bodega Harbor and Bodega Bay sometimes in waters less than 20 feet deep.

The distribution of sightings by water depth for all three years varied significantly from the expected if whales were distributed randomly (chi-square, $p<0.001$ all three years). This was tested by comparing the observed number of whales seen at a range of depths against that expected based solely on the proportion of effort in that depth class. In 1986, whale sightings were clustered at water depths of 200-500 feet; 97% of the sightings were made at these water depths. The 1987 sightings tended to be in deeper water (averaging 508 feet) and spread over a larger range of depths (all but three from 300 to >1000 feet). In 1988, whales were seen at wide range of water depths (similar to 1987) including some shallower water depths more typical of 1986.

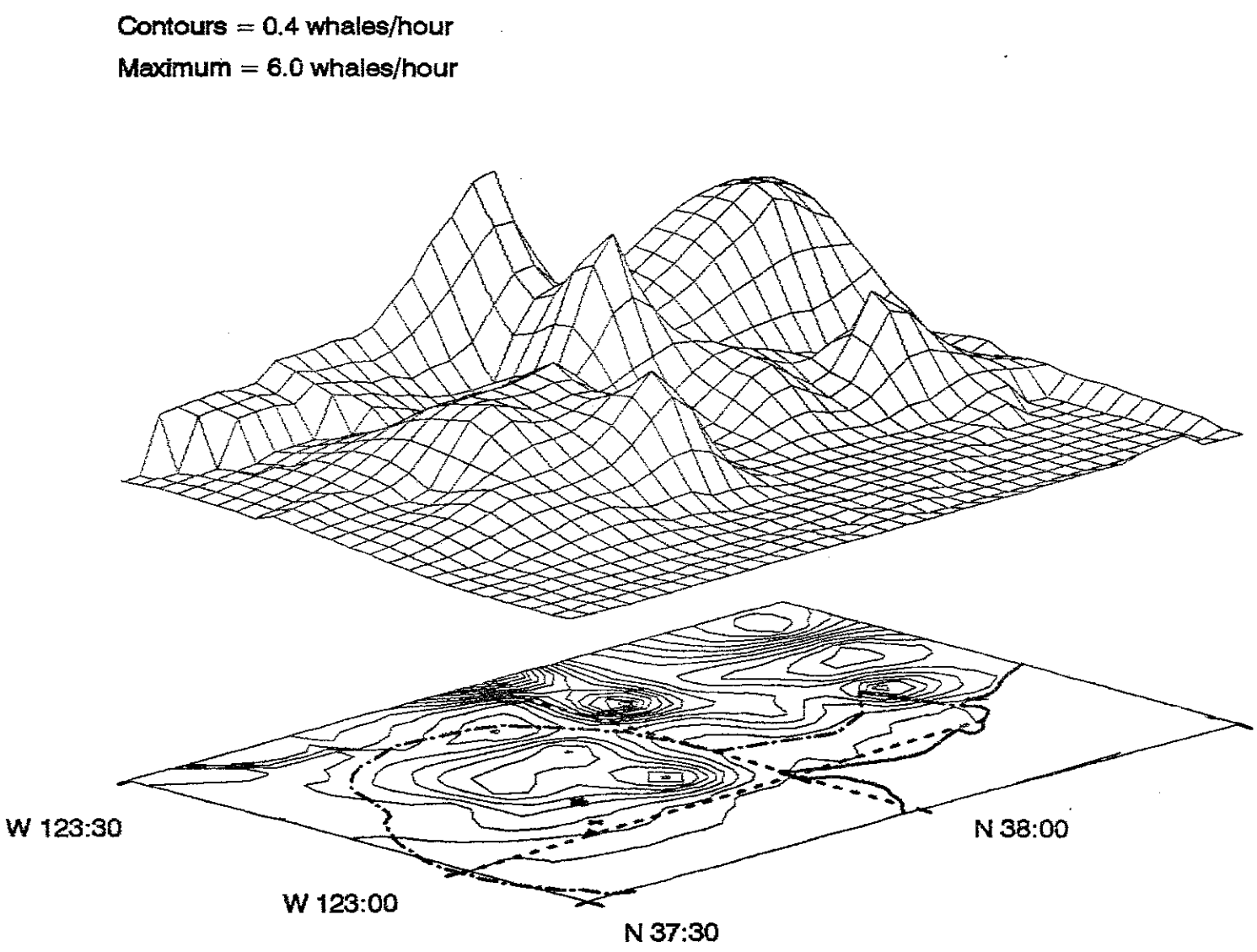


Figure 8. Effort-corrected sighting rate of humpback whales (per survey hour) from vessel surveys for 1986-1988. Data are summarized using cells (5 minutes latitude by 5 minutes longitude) with more than three hours of effort. Contours are smoothed by averaging neighboring cells.

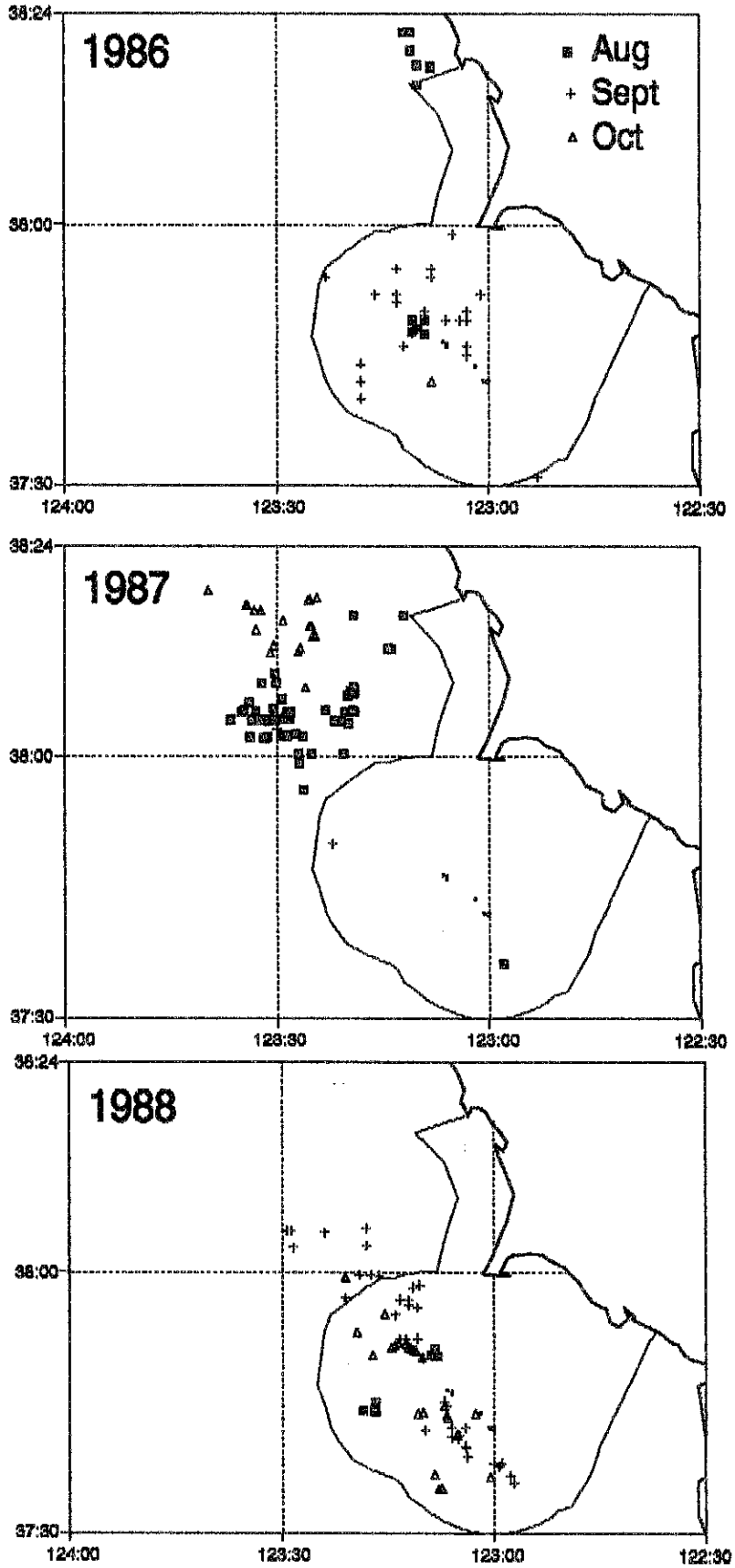


Figure 9. Locations of humpback whale sightings from aerial surveys 1986 to 1988. The month of each sighting is indicated by symbol.

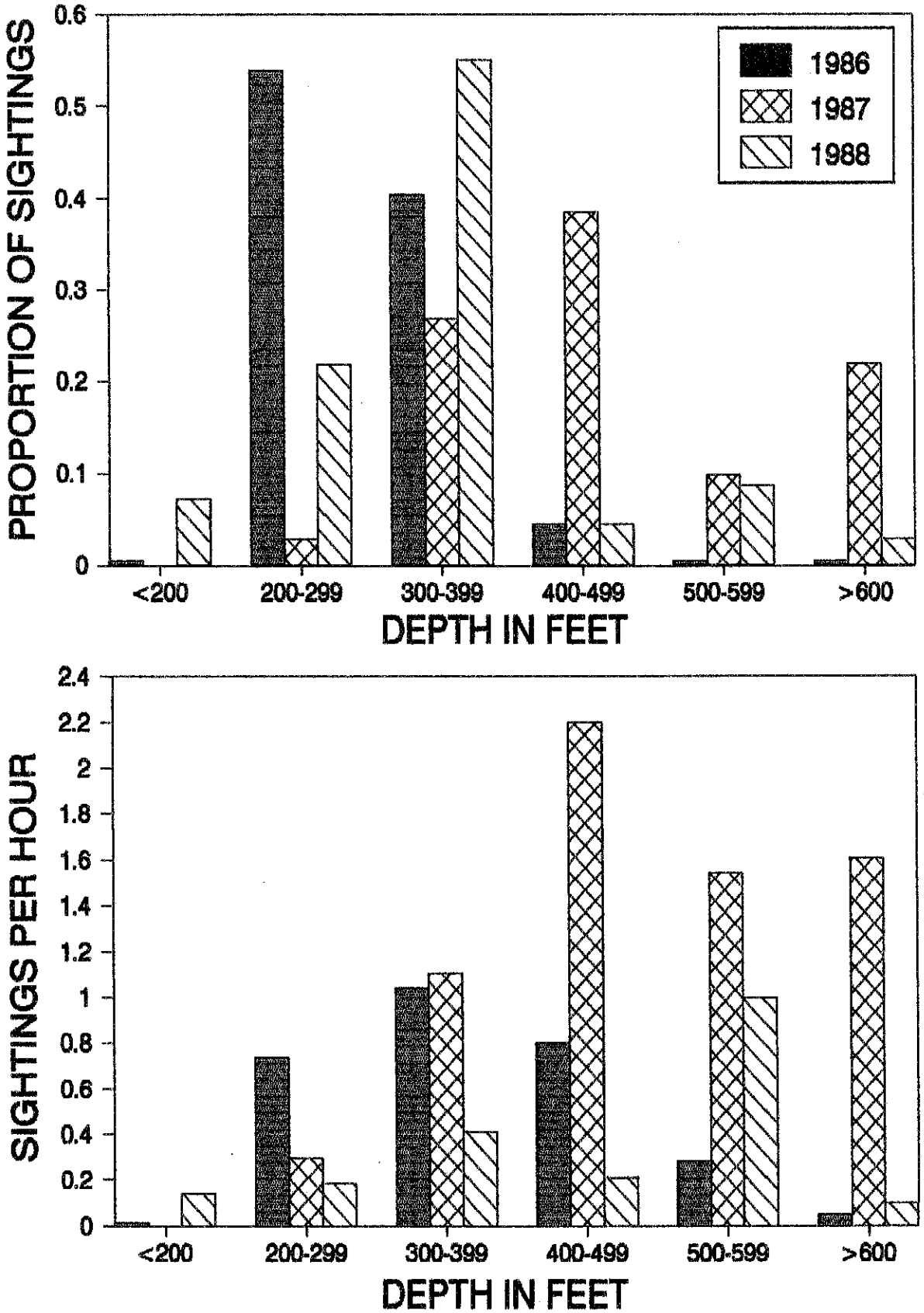


Figure 10. Sightings of humpback whales by water depth shown as the proportion of all sightings (top) and as effort-corrected sightings per hour (bottom). Data used are from vessels with depth sounders only.

Distribution and prey from whaling data 1956-65

The historical occurrence of humpback whales in central California is available from whaling data. Scammon (1874) reported humpback whales in the 19th century "in search of food" along the central California coast from April to December. He reported a northward seasonal movement of whales until September followed by a southward migration. Peak numbers of humpback whales near Monterey Bay were reported in October and November. Humpback whales were hunted extensively in the early 20th century along the California coast as well as other shore-based whaling stations to the north and south (Tonnessen and Johnsen 1982). Humpback whales were most recently hunted from 1956 to 1965 in the vicinity of the Gulf of the Farallones from two whaling stations operating out of San Francisco Bay (Rice 1963a, 1963b, 1974).

Examination of the records of humpback whales killed by whalers in the Gulf of the Farallones from 1956-1965 (provided by D. Rice) allowed comparison to our data. The largest number of humpback whales were killed in May, though fairly consistent numbers were caught from June to October (Figure 11). This timing probably reflected seasonal whale abundance in the area. The number killed by year declined rapidly from 1956 and 1965, suggesting that whaling depleted the population of humpback whales in the area.

Locations where humpback whales were caught within the Gulf of the Farallones from 1956 to 1965 were slightly different than the distribution of sightings in this study (Figure 12). We assume the capture locations reflected the distribution of humpback whales since whalers would concentrate their effort in areas of highest whale abundance. Locations where humpback whales were captured include areas farther south and offshore than where we operated. Captures were reported close to the coast as well as at a location corresponding to Drakes Estero. If these locations are accurate, they show a more coastal tendency of humpback whales than we saw (with the exception of the Humphrey sightings, see section under Individual Identification). Some of the major areas where whales were caught, including off Pt Reyes, north of Fanny Shoal and near Cordell Bank, correspond with locations we observed high densities. Several areas where we observed high densities in at least one year, including the west side of Cordell Bank, north of Bodega Canyon, and off Bodega Head, were not well represented in the whaling data either because the whales did not use these areas or the whalers did not search them.

Annual and seasonal variations in the distribution of humpback whales were apparent in the historical data, as in our results. Capture locations

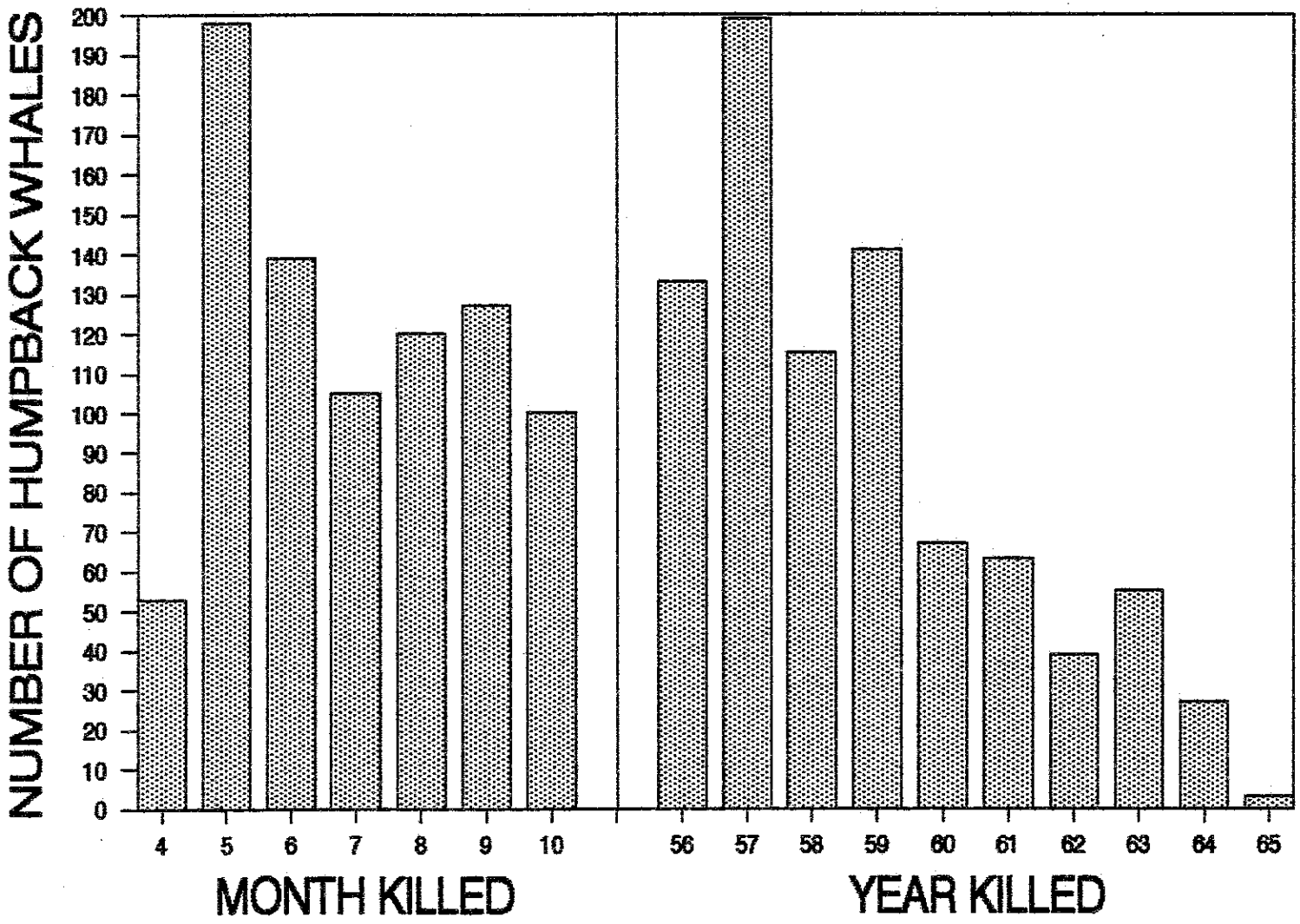


Figure 11. Number of humpback whales killed by month and year during whaling in the Gulf of the Farallones region between 1956 to 1965. Catch data provided by D. Rice (pers. comm).

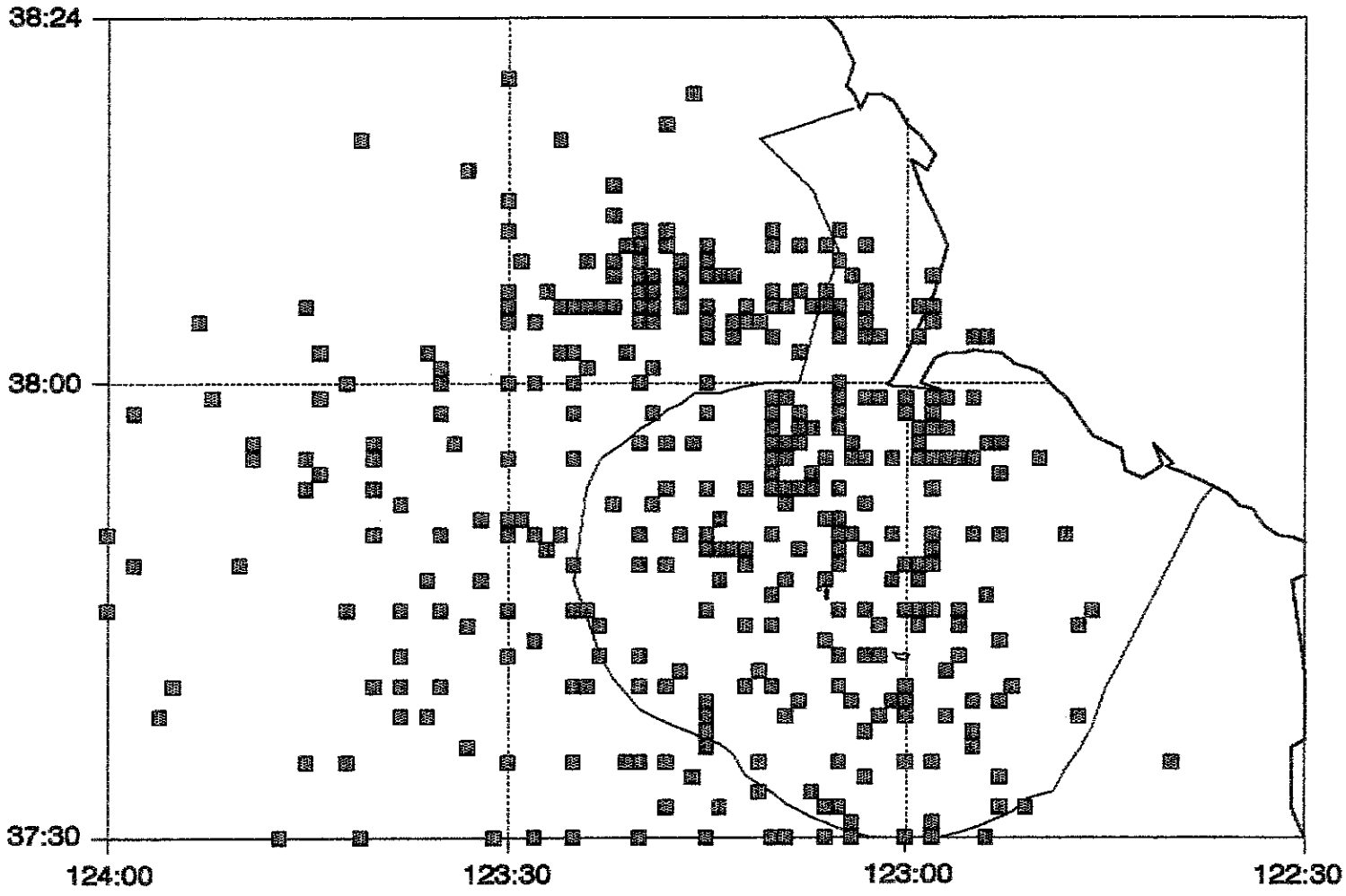


Figure 12. Locations where humpback whales were reported killed in the Gulf of the Farallones region between 1956 and 1965. Catch data provided by D. Rice (pers. comm).

varied significantly by both month and year (ANOVA, $P<0.005$ for latitude by year and $p<0.001$ for longitude by year and latitude by month and year). Humpback whale captures tended to be farther north ($n=628$, $r=0.12$, $p<0.01$) and east ($n=628$, $r=0.09$, $p<0.05$) in later months. In particular, capture locations in April tended to be the farthest south and offshore. Annual variations in the overall distribution and the pattern of seasonal distribution occurred but did not follow a consistent trend through the years. Figure 13 contrasts the locations by month for humpback whales caught in two consecutive years with large sample sizes. In 1957, humpback whales were caught primarily around Southeast Farallon Island; and in June, far offshore; and in August to October primarily east of Cordell Bank. The pattern in 1958 was different, whales caught in May and June were close to shore to the south and northwest of Pt. Reyes; sightings later in the year were scattered over a broad area.

The dominant prey reported by whalers for humpback whales caught in the Gulf of the Farallones were euphausiids and anchovy (Engraulis mordax) (Figure 14). These two prey items varied in prevalence by year with one dominating in different years. A variety of other prey were reported in lesser quantities including shrimp, fish (species not specified), and rockfish. There is the potential for inaccuracy in these categories since these data were reported by the whalers themselves. Rice (1977) reported the prey of humpback whales in California based on a more detailed examination of 215 stomachs containing food. He reported 60% contained northern anchovy, 40% Euphausia pacifica, 1% herring, and traces (<0.05%) of T. spinifera. Humpback whale prey in British Columbia consisted of T. spinifera and herring (Pike 1950). Prey of humpback whales in southeastern Alaska consisted primarily of euphausiids (mainly Thysanoessa raschii) as well as Pacific herring, capelin, and pollock (Krieger 1987). Humpback whales in the Gulf of Maine (North Atlantic) were associated with concentrations of sand eel (Payne et al. 1986).

There were significant differences in the locations for humpback whales caught with different prey reported in their stomachs (ANOVA, $p<0.05$ for latitude and $p<0.001$ for longitude). The predominant prey type varied annually therefore the location differences by prey type were related to the variations in location by year. Figure 13 shows differences between 1957 and 1958, for example, represent predominant feeding on euphausiids and anchovies, respectively.

Humpback whale occurrence in 1970s and 1980s

Sightings of humpback whales were made annually from the Farallon Islands from 1970 to 1984 (Ainley et al. 1977, 1978, Huber et al. 1979,

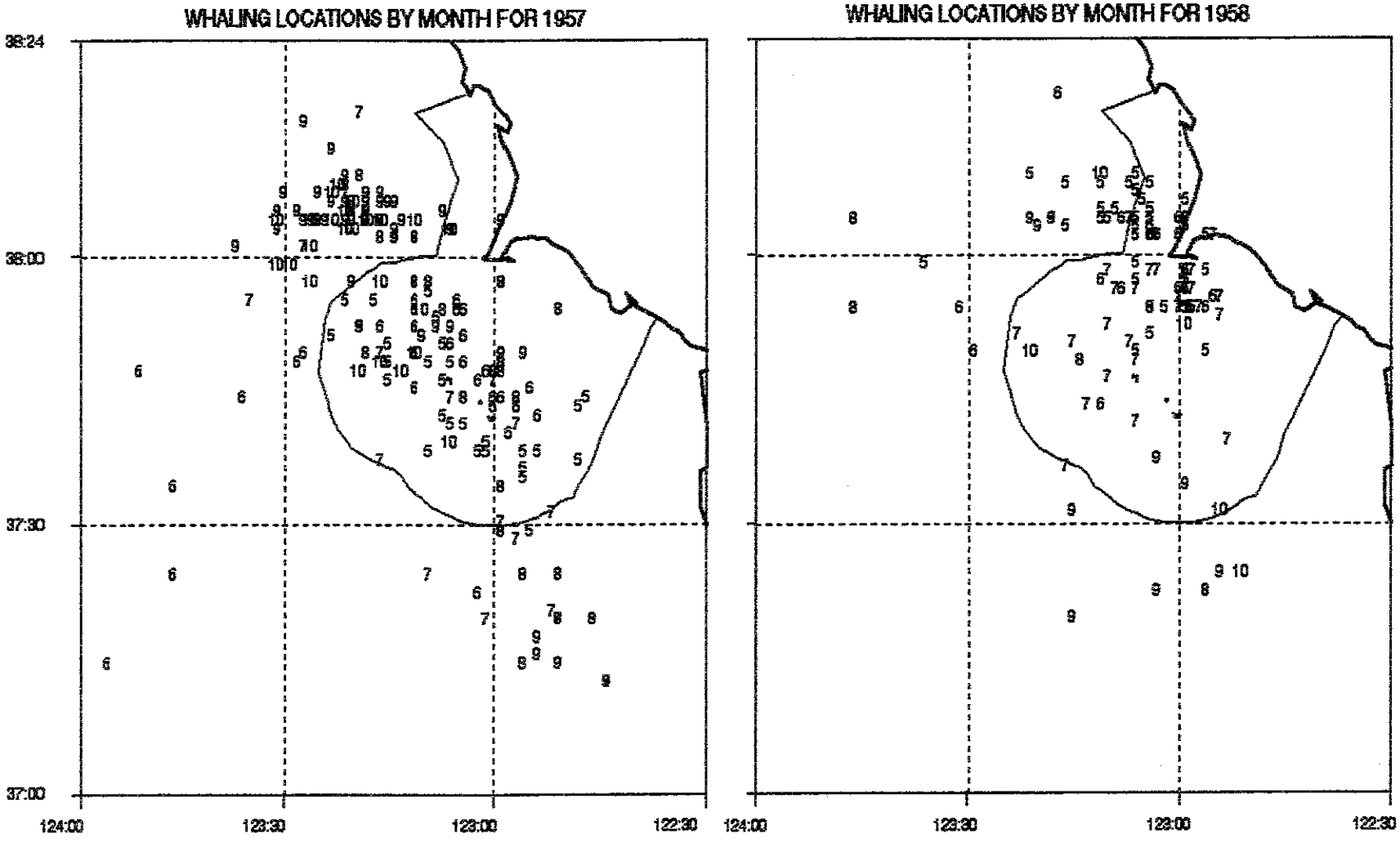


Figure 13. Locations from where humpback whales were taken by month (number of month where a whale was taken is plotted) in two years (1957 and 1958). Prey was predominantly euphausiids in 1957 and anchovies in 1958. Catch data were provided by D. Rice (pers. comm).

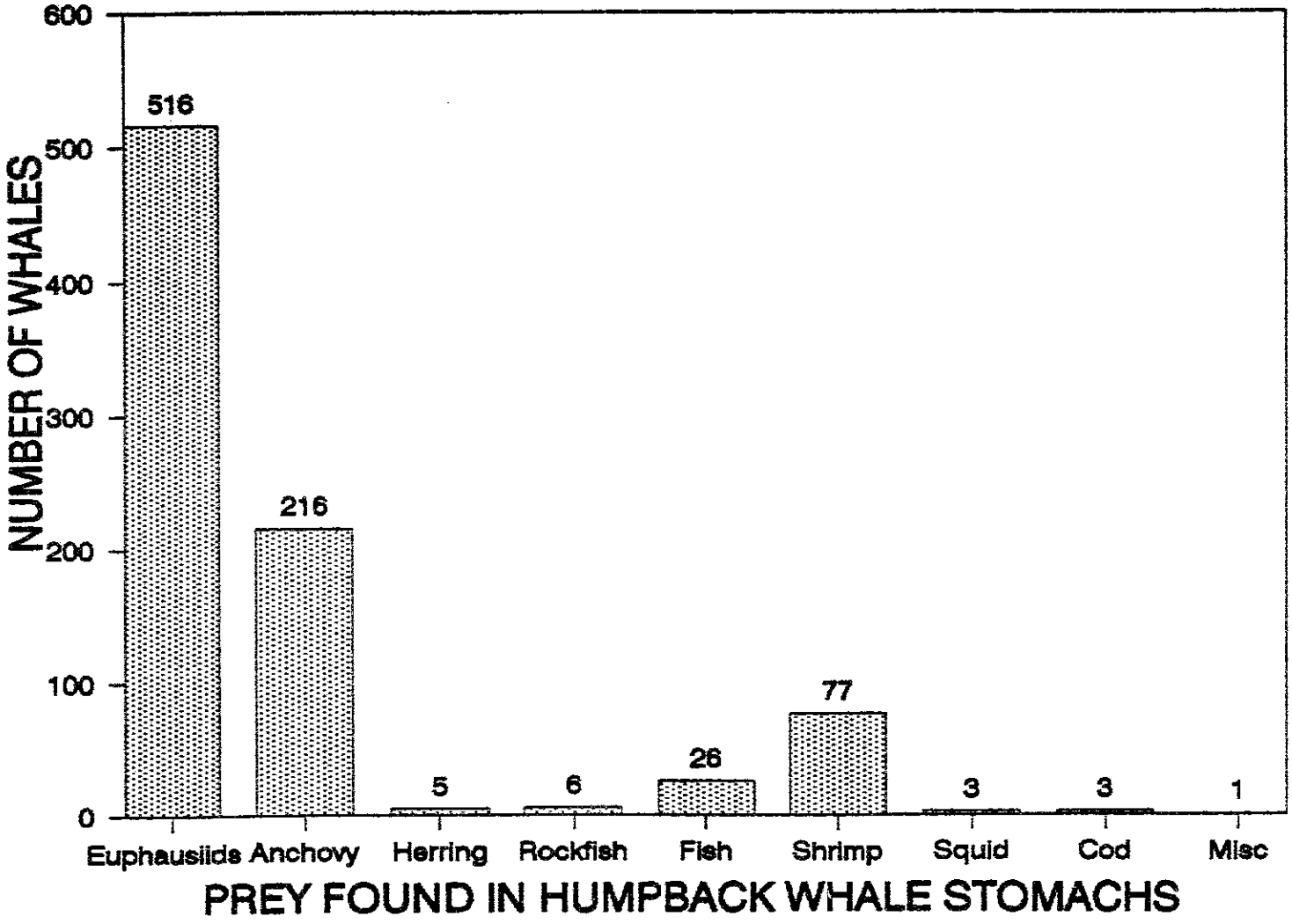


Figure 14. Prevalence of prey in humpback whales caught in the Gulf of the Farallones between 1956 and 1965. Prey type listed as reported by whalers, catch data provided by D. Rice (pers. comm).

1980, 1981, 1982, 1983, 1985, 1986). Humpback whales were seen every year except 1971, though there were large variations between years in the number and timing of the sightings (Figure 15). The highest number of whales were seen in 1982 (184) and 1973 (89). Sightings in August (160) and September (133) were the most common though whales were seen as early as April and late as December. Sightings of humpback whales in the spring (April and May) starting in 1977 were earlier than had been seen in previous years. The number of spring sightings was highest in 1980 and declined in the years after that. Frequent sightings of humpback whales in the early 1980s were reported from nature trips to the Farallon Islands and to Cordell Bank (Szczepaniak and Webber 1985, Webber and Cooper 1983, Rondeau 1987) but these did provide an indication of annual changes in abundance.

Humpback whale numbers in the Gulf of the Farallones were reported to have increased in the early 1980s but this appears to have been a short-term phenomenon. Sightings of humpback whales made from aerial surveys along the entire California coast from 1980 to 1983 were reported by Dohl et al. (1983) and Dohl (1984). The highest concentrations of humpback whales were found in the Gulf of the Farallones from August to November where the number of sightings increased from 1980 to 1983 (Dohl et al. 1983, Dohl 1984). Additional evidence of an increase came the spring sightings of humpback whales from the Farallon Islands seen staring in 1977 which led Huber et al. (1979, 1980) to speculate that these indicated a return of a "resident" whale population to the region. Spring sightings and total sightings of humpback whales from the Farallon Islands since 1982, however, have declined and no longer clearly indicate an increase (Figure 15). Similarly, the number of humpback whales seen in our research was less than found in 1982 (see Comparison of Population Estimates). Thus the increases reported by Dohl et al. (1983) and Huber et al. (1979, 1980) are probably a reflection of short-term variations in humpback whale distribution and seasonality rather than an indication of a long-term increase in abundance.

Association with prey abundance and oceanographic features

The large annual and seasonal variations in humpback whale distribution and occurrence are likely the result of variations in the oceanographic conditions that are responsible for the productivity of this region. The oceanographic province of the eastern North Pacific Ocean is dominated in spring through late summer by the the southward moving subarctic surface waters along the continental shelf and slope, known as the California Current (Strub et al. 1987). A countercurrent of inshore northward moving warmer waters, known as the Davidson Current, is of varying strength and extension in different years. These two currents and

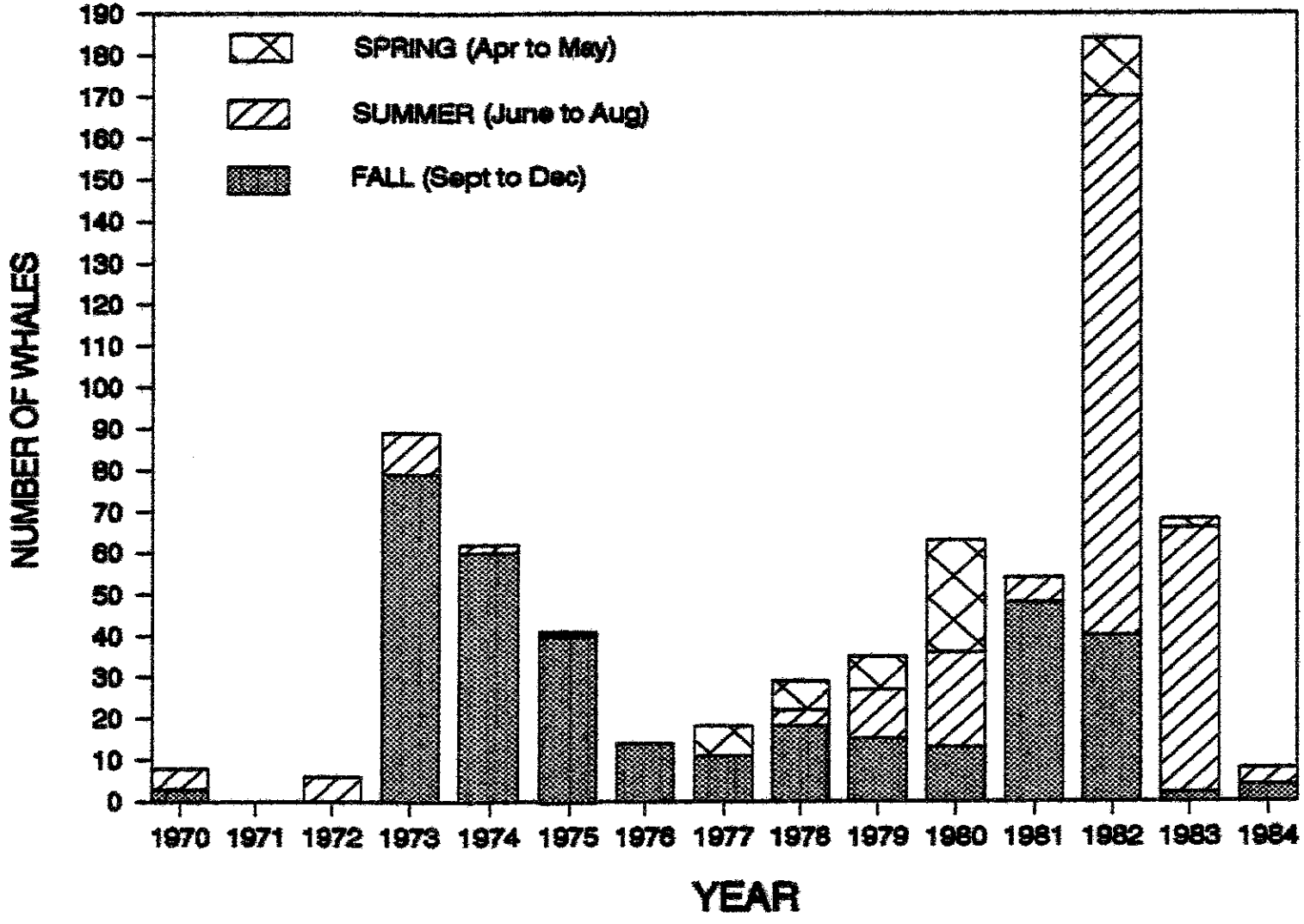


Figure 15. Number of whales sighted off the Farallon Islands by year and season reported in Ainley et al. (1977, 1978) and Huber et al. (1979, 1980, 1981, 1982, 1983, 1985, 1986, pers. comm.).

the coastal zone of upwelling from Point Conception to the Columbia River, are responsible for the high productivity of the California Current (Reid et al. 1958). The flow of the California Current is highly variable and consists of intense meandering current filaments intermingled with mesoscale-eddies (Moers and Robinson 1984). Zooplankton abundance in this region is related to surface water temperature (Colebrook 1977) and is the result of large-scale variations in the flow of the California Current (Chelton et al. 1982).

Behavior and Association with Other Species

Humpback whales observed in the Gulf of the Farallones were primarily feeding or traveling slowly (Table 6). Behavior that indicated feeding (milling and surface lunge-feeding) was seen in 45% and 66% of the groups observed in 1987 and 1988, respectively. Slow or fast travel was seen in 55% and 34% of the groups in 1987 and 1988, respectively. The significance of the differences in the frequency of travel and feeding between years is not clear. A number of other behaviors were seen frequently in both years including group affiliations and disaffiliations, breaching, pectoral fin slapping, and tail lobbing. Though data gathered in 1986 are not comparable to later years, behaviors noted in 1986 appeared to be similar to 1987 and 1988.

Trends in humpback whale movement through the season were tested in 1987. The average direction of 176 groups of humpbacks that were approached, followed for more than 10 minutes and photographed, was 291 degrees true or WNW. This direction of travel was statistically significant (Rayleigh test, $p<0.005$) and did not vary between the two study seasons in 1987 (Watson Williams test, $p>0.05$; 296 vs 281 degrees). Average speed of whales was 1.7 kts (s.d.= 1.1). Cluster analysis and multiple linear regression found no relationship of direction headed with time of day, day into the study season, whether feeding was seen, speed of animals, or location. Of other combinations of behavior and sighting variables, only size of group seen was related to other factors. In a multiple linear model larger groups tended to travel slower ($p<0.01$), and were found farther west ($p<0.05$).

Association with birds

Humpback whale occurrence was associated with the presence of marine birds on the water. In 1986 and 1987 (not tested in 1988) significantly more birds were present when humpback whales were seen than during regular effort observations (t-test and chi-square, $p<0.001$). Birds were present

Table 6. Primary and secondary behaviors of humpback whales approached by primary research vessels in 1987 (n=297) and 1988 (n=147). Percentages refer to the percentage of sightings where behavior was noted. Some type of feeding behavior was seen in 139 (47%) of approaches in 1987 and 97 (66%) of approaches in 1988. Data from 1986 were not included because behavior sampling was conducted using different sampling system.

Behavior	1987				1988			
	Primary		Secondary		Primary		Secondary	
	Num.	%	Num.	%	Num.	%	Num.	%
Slow travel	164	55	19	6	45	31	18	11
Fast travel	6	2	3	1	4	3	4	2
Milling	93	31	23	7	67	46	6	4
Feeding suspected	11	4	10	3	14	10	7	4
Surface lunge feed	15	5	30	9	10	7	23	14
Breaching	3	1	23	7	1	1	17	10
Tail-lobbing	2	1	13	4	0	0	11	7
Stationary	1	0	10	3	0	0	3	2
Fluke swish	0	0	34	11	0	0	19	11
Feeding with bubbles	0	0	3	1	0	0	1	1
Spy hop	0	0	3	1	0	0	3	2
Pectoral fin slap	1	0	16	5	0	0	5	3
Group affiliation	0	0	58	18	0	0	18	11
Group disaffiliation	1	0	52	16	0	0	20	12
Other noted	0	0	2	1	0	0	1	1
Total	297		300		147		156	

within 300 m of whales in 64% of photographic approaches to humpback whales in 1987 (n=321) and 83% of the approaches in 1988 (n=149).

The most common species of birds found near humpback whales were alcids (primarily Cassin's Auklets, Ptychoramphus aleuticus) and phalaropes (presumably Red Phalaropes, Phalaropus fulicaria, or Red-necked Phalaropes, P. lobatus). Alcids were present during 25% of all approaches in 1987 and 49% of approaches in 1988. Phalaropes were present during 22% and 42% of approaches in 1987 and 1988, respectively, and were seen in the densest groups (when phalaropes were present, an average of 85 phalaropes in 1987 and 89 in 1988 were within 300 m of humpback whales). Other birds seen in over 10% of the humpback whale approaches included gulls and shearwaters in both years, and terns in 1988.

Cassin's Auklets and phalaropes feed primarily on zooplankton. Near the Farallon Islands, both species feed on euphausiids, most notably Euphausia pacifica and Thysanoessa spinifera (Manuwal 1974, Briggs et al. 1984, Briggs and Chu 1987, Ainley et al. 1987). Other studies have reported the association of feeding humpback whale with Alcids (Webber and Cooper 1983, Hoffman et al. 1981); Calambokidis et al. (1989) reported the same association between the presence Cassin's Auklets and phalaropes with feeding blue whales in the Gulf of the Farallones.

Interactions with other marine mammals

Dall's porpoise and California sea lions were seen swimming in the wake or around the head of humpback whales as they surfaced. No direct interactions were observed with other large cetaceans; it was not unusual to observe humpback whales and blue whales feeding in the same area, however, no cooperative behavior was observed between these species.

Age and Size Classes of Humpback Whales

Lengths of humpback whales

The average length of humpback whales in the Gulf of the Farallones, determined through aerial photogrammetry, was 12.0 m (n=24, s.d.= 0.76). Whale lengths ranged from 10.5 m to 13.6 m. The length distribution of whales measured is shown in Figure 16.

The lengths of humpback whales we measured through photogrammetry were generally smaller than whales caught during whaling. We calculated the length distribution of humpback whales taken from the Gulf of the Farallones region during whaling between 1956-65 (Figure 16) from data

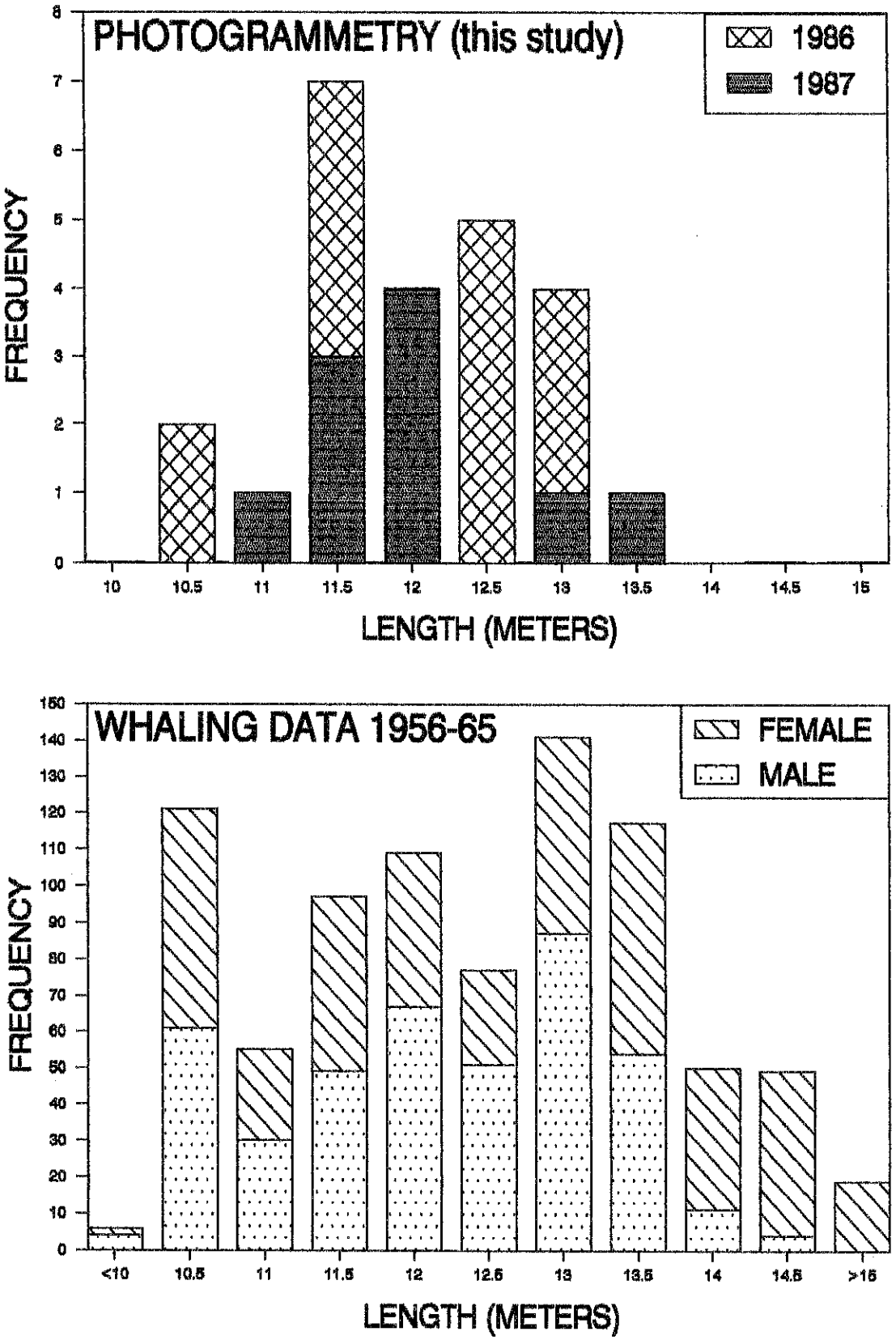


Figure 16. Length of 24 humpback whales measured through aerial photogrammetry in 1986-1987 (top) and of humpback whales taken during whaling between 1956-1965 (bottom) in the Gulf of the Farallones. Catch data provided by D. Rice (pers. comm.).

provided by D. Rice (pers. comm.). Lengths ranged between 8.4 m and 15.8 m and averaged 12.1 m for males (n=418, s.d.=1.1) and 12.6 m for females (n=423, s.d.=1.4). Although the average lengths are only slightly higher than lengths measured through photogrammetry, the comparison of length distributions (Figure 16) shows that larger whales were present historically. Due to potential biases in measurement methods, differences between lengths from whaling data and lengths measured through photogrammetry may be partly the result of methodological differences.

The average lengths of humpback whales taken in the Gulf of the Farallones were similar to whales taken off British Columbia between 1948-1959 (12.0 m for males and 12.1 m for females, calculated from Pike 1962) and similar to whales taken in the Ryukyuan waters in 1959-1960 (11.9 m for males and 12.7 m for females, n=346, calculated from Nishiwaki 1959, 1960). Farallon humpback whales are larger than humpbacks taken in the Gulf of Alaska taken between 1924 and 1939 (off Akutan, 10.9 m for males and 11.1 m for females, n=845, and off Port Hobron, 11.4 m for males and 11.7 m for females, n=1561, calculated from Reeves et al. 1985).

Most humpback whales measured photographically in the Gulf of the Farallones were estimated to be sexually mature but not physically mature. Determining age classes is difficult because the length of whales at maturity varies by region and sex. Rice (1963a) determined lengths at maturity for humpback whales taken off central California during whaling. Length at sexual maturity was 12.0 m for females and 11.7 m for males; length at physical maturity was 14.8 m for females and 13.6 m for males (Rice 1963a). By applying these lengths to the whales measured in the Gulf of the Farallones, 25% (6 of 24) would be immature (< 11.7 m), 71% (17 of 24) would be sexually but not physically mature (11.7-13.5 m long), and 4% (1 of 24) would be physically mature (> 13.5 m).

Occurrence of Cows and Calves

The number of cows and calves in the Gulf of the Farallones was low, however, the number of calves recorded did increase each year. In 1986, 3 of 711 (0.4%) humpback whales sighted from vessels were calves; in 1987, 19 of 1,129 (1.7%) were calves; and in 1988, 23 of 435 (5.3%) were calves. During aerial surveys, no calves were seen in 1986 or 1987, and two were observed out of 212 (1%) humpback whales seen in 1988. Although it was sometimes difficult to discriminate a calf from a yearling (calves were at least six months old by the time they were in the Gulf of the Farallones), calf sightings clearly increased over the three years.

In 1987, we photographically identified four whales as cows (two of them tentative identifications) and four whales as calves (including three tentative); in 1988, we identified four cows and three calves (Table 7 and 8). Whales were listed only if good evidence supported calling them a cow or calf, tentative identifications were given if notes were ambiguous. The examination of the identities of some animals showed that, in two cases, "calves" had been seen in previous years (and therefore were not calves). Cows comprised 0-3% all the humpback whales identified by year; this was slightly lower than the proportion of calves sighted (see above). No cows were identified in 1986, four cows were identified in 1987 (3% of the whales identified), and 4 cows were identified in 1988 (3% of the whales identified).

The percentage of cows and calves in the Gulf of the Farallones was low compared to other regions. Birth rates for humpback whales in other regions have been reported between 4 and 12% (Chittleborough 1965, Herman and and Antinoja 1977, Whitehead 1982, Clapham and Mayo 1987). The low percentage of calves seen in the Gulf of the Farallones appears to indicate a low reproductive rate for this population, though geographic age-class segregation of whales is also possible.

Behavior of cows and calves

More cows were identified than calves because cows were more likely to fluke than were their calves. Of the seven cows identified in 1987 and 1988, two were observed with a calf that did not fluke. Cow #10113 was observed seven times in 1988, and the calf (10253) raised it fluke only once (partially) on one occasion. This cow was observed in late October off Monterey Bay (photographed by T. Jefferson, Moss Landing Marine Lab), again the calf did not fluke. Studies of humpback whales in other regions have found that calves raise their flukes out of the water less frequently than older animals (Kaufman et al. 1987, Perkins et al. 1985).

Residency patterns of cows and calves

Most cow and calf pairs identified appeared to remain in the the Gulf of the Farallones for over a month. Days elapsed from first to last sightings of cows averaged 33 days (s.d.=22.9) and ranged from 1 to 59 days. Four of eight cows were observed from the beginning to the end of our study period (Aug-Oct), and two were first observed late in the field season (October)(Table 7).

In other regions, cow-calf pairs tended to remain on wintering grounds longer and arrive at feeding grounds later than other age-classes (Pike

Table 7. Identified females observed with calves that were noted in field observations.

ID mother	Range of dates observed with calves	Yrs seen in GF	Comments
10044	19 Aug-30 Aug 87	86 87 88	calf doesn't fluke
10165	30 Aug-11 Oct 87	87	calf is 10135
10065	24 Sep-30 Oct 88	86 87 88	calf is 10211
10159	01 Oct-07 Oct 88	87 88	calf is 10216
10230	30 Oct 88	88	calf doesn't fluke
10113	29 Aug-27 Oct 88	81 87 88	calf is 10253
Tentative identification			
10064	20 Aug-11 Oct 87	86 87 88	calf is 10105?
10163	19 Aug-11 Oct 87	87 88	calf is 10138?

Table 8. Calves identified in field observations.

ID calf	Date of first record	Comments
10135	30 Aug 87	calf of 10165
10211	23 Sep 88	calf of 10065
10216	02 Oct 88	calf of 10159
10253	02 Sep 88	calf of 10113
Tentative identifications		
10105	18 Aug 87	calf of 10064?
10138	19 Aug 87	calf of 10163
10181	26 Aug 87	cow not known

1962, Dawbin 1966, Herman and Antinoja 1977, D'Vincent et al. 1988). It is possible that the sightings of cow-calf pairs seen in the Gulf of the Farallones were affected by temporal age-sex differences in migration, however, this is not supported by the early season (August) sightings of over half of the cows with calves.

Sighting histories and regional fidelity of cows and calves

Cows identified in the Gulf of the Farallones were resighted across years (1986-88) more frequently than other humpback whales. Six of the eight cows (75%) identified were sighted in more than one year, and three of eight (38%) were observed in all three years (Table 7). In contrast, resighting rates for all humpback whales were lower; 46% seen more than one year and 17% seen all three years (see Individual Identification). Baker et al. (1987) reported that 68% of the females identified in southeastern Alaska (over 6 years) were resighted across years. One female (#10113) was seen in the Farallones across seven years; female #10113, was first photographed in the Gulf of the Farallones in 1981 (by Farallon Research Associates) and was seen with a calf in 1988.

None of the four calves identified in 1987 were seen in the Gulf of the Farallones in 1988, the only year where calf resightings can be examined. Studies in other areas have demonstrated site-fidelity by juveniles (Mayo and Clapham 1983, Baker et al. 1987, Clapham and Mayo 1987). The low return rate of yearlings to the Gulf of the Farallones could be due to the small sample or that yearlings feed in another region.

Two females identified in the Gulf of the Farallones were observed in other feeding regions. Female #10165 was observed with a calf in the Gulf of the Farallones in 1987; in 1988, it was not seen in this region but was observed off San Luis, California, with a yearling or calf (which was not identified). Female #10128, identified in the Gulf of the Farallones in 1987, was seen with a calf off Monterey Bay, California, in 1988.

Individual Identification

From 1986 to 1988, 225 individual humpback whales were identified based on fluke markings in the Gulf of the Farallones region (southern boundary of the marine sanctuary to off Bodega Bay). Three additional individuals were identified prior to 1986 and not seen 1986-1988. The number of individuals identified varied from 90 in 1986 to 141 in 1987 (Table 9). The differences in the number of whales identified is partially the result of the increased effort later in the season (October) in 1987 and 1988 compared to 1986 when dedicated vessel surveys ended in mid-September. More whales were identified in October than August or September. A majority of the identified whales (122) were seen in only one of the three years, 65 were identified in two of the years, 38 were identified in all three years; 63% to 73% of the whales seen each year were seen on a second year from 1986-88.

Rate of discovery

The rate at which new whales were "discovered" (discovery rate) provides insight into the number and arrival times of new whales in the area. The cumulative discovery rate for all three years increased sharply at the start of each year (Figure 17, top), then tended to decrease through the season. Differences in the timing of effort each year are not responsible for this pattern, because in all three years most of the animals were not identified until late August and September. We conclude that the increased rate of discovery of new whales at the start of each year reflected the arrival of a substantial number of whales that had not been in the study area the previous year(s). However, despite this apparent infusion of new whales each year, a growing proportion of the population that visited the study area was identified over the three years of the study as indicated by the progressively shallower slope of the discovery curve through the years (Figure 17,top).

The rate at which new whales were discovered within each year indicated differences in the number of whales present each year (Figure 17, bottom). The proportion of whales that had been seen previously in the season was highest at the end of sampling in 1986, as indicated by the shallow slope of the curve. The opposite was true in 1988 when a high proportion of the whales identified at the end of the season had not been identified previously that year. Two factors could account for the differences between years: 1) different numbers of whales were present each year (the least in 1986 and the most in 1988), or 2) new whales tended to continued to arrive late in the season and so the later effort each year

Table 9. Individual humpback whales identified each year in the Gulf of the Farallones 1986-88.

Year	# identified	Unique IDs	Times seen		Unique IDs by month					Matches by year		
			mean	S.D.	Jul	Aug	Sep	Oct	Nov	86	87	88
1986	466	90	5.2	4.0	0	68	59	1	0	-	56	48
1987	793	141	5.6	4.5	6	11	51	73	0		-	75
1988	398	135	2.9	2.1	1	14	57	106	5			-
1986-88	1,658	225										
Prior to 1986	19	16	-	-						6	9	11
All	1,777	228										

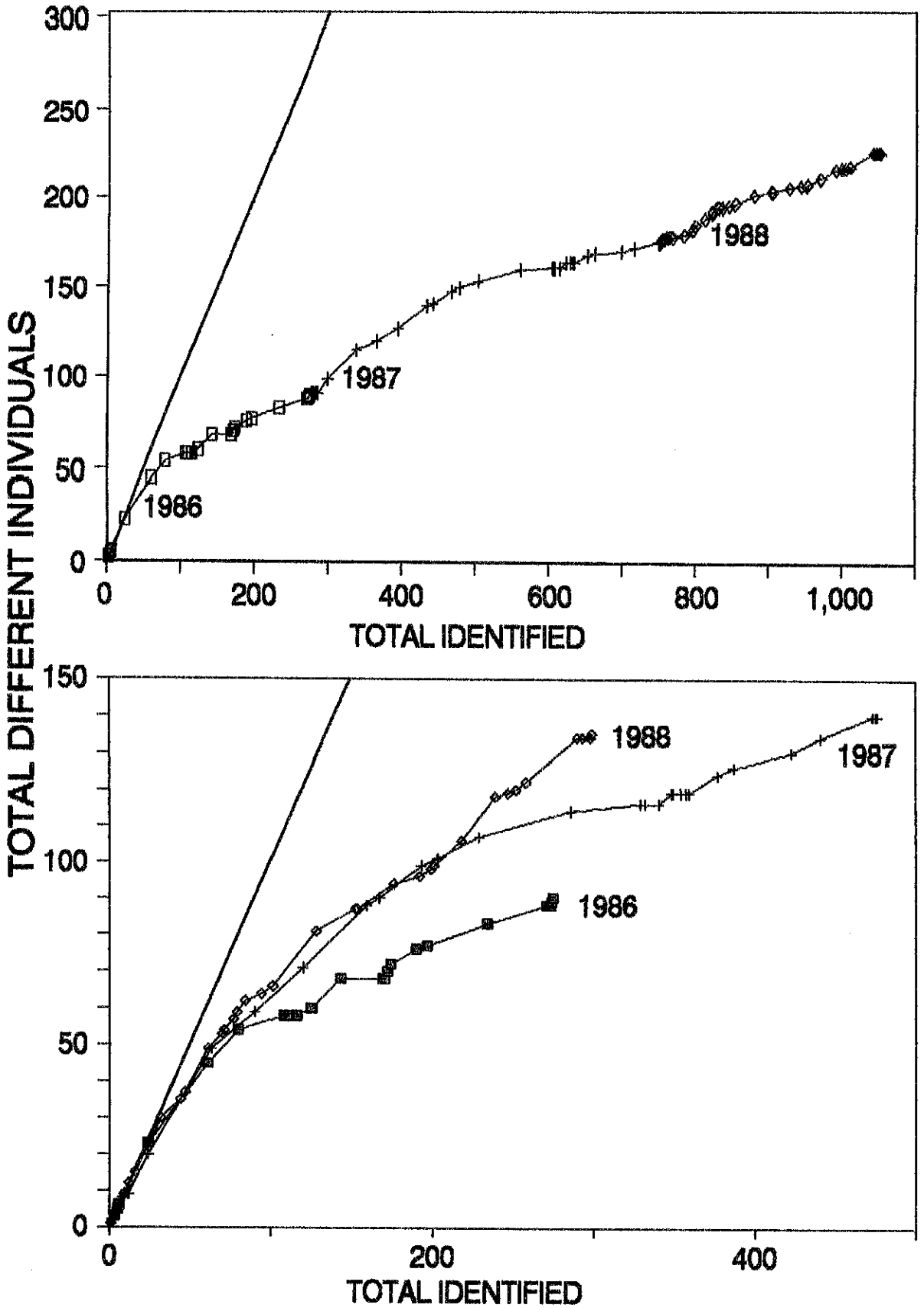


Figure 17. Rate at which new humpback whales were identified (rate of discovery) in relation to total whales identified over all three years (top) and within each year (bottom). The straight line shows rate if all whales were seen once. Each point is a single day. Multiple sightings of the same whale in a day are counted once.

sampled more of these new whales. We suspect both these factors partly were responsible for the observed annual differences.

Resightings of humpback whales identified prior to 1986

A high proportion of humpback whales photographed in the study area by other researchers (M. Webber, I. Szczepaniak, C. Ewald, J. Ostman, and H. Rondeau) prior to 1986 were seen during our research. Sixteen individuals were identified from photographs taken from 1981 to 1985. All but three of these have been seen in the Gulf of the Farallones from 1986 to 1988. One of these three was seen in 1988 off San Luis, California. One of the remaining two was an individual that matched to Hawaii and reported in Baker et al. (1986). Of three humpback whales first identified in 1981, two were seen in 1988, seven years later.

Resighting rates

Whales were usually identified on multiple days each season (Figure 18). In both 1986 and 1987, whales were identified an average of more than five times during the year (Table 9). The average within-season resighting frequency was much lower in 1988 (2.9) when close to half of the identified whales were seen on only one day.

Resighting rates each season for whales seen in multiple years varied significantly from the rates of whales seen in only one year (Figure 19). The number of times and days a whale was seen in each of the three years was significantly different among those whales that been seen only one year, two years, 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 also 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 the last sighting each year). Differences in tenure were significant for 1987 and 1988 (ANOVA, $p<0.05$ and $p<0.001$, respectively) when whales that had been seen all three years were seen an average of 15 days longer than whales seen in the one year only. Significant differences in tenure were not in 1986 (ANOVA, $p>0.05$).

The longer tenure for whales seen across years was the result of later sightings of these whales in 1987 and earlier sightings in 1988. In 1987, there were significant differences in the last day whales were seen among whales that had been seen different numbers of years (ANOVA, $P<0.05$). Whales seen all three years were seen 12 days later on average in 1987 than whales that were seen in 1987 only. Dates of first sightings in 1987 did not differ significantly (ANOVA, $p>0.05$). Arrival dates varied

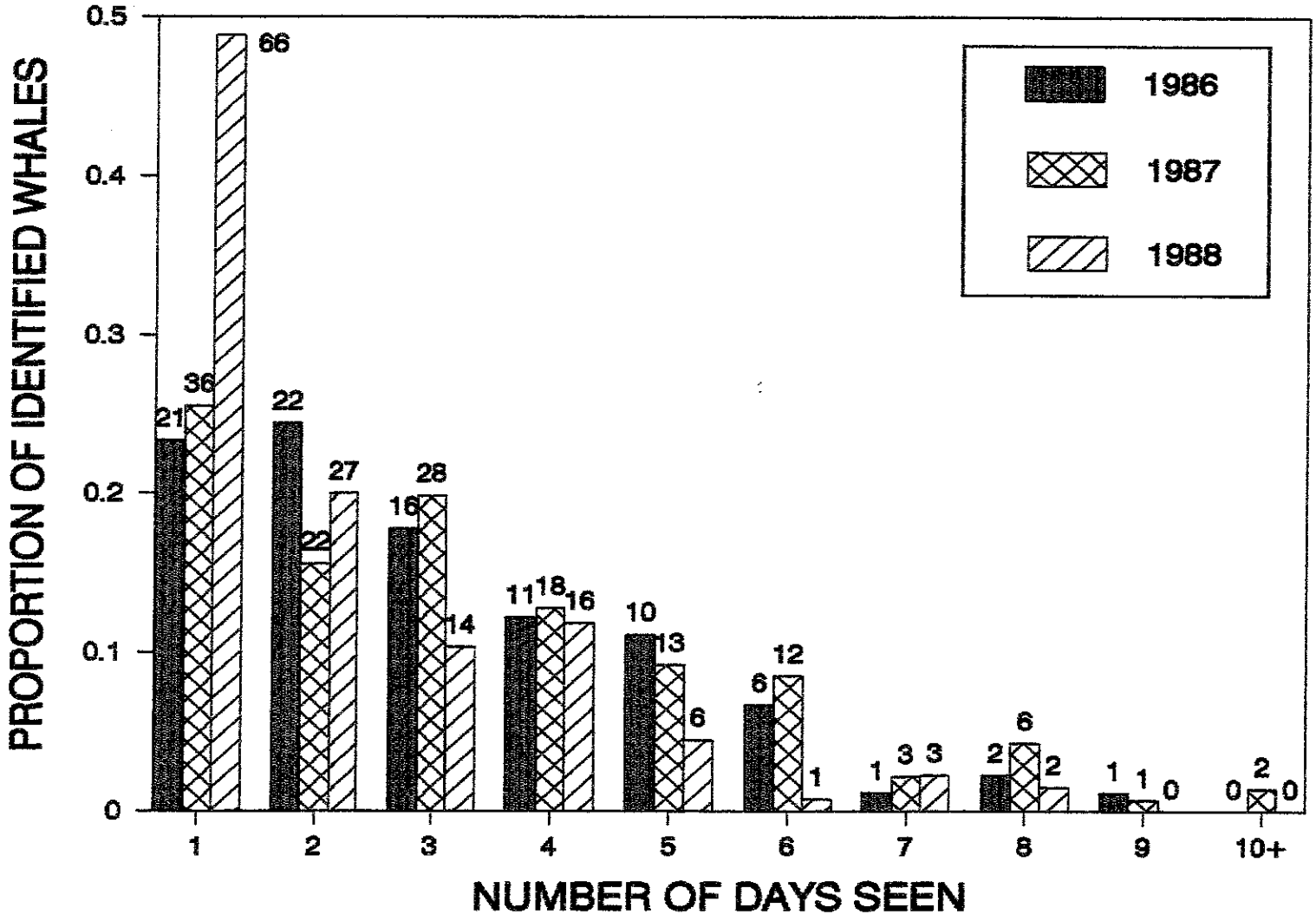


Figure 18. Resighting frequencies of identified humpback whales for 1986 to 1988. Numbers above bars are number of whales.

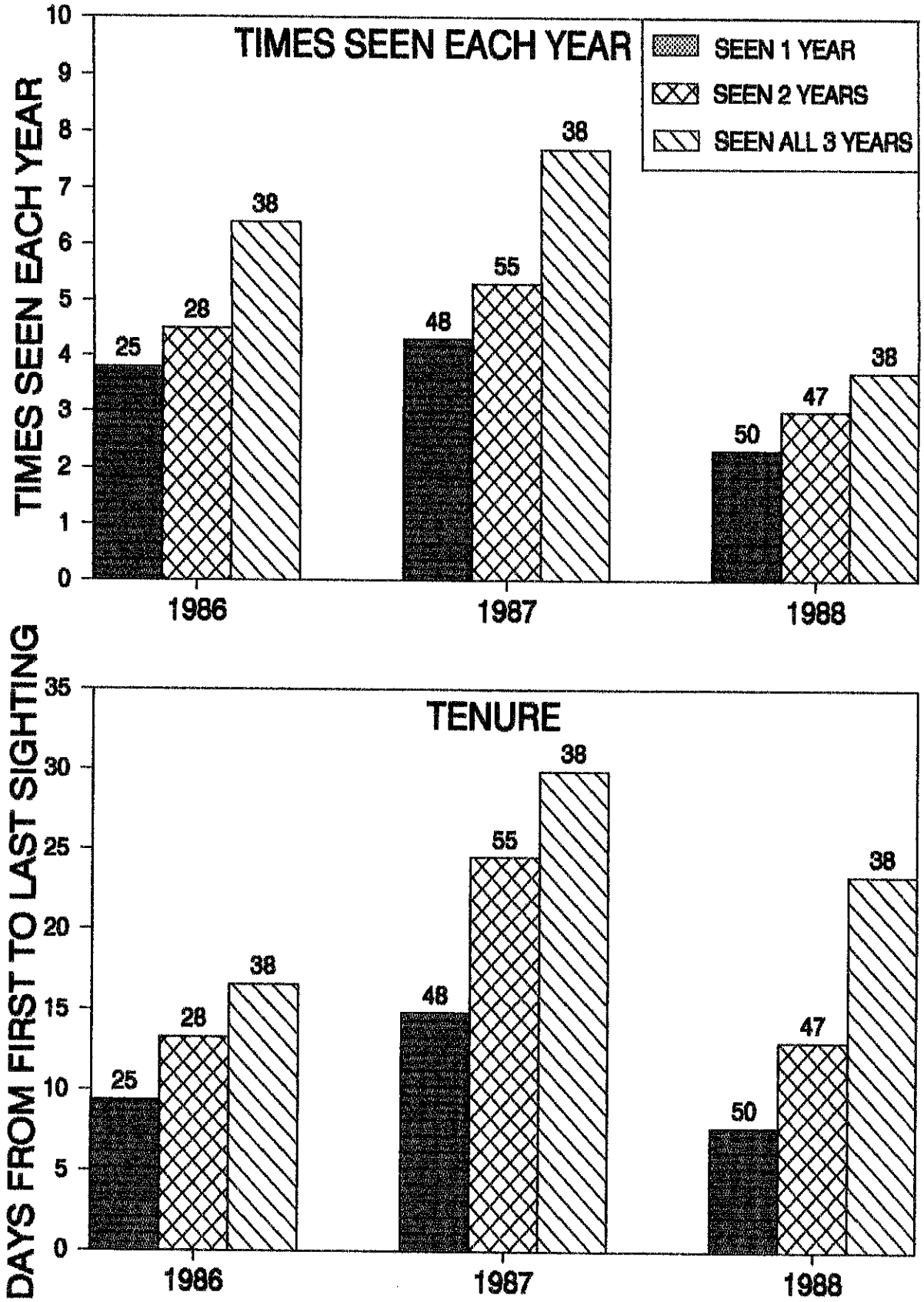


Figure 19. Times seen each year and tenure (days elapsed from first to last sighting each year) for individual whales identified in different numbers of years in the Gulf of the Farallones. Numbers above bars are number of whales.

significantly in 1988 among the whales that had been seen different numbers of years (ANOVA, $p<0.005$). Whales seen all three years were seen 14 days earlier on average in 1988 than whales that were seen first in 1988.

Our findings indicate at least two subgroups of humpback whales visit the Gulf of the Farallones. One group occurs in successive years and consistently stays longer each year. Another group appears less likely to be seen across years and does not stay as long each year. These findings show that one of the assumptions in conducting mark-recapture population estimates has been violated; all individuals in the population do not have an equal probability of capture (heterogeneity of capture probabilities).

Movements of Humphrey and other individuals

Several times each year, we resighted "Humphrey" (Table 10), the humpback whale that captured the public's attention in 1985 when it swam up the Sacramento River. Humphrey was first identified off Isla Isabel, Mexico in December 1983 (Alvarez 1987). In 1986, we sighted Humphrey 3 different days. On 16 August 1986, sightings were made from 0811 to 1357 between Pt. Reyes and the North Farallon Islands (Figure 20). Humphrey was associated with several different groups of humpback whales and appeared to be feeding. Other observations in 1986 were made in the same area on 20 August and off Bodega Head, 25 nm north of the previous sightings, on 28 August. In 1987, we observed this whale on three occasions on two different days. On 21 August 1987, Humphrey was seen apparently feeding with two other whales northeast of Cordell Bank. On 29 August 1987, Humphrey was seen with two other whales traveling north off Bodega Bay.

Unlike the sightings in 1986 and 1987, the sightings in 1988 all occurred in unusual areas. On 1 October 1988 Humphrey was observed for several hours in shallow water in Drakes Bay. Blows heard earlier suggested Humphrey arrived the previous evening. On 2 and 4 October, Humphrey again was seen in shallow water, this time in Bodega Bay and for short periods, Bodega Harbor. In all the 1988 sightings no other humpback whales were observed in these waters. These sightings were the only sightings of humpback whales at these locations or water depths made during this study.

Movements of another identified whale seen in all three year demonstrates the wide ranging movement of individual humpback whales in the Gulf of the Farallones (Figure 20). This individual (ID # 10001) was generally seen at the locations were the major concentrations of whales were seen each year.

Table 10. Sightings of Humphrey during study. Earliest sighting predates incident in the Sacramento River in 1985 and is from photoidentification research in Mexico (Alvarez 1987).

Date mo/dy/yr	Time	Location lat.	Location long.	Location description	Grp size	Depth (ft)	Other individuals in group	Comments
12/29/83				Isla Isabel, Mexico	3		2M84I004(UNAM)	by C. Alvarez
11/--/85				Sacramento River		<50		for > 1 month
08/16/86	0811	37:55.6	123:02.9		3	250	10051 10075	
08/16/86	0830	37:55.8	123:04.3		3	270	10051 10075	
08/16/86	0958	37:54.	123:04.		4	200	10051 10075 10019	
08/16/86	1245	37:56.5	123:06.6		2	300	10060	
08/16/86	1328	37:56.2	123:06.5		2	287	10068	
08/16/86	1357	37:58.4	123:07.7		6		10008 10045 10048 10060	
08/20/86	1309	37:54.7	123:05.4		2	295	10075	
08/20/86	1425	37:55.0	123:03.3		3	265	10044 10068	
08/20/86	1530	37:54.0	123:05.7		3	308	10049 10074	
08/28/86	1100	38:20.0	123:09.0		2		10004	
08/28/86	1155	38:19.4	123:09.1		10		10005 10010 10069	
08/28/86	1638	38:19.6	123:09.0		4	285	10024 10052 10069	
08/21/87	1620	38:03.4	123:19.8		3	426	10028 10064 10069	
08/29/87	0911	38:11.7	123:10.2		3		10148 10149	
08/29/87	0955	38:13.7	123:10.6		3	315	10148 10149	
10/01/88	0941	37:58.5	122:56.5	Drake's Bay	1	16		
10/01/88	1002	37:58.5	122:56.5	Drake's Bay	1	14		
10/02/88	0936	38:18.2	123:03.0	Bodega Hbr. and Bay	1	<30		
10/04/88	1740	38:18.5	123:02.0	Bodega Hbr. entrance	1	<30		

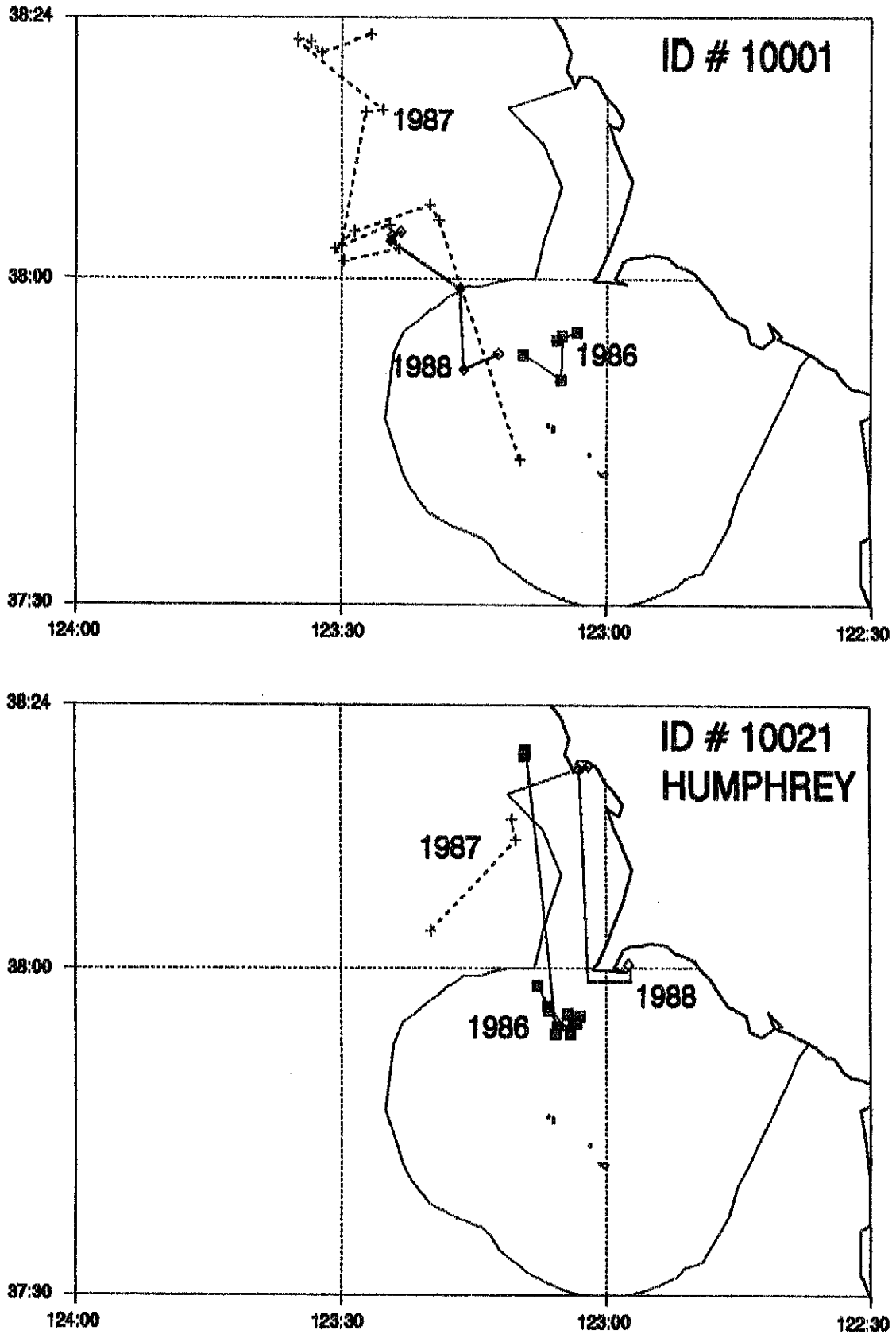


Figure 20. Examples of seasonal and annual movements of individual whales identified in the Gulf of the Farallones in 1986-1988. Movements of whale #10001 and #10021 (Humphrey) are shown. Lines connect sighting locations and do not necessarily reflect route of travel.

Migration Routes and Population Structure

Movements within California

Humpback whales identified in the Gulf of the Farallones were also seen in other coastal areas of California to the north and south (Figure 21). Most of these photographs from other regions in California were from 1988 and were provided in part by other researchers (see Methods).

The largest proportion of matches between the Gulf of the Farallones and other regions of California was with the Monterey Bay area, where 15 of the 22 whales identified there were also seen in the Gulf of the Farallones. Eight of these 15 whales were found in both the Gulf of the Farallones and Monterey Bay in the same year (1988). Most of the Monterey Bay whales were seen earlier in the season (21 June to 29 August) than the majority of the whales in the Gulf of the Farallones. Seven of the eight matched whales were seen first off Monterey Bay and from 5 to more than 80 days later in the Gulf of the Farallones. The single match that occurred earlier in the Gulf of the Farallones was a mother and calf discussed previously (see section on cows and calves). Most of the humpback whales seen off Monterey Bay appeared to be in transit to other areas, often to the Gulf of the Farallones. Four individuals, however, were identified multiple times from 2 to 43 days apart, indicating a few individuals remain for prolonged periods in Monterey Bay area.

Smaller numbers of humpback whales were identified in other areas adjacent to the Gulf of the Farallones including off Pt. Sur, Half Moon Bay, and Pt. Arena. All or most of the whales from these locations matched those seen in the Gulf of the Farallones, though again not always in the same year. Of six humpback whales identified off Pt. Arena (5 in 1988), five have been seen in the Gulf of the Farallones but only two were seen in both areas in the same year (1988).

Matches of identified humpback whales between the Gulf of the Farallones and areas in northern and southern California was much lower than those seen in central California. Of 62 humpback whales identified in the Port San Luis area between Pt. Buchon and Pt. Conception (primarily in 1988), only 13 were identified in the Gulf of the Farallones and only four in the same year. The four that traveled between the two regions (about 180 nm apart) in the same year were seen between 24 July and 12 August off San Luis and between 21 September and 30 October in the Gulf of the Farallones. Similarly only one individual of 11 that were identified in northern California, about 200 nm north of the Gulf of the Farallones, had been seen previously in the Gulf of the Farallones. This single match was

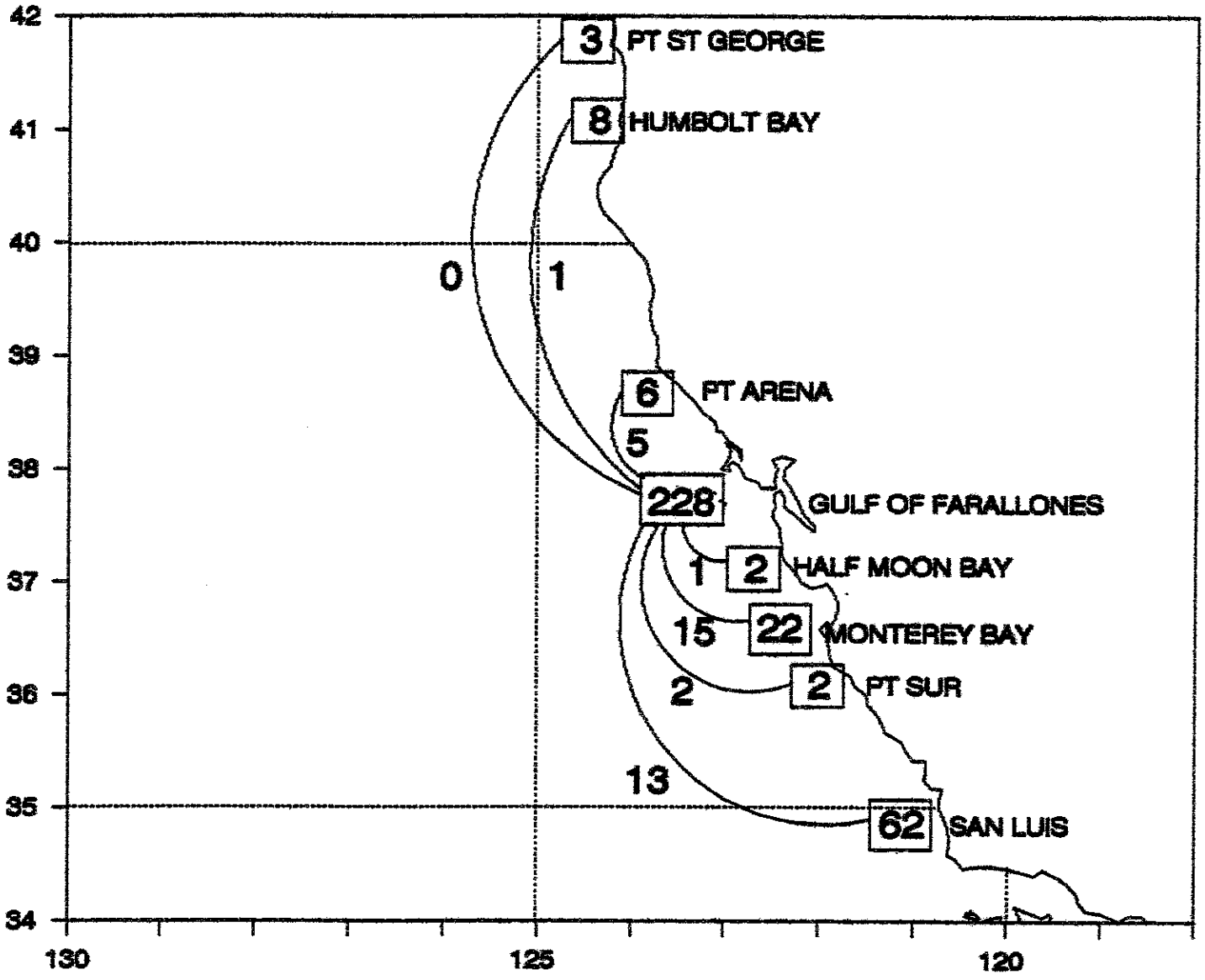


Figure 21. Number of matches (next to lines) found between humpback whales identified in the Gulf of the Farallones and whales identified in other areas of California. Number of humpback whales compared for each area are shown in boxes. See text and Table 3 for details on collaborators and samples compared.

of a whale seen in the Gulf of the Farallones on 28 August 1988 and identified on 10 October 1988 off Humboldt Bay.

The proportion of humpback whales seen in the Gulf of the Farallones that also were found in other areas of California varied with distance. A high proportion of humpback whales identified in central California from Pt. Sur north to Pt. Arena matched with those seen in the Gulf of the Farallones. A much smaller matching rate was seen between the Gulf of the Farallones and locations in southern and northern California though a few individuals travelled between these areas in the same year (Figure 22).

Matches to feeding areas outside of California

North Pacific humpback whales have been identified at feeding grounds in Alaska. Though humpback whales also occur in the summer along the coasts of Oregon, Washington, and British Columbia, only a small number of individuals have been identified from these regions. To date no matches have been found between humpback whales seen in feeding areas in California and those identified at feeding areas in Washington, British Columbia, or Alaska (Figure 23). A few individuals may travel between the Gulf of the Farallones and Alaska, but the lack of matches suggests it is rare.

Matches to breeding/wintering areas in Hawaii, Mexico, and Central America

A few humpback whales from the Gulf of the Farallones winter in Hawaii (Figure 23). Three individuals have been seen in both the Gulf of the Farallones and Hawaii. One of these, a match between the Gulf of the Farallones in 1981 (by M. Webber) and Hawaii in March 1980 and 1982, was reported by Baker et al. (1986). The whale identified in this match was one of the few photographed prior to 1986 in the Gulf of the Farallones not seen in our study. The two other matches to Hawaii were seen in Hawaii in 1980 or 1982 (catalogued by the University of Hawaii in Perry et al. 1988) and seen in the Gulf of the Farallones in both 1987 and 1988.

Matches of humpback whales seen in the Gulf of the Farallones to those seen in Mexico were far more common. In collaboration with Mexican researchers, 23 whales seen in the Gulf of the Farallones have been matched to whales identified in Mexico. Nineteen of these humpback whales were identified in Bahia de Banderas and Isla Isabel, Mexico from December to February of 1983 to 1987 by researchers with the Universidad Nacional Autonoma de Mexico (UNAM, Anelio Aguayo, Carlos Alvarez, and Jorge Urban). Seven matches were to humpback whales identified near the southern tip of Baja in February and March of 1988 and 1989 photographed by Jorge Urban, Ken Balcomb, and co-workers. Movements of whales between Mexico and Gulf

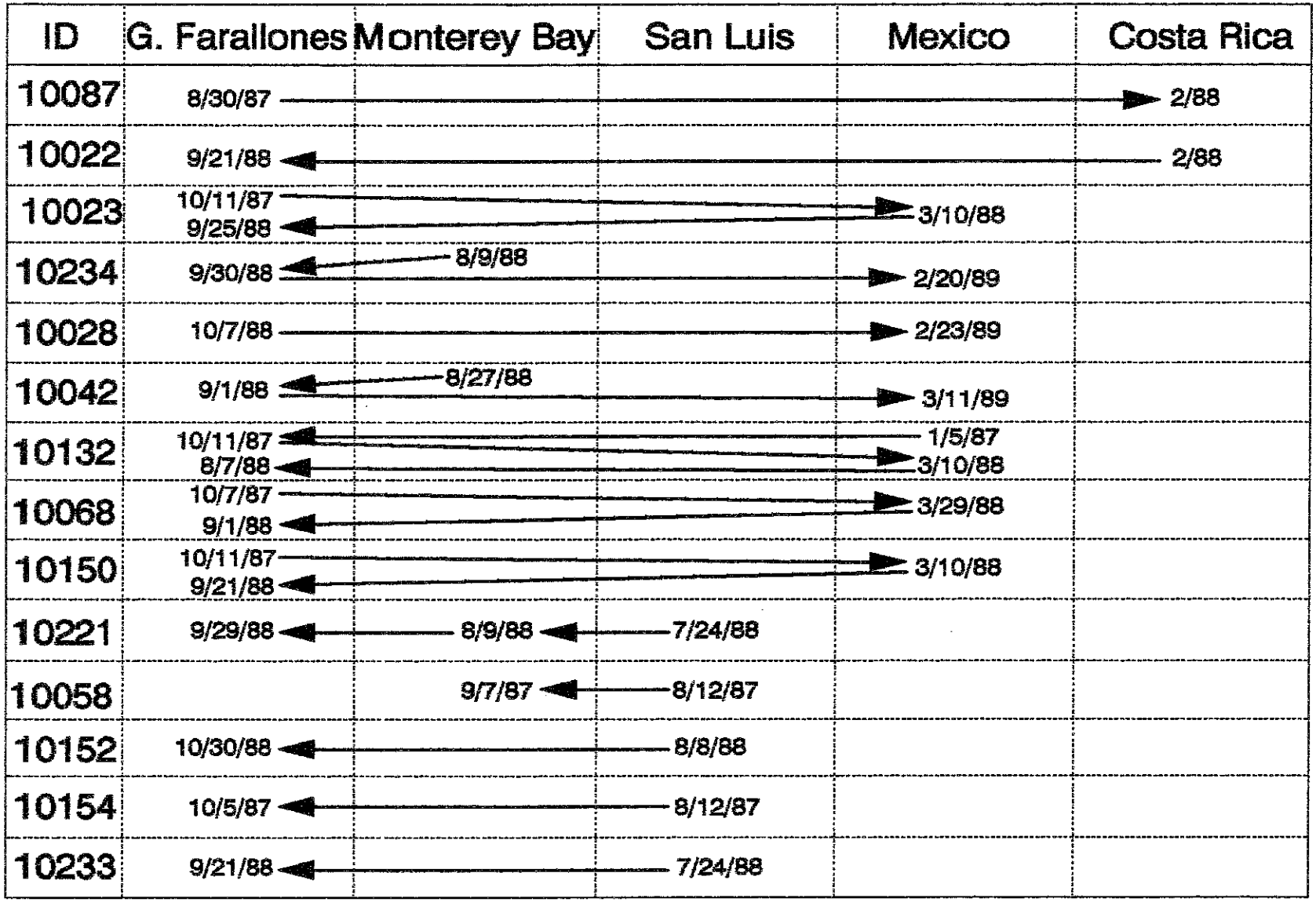


Figure 22. Movements of identified whales between the Gulf of the Farallones and other regions. Only long-range movements occurring over less than 9 months are shown.

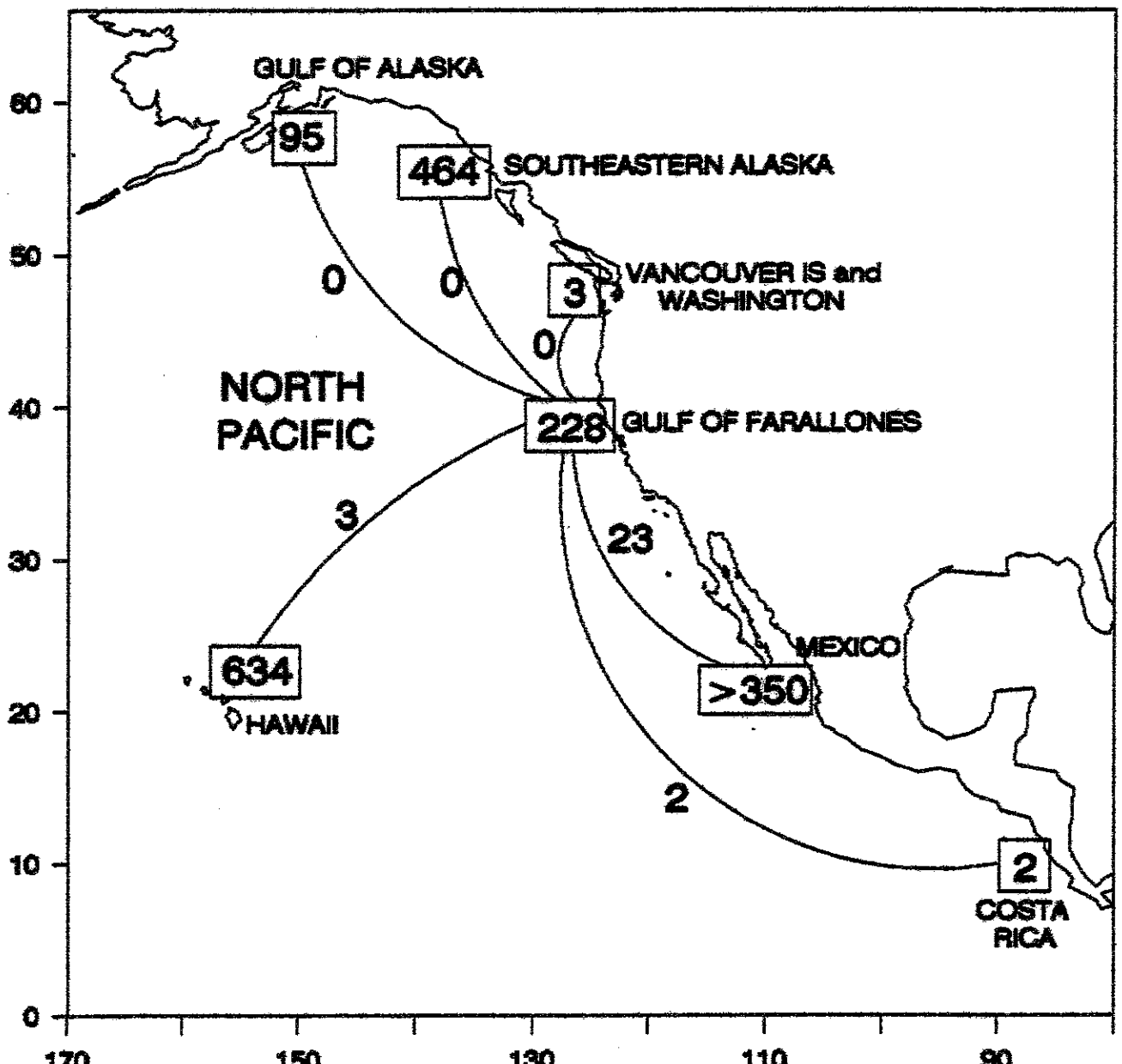


Figure 23. Number of matches (next to lines) found between humpback whales identified in the Gulf of the Farallones and whales identified in other regions. Number of humpback whales compared shown for each region are shown in boxes. See text and Table 3 for details on collaborators and samples compared.

of the Farallones in the same year were noted for seven individuals (Figure 23). One humpback whale (ID# 10132) was seen on 5 January 1987 in Bahia de Banderas, on 11 October 1987 in the Gulf of the Farallones, on 10 March 1988 off southern Baja, and from 7 August to 2 November 1988 in the Gulf of the Farallones. Two other trips from the Farallones to Mexico and back were documented with these matches. Additional matches to Mexico likely exist within our catalog because comparisons between the whales first identified in the Gulf of the Farallones in 1988 and the whales identified in Mexico is not complete.

No matches were found between humpback whales we identified in California and more than 70 individuals identified at the Revillagigedo Archipelago, Mexico, an area over 200 nm south of Baja and 300 nm offshore from mainland Mexico. Given the high rate of matching we found with other areas of Mexico, the lack of matches to the Revillagigedos suggests the whales in this area have a different migratory destination than humpback whales wintering off mainland Mexico and Baja. Matches have been reported between the Revillagigedos and Prince William Sound, Alaska (Baker et al. 1986) and Hawaii (Baker et al. 1986, Darling and McSweeney 1985). Urban and Aguayo (1987) summarize information on the seasonal and spacial distribution of humpback whales in the Mexican Pacific; the seasonal occurrence of humpback whales at the Revillagigedos is similar to the Mexican mainland.

Several matches between regions other than the Gulf of the Farallones were also noted. A fourth match between California and Hawaii (University of Hawaii, Perry et al. 1988) was made for an individual seen in the San Luis area of southern California in 1988 (but not seen to date in the Gulf of the Farallones). Two matches were made between Baja, Mexico (K. Balcomb and J. Urban, and M. Webber from tour boat) and Hawaii (University of Hawaii, Perry et al. 1988) and one match between Baja, Mexico (K. Balcomb and J. Urban) and southeast Alaska (University of Hawaii, Perry et al. 1988).

Two humpback whales photographed by Richard Sears (Mingan Island Cetacean Study) near Isla Canos, Costa Rica in the winter of 1988 were both whales identified in the Gulf of the Farallones. One individual (ID# 10022) was seen in the Farallones in 1986 prior to the sighting off Costa Rica and was seen again about 7 months after the sighting from 21 September to 6 October 1988 in the Gulf of the Farallones. The second individual (ID# 10087) was seen in the Gulf of the Farallones in 1986 and in 1987 (through 30 August) before being seen off Costa Rica. These are the only two individuals identified from off Central America. Despite the small sample, these two individuals may reflect a larger presence of more southern breeding areas off Central America for California humpback whales.

Stock structure

Humpback whales from a different feeding areas congregate on the breeding grounds. Humpbacks migrate from Hawaii to several feeding areas including the western Gulf of Alaska (Baker et al. 1986), Prince William Sound, Alaska (Baker et al. 1986, Darling and McSweeney 1985), southeastern Alaska (Baker et al. 1986, Darling and McSweeney 1985, Darling and Jurasz 1983), British Columbia (Darling and McSweeney 1985), and California (this study, Baker et al. 1986). Similarly, humpback whales that congregate in Mexico migrate to feeding areas in the Prince William Sound (Baker et al. 1986), southeast Alaska (Baker et al. 1986, this study) and central California (Baker et al. 1986, Urban et al. 1987, this study). This demonstrates that humpback whales on each feeding ground migrated to different breeding areas. The rate of interchange between different areas, however, are not equivalent. The relatively low number of matches between California and Hawaii, despite an extensive comparison, indicates this is not a common migration route in contrast to the movement between California and Mexico or Costa Rica, where a much higher proportion of matches was found.

Interchange of humpback whales between different feeding areas occurred to a limited degree. Baker et al. (1985, 1986) reported movements between southeastern Alaska and both Yakutat Bay and Prince William Sound. Darling and McSweeney (1985) reported movement of one whale between British Columbia and southeastern Alaska. We found that the degree of interchange along the California coast varied as function of the distance between the areas. Humpback whales at areas along the central California coast (Pt. Sur to Pt Arena) showed a high rate of matching, while there was a much lower rate of interchange with areas in southern and northern California. No matches have been found to date between the humpback whales along the California coast and the more distant feeding areas in Alaska. Some matches would be expected between these areas because some of the whales that have been matched between Mexico and Alaska probably migrate along the California coast. Humpback whales in the western North Atlantic form discrete feeding areas with little interchange between areas (Katona et al. 1980, Whitehead et al. 1983).

Mark-recapture Population Estimates

Mark-recapture estimates were used to estimate the size of the humpback population in the Gulf of the Farallones. These calculations were based on resighting rates of identified individuals that are conditional on a number of assumptions being met. We found clear evidence that some of these assumptions were violated in our data. An examination of the assumptions, limitations, and results of mark-recapture populations are provided below.

Limitations and assumptions

Limitations and assumptions of mark-recapture calculations are presented by Seber (1982) and their application to using naturally marked whale populations reviewed by Hammond (1986). Both a closed population estimate (two-sample Petersen) for within season estimates and an open population estimate (Jolly-Seber) for between year samples were used in our analyses.

The Petersen estimate is a two sample closed population model. We employed this estimate within-years, treating the first half of each season as the marking sample, and the second half as the recapture sample. Across-year estimates treated each year as a sample. Assumptions for these calculations and evidence we have of their validity are as follows:

1) The population is closed; there is no immigration, emigration, mortality, or birth between the two samples.

Because the within-year samples are taken only a few weeks apart, mortality and natality are not problems. Between-year samples are subject to some bias from mortality and natality but this would be minimal because those rates are low for whales. Immigration and emigration, however, are likely occurring between the sample periods, as evidenced by movements between other feeding areas along the California coast and the seasonal shifts in distributions of animals within the study area. The magnitude of the immigration and emigration appeared to be limited, because the resighting rates of individual whales were high and the same individuals were seen throughout the study period. Violations of this assumption would result in an overestimate of the number of humpbacks in the study area at the time of either sample. This estimate, however, underestimates the size of the entire humpback whale population because we have sampled only one geographic area.

2) All animals have the same probability of being "caught" in the first sample.

We found some evidence of violation of this assumption. Calves did not fluke as often as adult animals, as has been shown in other areas (Kaufman et al. 1987, Perkins et al. 1985). The rate at which whales fluked (tested for 1987) varied significantly among individuals (ANOVA, $p<0.05$), though the fluking rate did not correlate with the number of times an individual was seen ($n=141$, $p>0.05$). The effect of

the difference in fluking rate therefore was not likely a major source of bias in the calculations. The existence of a "resident" subgroup of whales more likely to be seen within and across years (discussed previously) indicated heterogeneity of capture probability and therefore a violation of this assumption. An unequal capture probability would result in an underestimate of population size.

3) Marking does not affect the catchability of an animals.

We saw no subjective evidence that animals altered their behavior to avoid capture later in the season.

4) The second sample is a random sample.

Our vessel surveys were not random and so this assumption is only met if animals have mixed and redistributed randomly between the two samples. In 1987 and 1988 there was a two to three week gap between the two samples. Whale distribution in all three years was different between the two sessions. Both these factors would contribute to the second sample being random. Non-random selection of whales in the second sample could result in over or underestimates of population size.

5) All marks are permanent.

Changes in marks have been seen in the flukes of individual humpback whales in our study as well as others (Carlson and Mayo 1983). These changes occurred over one or more years of time and generally were not dramatic enough to prevent identification.

6) All marks (matches) are identified and recorded.

A few matches of whales with dark indistinct flukes may have been missed. Several matches among catalogued whales in 1986 and 1987 catalogs were not discovered until one or two years later. It is possible that some internal matches may still be unrecorded, though the number is likely very small. Failure to identify matches would result in overestimates of population size.

The Jolly-Seber open-population model has many of the same assumptions as explained above for the Petersen closed-population model. The estimate using the Jolly-Seber model treated each year as a sample. The closed population assumption is no longer required, however, emigration, should it

occur, is assumed to be permanent. This is not the case, because some animals appeared to leave the study area for one year and return the next.

Single-year estimates

Within year population estimates were made for all three years using the Petersen estimate (Table 11). Estimates of the humpback population in the Gulf of the Farallones in each year ranged from 109 to 211. The number of whales estimated was lowest in 1986, numbering just over 100 whales. Estimates for 1987 and 1988 were 166 and 211, respectively.

In each year the mark-recapture population estimates are only slightly higher than the number of individuals identified that year. This is consistent with our conclusion that we identified a majority of the individuals present each year. The cumulative number of whales identified in all three years, 224, is higher than any of the single year estimates. The estimates generally increased from 1986 to 1988, however, this should be viewed with some caution. The 1986 estimate was lower than for 1987 and 1988. The timing of the effort was different in 1986 than 1987 and 1988; effort ended earlier (mid-September) in 1986 and was not divided into two separate sessions. The shorter time period where whales were sampled and the lack of clear division in the sampling periods may have biased the estimate downward for 1986.

Multiple-year estimates

Between-year Petersen estimates calculated using each year as a sample yielded higher estimates than the within-year estimates (Table 11). These estimates are based on the premise that humpback whales return to the same feeding areas in different years, and therefore simulate a closed population. Estimates were 226 and 253 for 1986-87 and 1987-88, respectively. The only within-year calculation that yielded a similar estimate of over 200 whales was for 1988.

The number of whales present using the Jolly-Seber estimate from resightings in multiple years yielded similar results to some of the Petersen estimates. The Jolly-Seber estimate cannot be calculated for the first and last sample in a series. Because data from only three years is available (1986-88), an estimate can only be made for 1987. The estimate for this period was 188 whales.

The various mark-recapture estimates may not reflect the true population size. Several assumptions of these calculations were violated and biased the resulting estimates. Estimating the population within a

Table 11. Mark-recapture population estimates using within-year resightings in different time periods. Sampling was without replacement and counted individuals only once in the second sample and used the Chapman modification of the Petersen estimate. See text for limitations and assumptions of these calculations.

Year	Cut-off date for periods	Period 1 marked	Period 2 # seen	Number matching	Esti-mate	Var-iance	95% C.I. Low	95% C.I. High
Within-year estimates								
1986	1 Sept	68	61	38	109	49	95	123
1987	15 Sept	120	75	54	166	75	149	183
1988	15 Sept	38	135	24	211	507	167	255
Between-year estimates								
1986-87	-	90	141	56	226	198	198	254
1987-88	-	141	135	75	253	172	227	279

specific geographic region (like the marine sanctuary) was also not possible because the whales moved in and out of this area during the season. The above estimates, however, provide some indication of the number of animals present during a single season and rough estimates of the number present over multiple years. They do not serve as an accurate estimate of the overall humpback population in central California.

Aerial Line-transect Estimates

Estimates of humpback whale numbers from aerial line-transect flights were possible for one flight each year. The line-transect estimates incorporated an adjustment for whales that would have been missed (even on the transect line) because they were underwater (see Methods).

The number of humpback whales estimated from aerial line-transects (Table 12) were all lower than the population size estimated from mark-recapture calculations. As in the mark-recapture estimates, the estimate for 1986 (60) was lower than for 1987 (90) and 1988 (109). These estimates were also lower than the number of individuals identified each year. The lower estimates from the line-transect flights suggests only a portion of the humpback whale population was present in the study area at the time of the flights. This was also apparent from sightings of humpback whales outside the Gulf of the Farallones concurrent with our research. For example, on 17 August 1986, we encountered large numbers of humpback whales in the study area while on the same day 36 humpback whales were sighted near Pioneer Canyon southwest of the study area (T. Dohl, pers. comm.).

Comparison of Population Estimates

Population estimates for humpback whales in the Gulf of the Farallones in 1982 were higher than we found in 1986 to 1988. Dohl et al. (1983) estimated 346 humpback whales in the Farallon Basin in September 1982, the time period when they found the highest numbers present. The same study reported a mean estimate of 338 humpback whales for the entire California coast during the period of peak occupancy (August-November). Either the entire California humpback population was present in the Gulf of the Farallones in September 1982 or one of the two estimates above was in error. Our survey results indicated much lower numbers of whales present in the Gulf of the Farallones than found in these earlier surveys.

We propose an hypothesis to explain the divergence in some of the population estimates we found and those reported previously. Humpback whales form feeding aggregations at a number of locations along the California coast. Whales tend to return to the same region to feed in

Table 12. 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 km	SE density	Area[2] surv. km	Estim. groups	Group size	% sub-merged[3]	Estim. number
16 Sept 86	4	222	.28	.0062	.0020	1,646	10.2	2.18	.37	60
21 Aug 87	11	624	.28	.0033	.00089	4,623	15.2	2.18	.37	90
26 Sept 88	46	350	.28	.0047	.0014	2,596	12.2	2.18	.37	72
26 Sept 88	46	350	.28	.0047	.0014	3,929	18.5	2.18	.37	109

[1] Number seen likely includes some duplicate animals seen from adjacent survey lines.

[2] Because study area was surveyed systematically, only area covered by survey lines is used, except in second estimate for 25 Sept 1988 where portion of study area where whales were seen in previous day (but could not be surveyed due to fog) is included as an alternate estimate.

[3] See Methods for calculation.

successive years, but there is also some movement among these locations. Presumably, the movement among locations was in response to prey availability in the different areas. During the early 1980s, when warmer oceanographic conditions were present along the California coast, whales concentrated in the Gulf of the Farallones. During other "normal" years humpback whales were distributed among a number of feeding locations. The total size of the humpback population at all feeding areas along the California coast exceeds 284 (the number of individuals already identified in the Gulf of the Farallones and, with fairly limited effort, in other areas). The number returning to the Gulf of the Farallones in the late summer and fall of any year, however, appeared to be 100-200.

Other Marine Mammals

In addition to humpback whales, sixteen other species of marine mammals were encountered during surveys in the Gulf of the Farallones between 1986 and 1988. Sightings of these species are summarized here. Figures of the distribution of sightings are given for most species; caution should be used in interpreting differences that could be due to shifts in study effort. Additional research conducted on blue whales in conjunction with this study was reported separately (Calambokidis et al. 1989). Although not a marine mammal, sightings of leatherback turtles are also reported here.

Blue whale

Over 700 sightings of 1,315 blue whales (Balaenoptera musculus) were made from boat and aerial surveys in the Gulf of the Farallones region between 1986 and 1988 (Calambokidis et al. 1989). Increasing numbers were seen in each season. The distribution and timing of blue whale sightings were somewhat variable among years; peak numbers were generally present in August to early October. A total of 179 individual blue whales were photographically identified in the Gulf of the Farallones from 1986 to 1988. Most individuals were identified in 1988 (101) and 1987 (75).

Estimates of the number of blue whales that occurred in the Gulf of the Farallones were possible from photoidentification data and from aerial line-transect flights (Calambokidis et al. 1989). A single line-transect flight conducted on 26 September 1988 provided area-dependent estimates of 160 and 250 whales in the study area, the highest numbers that we saw during the study. Mark-recapture estimates for 1988, despite the violation of a number of assumptions, yielded similar estimates of about 200 animals, depending on the time period and sides of whales used in these

calculations. Population estimates in 1986 and 1987 indicated lower number of blue whales than in 1988.

Fin whale

Seven sightings of seven fin whales (Balaenoptera physalus) were made during vessel and aerial surveys between 1986 and 1988. Five of the seven sightings were in August and September 1988, one was in August 1986, and one in August 1987. All but two of the sightings were between Point Reyes and Bodega Head, between 6and 8 nm offshore; one sighting was at Cordell Bank in 1987 and one at 22 nm west of Half Moon Bay (south of the sanctuary)(Figure 24). Fin whales were always observed singly, except on one occasion on 24 September 1988 when a fin whale as seen surface feeding with blue whales as a group.

Sei whale

Eleven sightings of 11 sei whales (Balaenoptera borealis) were made during vessel and aerial surveys between 1986 and 1988. Five sightings were in September 1986, and all others were between August and October 1988; we saw no sei whales in 1987. All sightings were made between Point Reyes and Bodega Canyon (Figure 25).

The species identification of an individual whale that we report here as a sei whale is uncertain. Experienced researchers disagreed on whether this animal is a sei or fin whale. Though photoidentification, it has been seen in 1984 and 1987 by researchers working with the Oceanic Society and we have identified it once in 1986 and on four occasions in 1988. In both 1986 and 1988, we observed this whale with blue whales swimming and surface feeding in close association.

Minke whale

Twenty-nine sightings of 31 minke whales (Balaenoptera acutorostrata) were made during vessel and aerial surveys between 1986 and 1988. In 1986 and 1987, most of the sightings were in August (10 of 11 sightings in 1986 and 10 of 12 sightings in 1987); in 1988, minke whales were seen throughout the season (2 sightings in August, 2 sightings in September, 2 sightings in October).

Sightings were distributed from south of the Southeast Farallon Islands to Bodega Head (Figure 26). The average water depth of sightings was 325 ft (n=15 for sightings made by vessels with depth sounders, s.d.=72). One sighting was made close to shore off Chimney Rock in Drake's

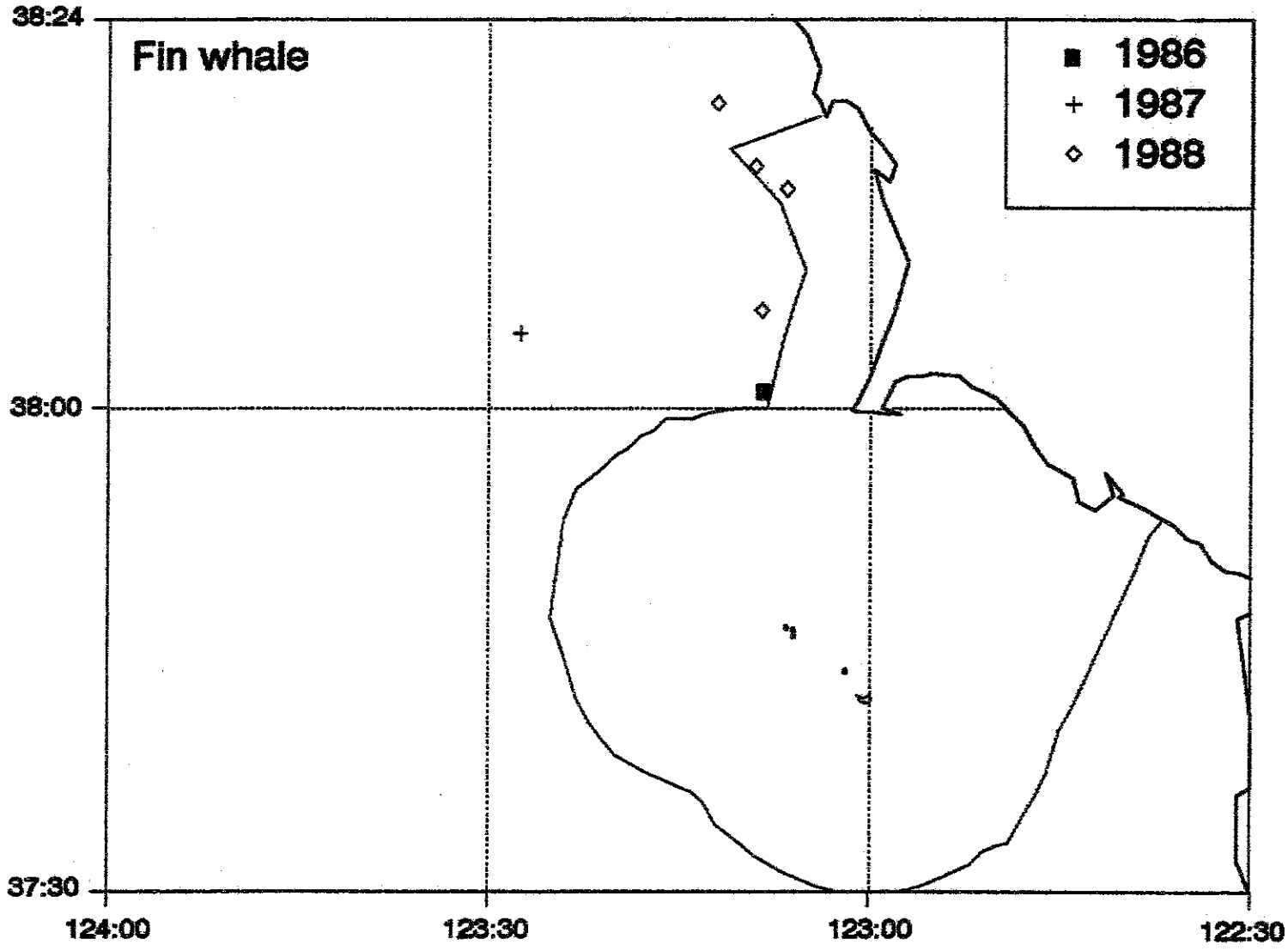


Figure 24. Location of fin whale sightings made from vessels and aircraft by year.

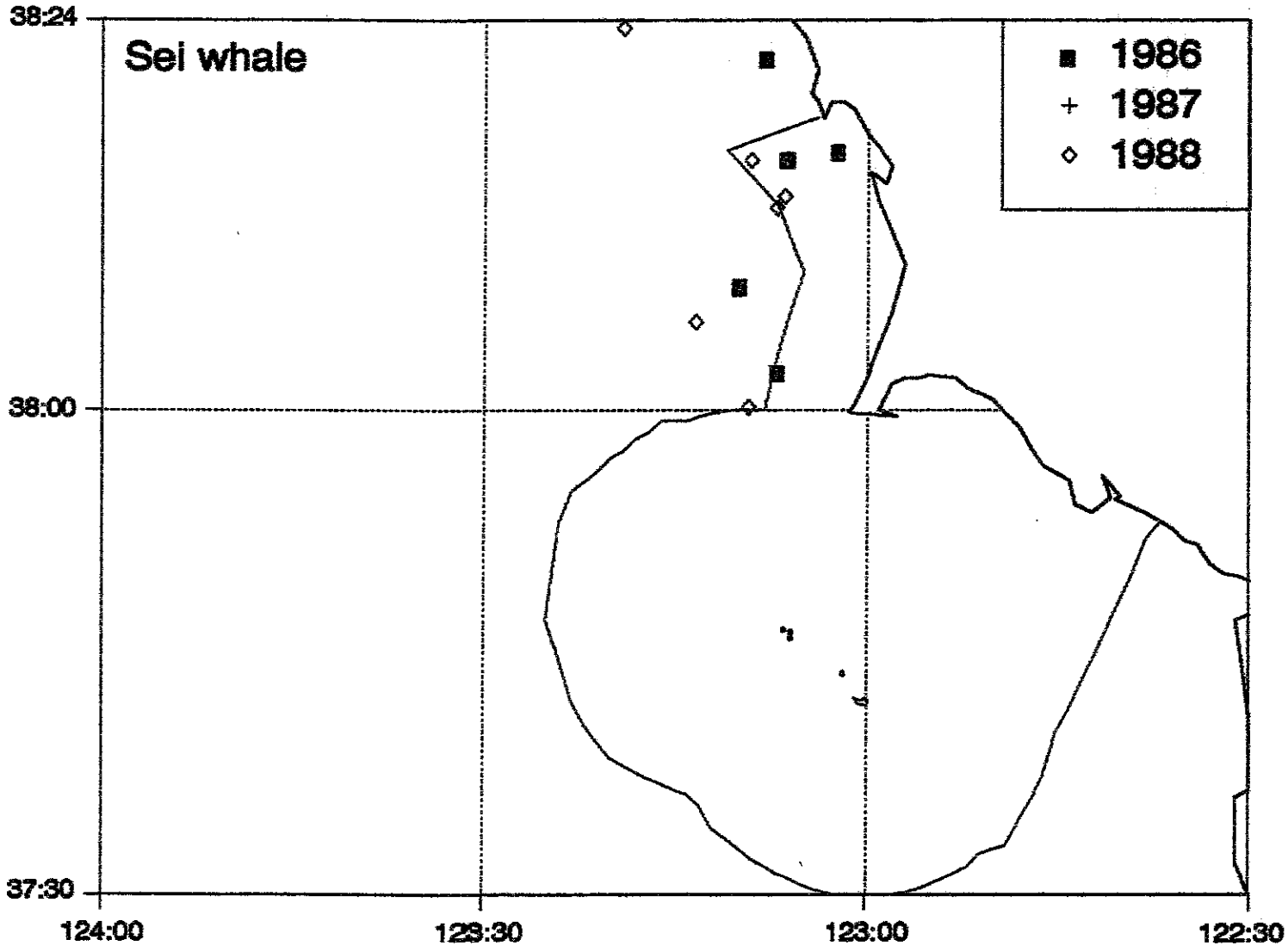


Figure 25. Location of sei whale sightings made from vessels and aircraft by year.

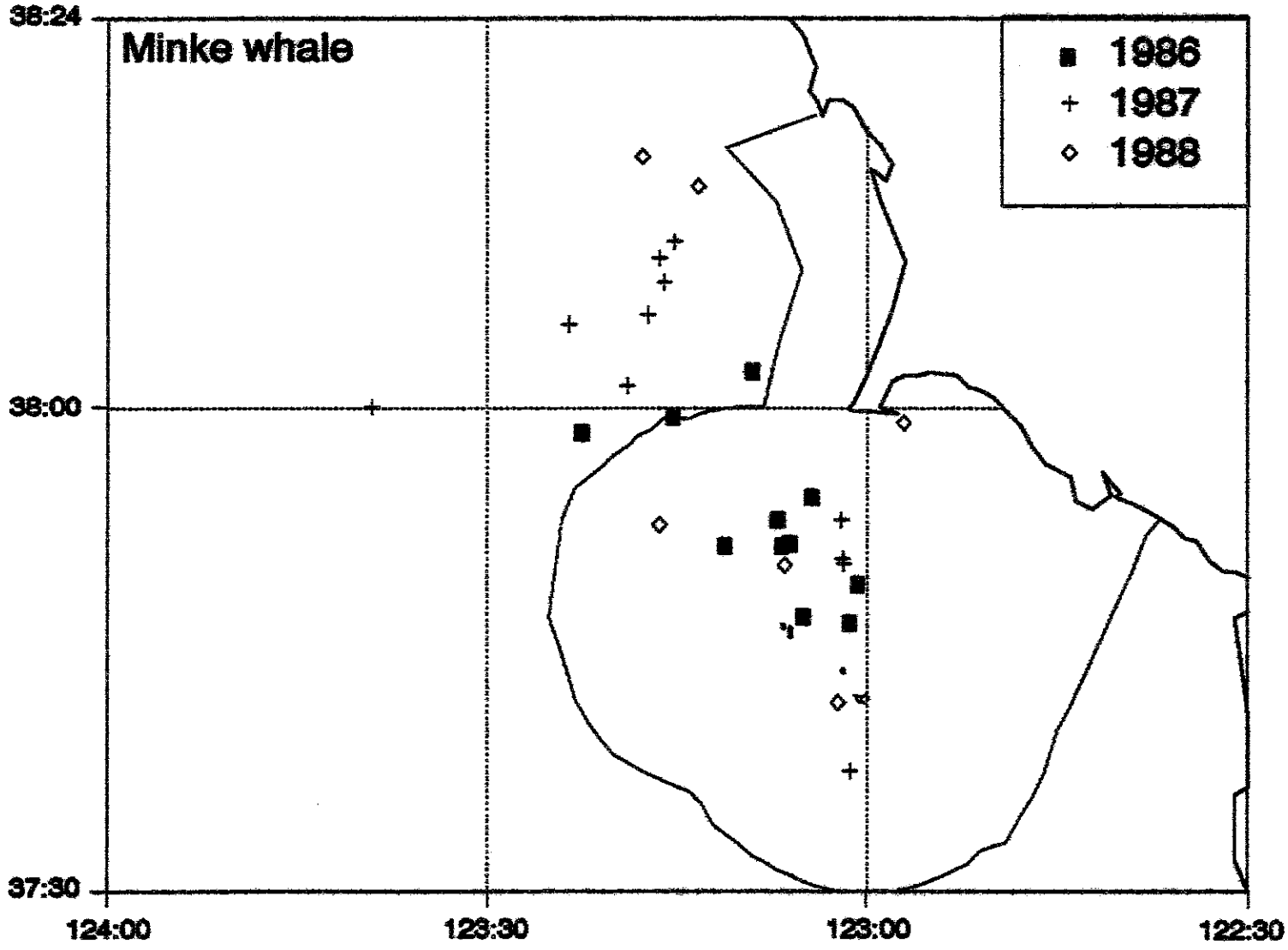


Figure 26. Location of minke whale sightings made from vessels and aircraft by year.

Bay on 28 August 1988; one sighting was made far offshore, 11 nm west of Cordell Bank. Some milling and feeding behavior was observed, however, the primary behavior seen was slow travel. A minke whales seen off Bodega Head on 22 August 1988 was an estimated 4 m long and appeared to be a recently weaned calf.

Baird's beaked whale

One sighting of two Baird's beaked whales (Berardius bairdii) was made during our study during an aerial survey on 9 October 1987 just outside the southwestern edge of the sanctuary. This sighting was at a water depth of 7,500 feet, consistent with this species' deep water habitat (Leatherwood and Reeves 1983).

Killer whale

Eight sightings of 25 killer whales (Orcinus orca) were made during vessel and aerial surveys between 1986 and 1988. All of our sightings were in 1986 and 1987. We had no sightings in 1988, however, we did receive a number of reports of killer whales off Point Reyes and the Farallon Islands in 1988 from fishermen and other researchers. In 1986, whales were seen in the vicinity of Point Reyes; in 1987, most sightings were near the Bodega Canyon (Figure 27). Ten killer whales were seen on 7 September 1987, southwest of the Farallon Islands; all other sightings were of groups of two or three animals.

Risso's dolphin

Six sightings of 112 Risso's dolphins (Grampus griseus) were made during vessel and aerial surveys between 1986 and 1988 (Figure 28). In 1986, animals were seen in August and September on two occasions; in 1987, two sightings were in September and October; and in 1988, two sightings were in October. Sighting locations included both deep and shallow waters. Group size ranged from 1 to 40 animals.

Pacific white-sided dolphin

Forty sightings of 2474 Pacific white-sided dolphin (Lagenorhynchus obliquidens) were made during vessel and aerial surveys between 1986 and 1988. Most sightings were in 1987 (32 of 40); there were five sightings in 1986 and three in 1988. Sightings in 1987 occurred primarily at Cordell Bank, between the bank and Bodega Bay, and north of the Bodega Canyon (Figure 29). There were a number of sightings to the south and west of the Farallon Islands. Average water depth of sightings was 585 ft (n=16,

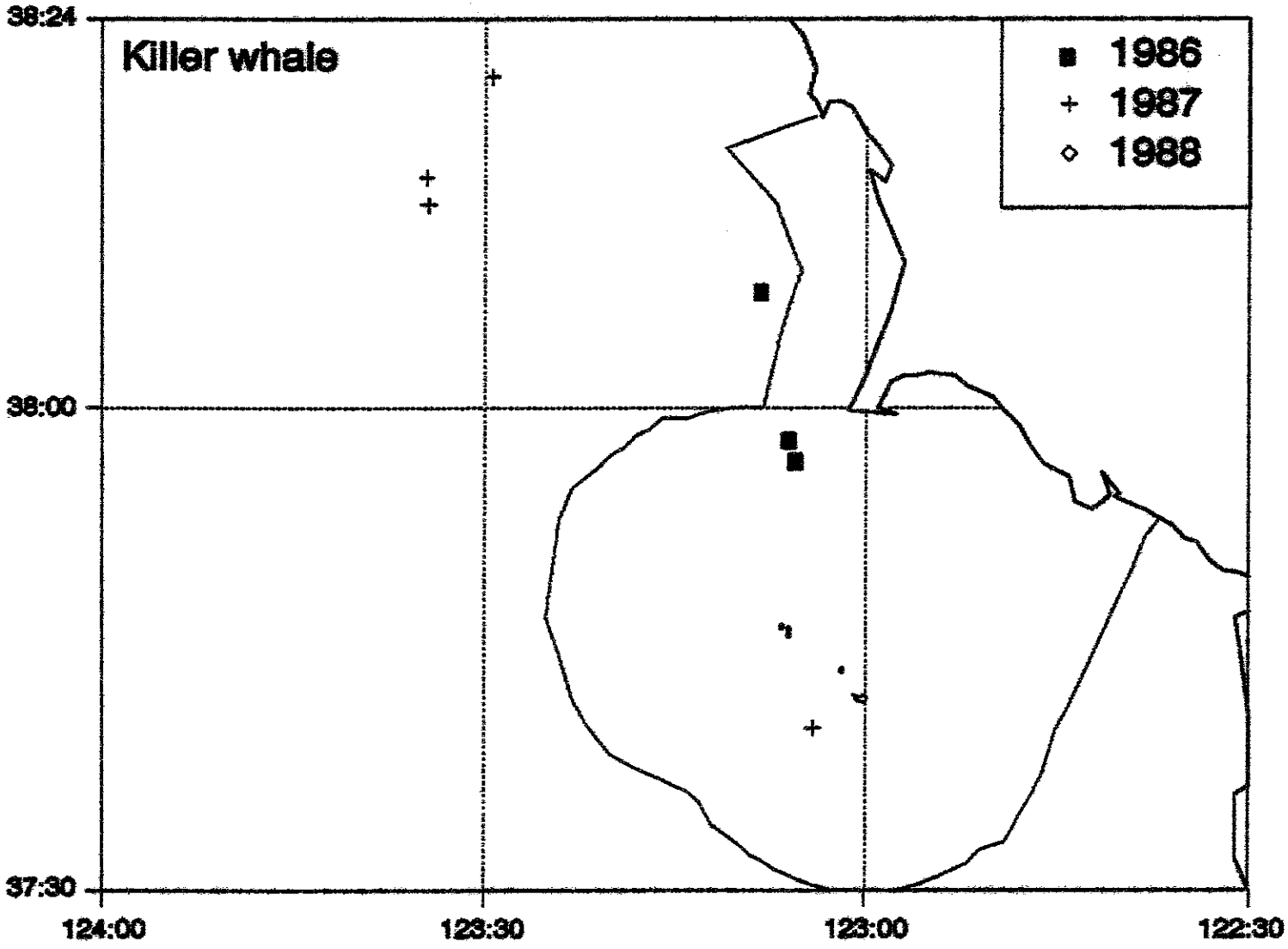


Figure 27. Location of killer whale sightings made from vessels and aircraft by year.

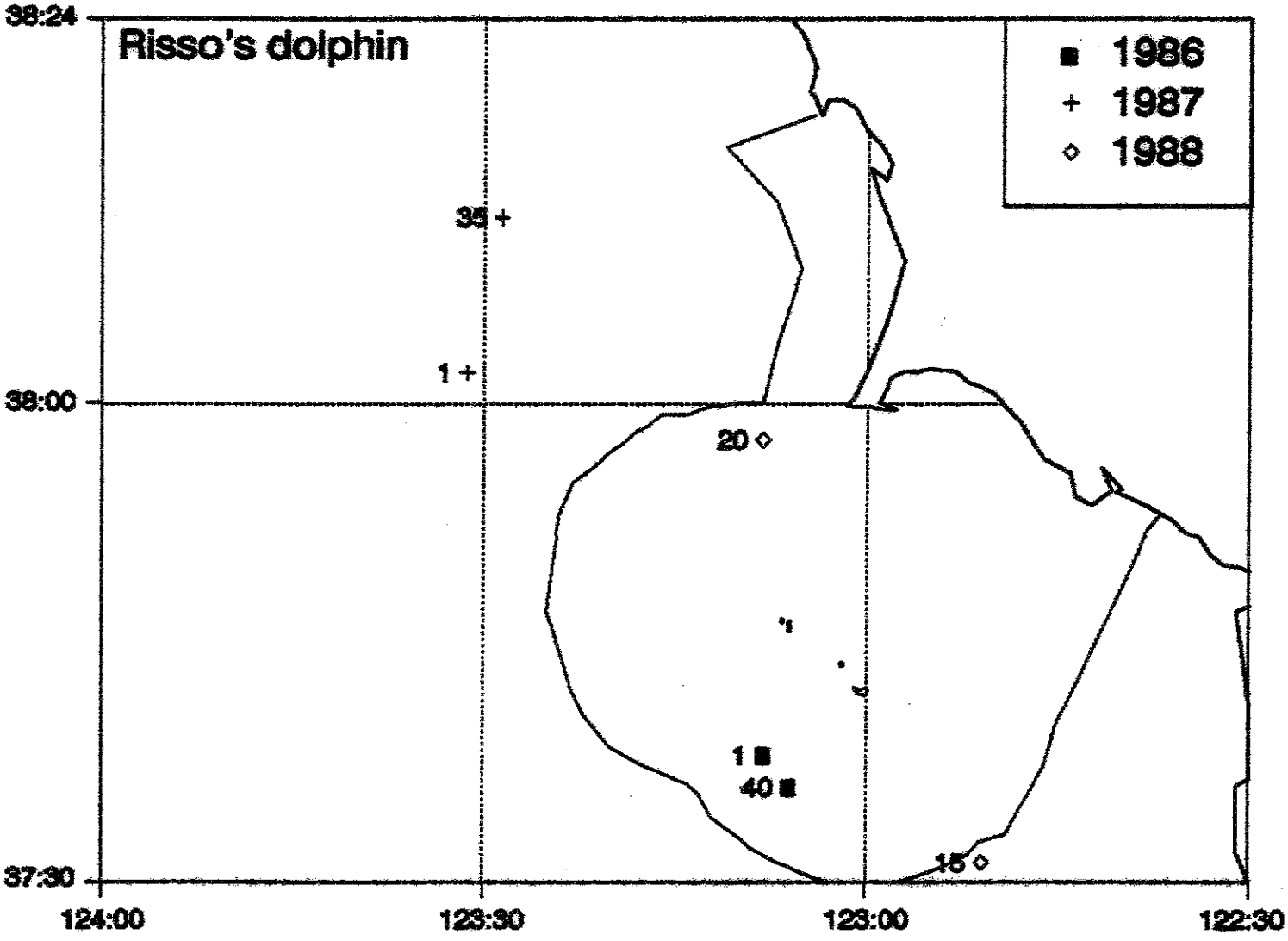


Figure 28. Location of Risso's dolphin sightings made from vessels and aircraft by year. Group size is indicated.

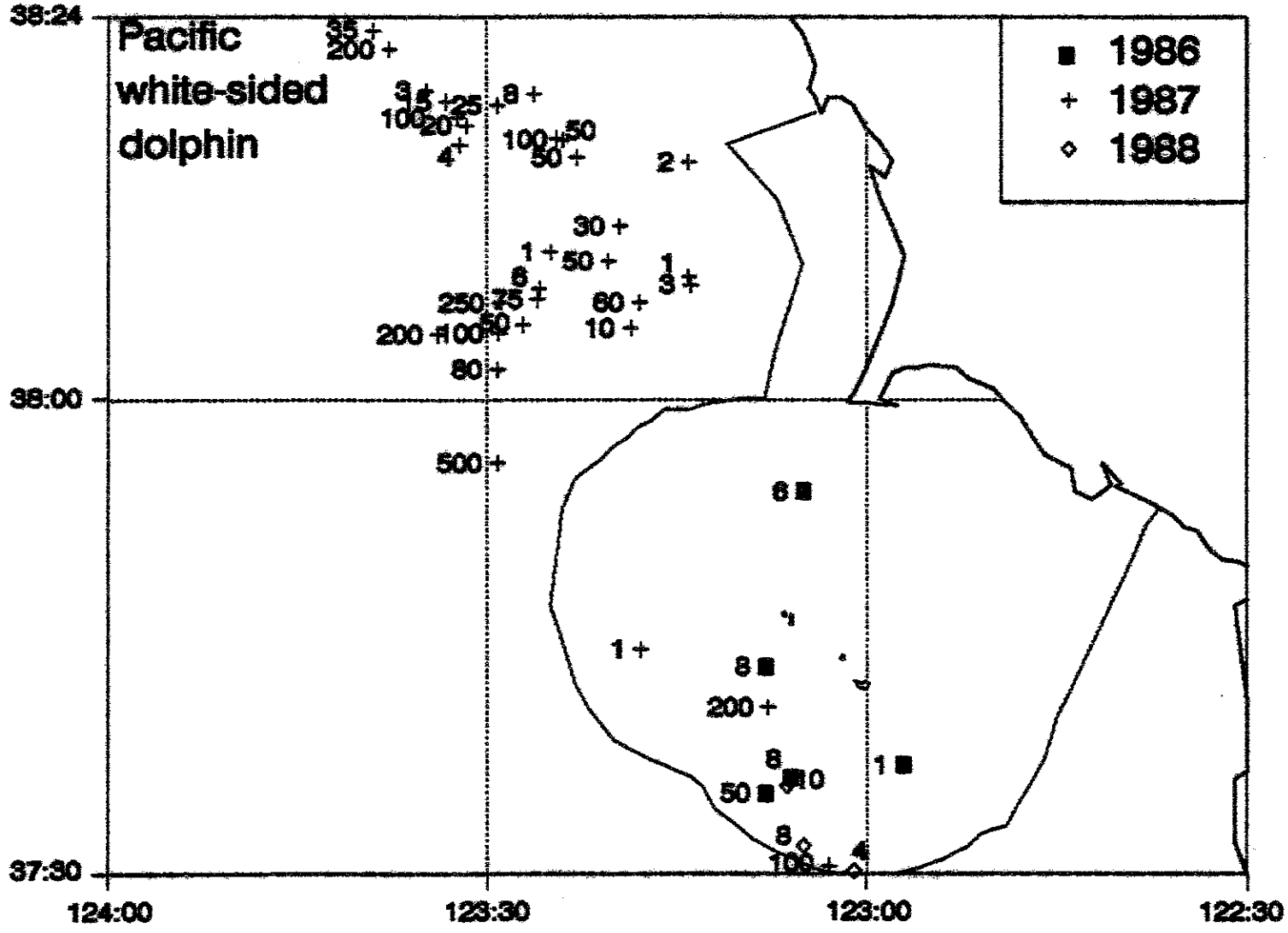


Figure 29. Location of Pacific white-sided dolphin sightings made from vessels and aircraft by year. Group size is indicated.

s.d.=267). Group size ranged between 1 and 500 animals and averaged 62 (s.d.=95), five sightings were of groups of 200 or more porpoise.

Northern right whale dolphin

Nine sightings of 454 northern right whale dolphins (Lissodelphis borealis) were made during vessel and aerial surveys during the study, all were in 1987. Most sightings were in October; there was one sighting in August and one in September. All sightings were made west of the Gulf of the Farallones sanctuary, near Cordell Bank and the Bodega Canyon (Figure 30). Average water depth of sightings was 774 ft (n=5, s.d.=214). Group size ranged between 3 and 250 animals and averaged 50 (s.d.=77). Northern right whale dolphins were observed in groups with Pacific white-sided dolphins in all but one sighting.

Harbor porpoise

Sixty-one sightings of 124 harbor porpoise (Phocoena phocoena) were made during vessel and aerial surveys between 1986 and 1988. There were 22 sightings in 1986, 17 in 1987, and 22 in 1988. Harbor porpoise were seen in every month sampled during the study (except for the one day of effort in November); there were 15 sightings were in July, 12 in August, 12 in September, and 22 in October. Calves were seen in August 1986 and October 1988.

Most of the sightings were nearshore, off the entrance to San Francisco Bay and off Point Reyes and Bodega Bay (Figure 31). However, there were some sightings further offshore; there were several sightings near the Bodega Canyon, one near Fanny Shoal, and one 11 nm west of Point Reyes. The average depth for the 21 sightings with depth data was 231 feet (s.d.=103). The proportion of offshore sightings is biased upwards by our extensive effort in offshore waters where harbor porpoise are not common. Additionally, we had one sighting of three harbor porpoise inside San Francisco Bay (off Point Cavallo) when the Noctilio leaving harbor on 28 August 1988. Average group size was 2 (s.d.=1.3) and ranged from 1 to 6 animals.

Dall's porpoise

There were 177 sightings of 782 Dall's porpoise (Phocoenoides dalli) seen during vessel and aerial surveys between 1986 and 1988. There were 59 sightings in 1986, 49 sightings in 1987, and 69 sightings in 1988. Dall's porpoise were seen in every month sampled during the study; there were 23 sightings were in July, 55 in August, 41 in September, 55 in October, and 3

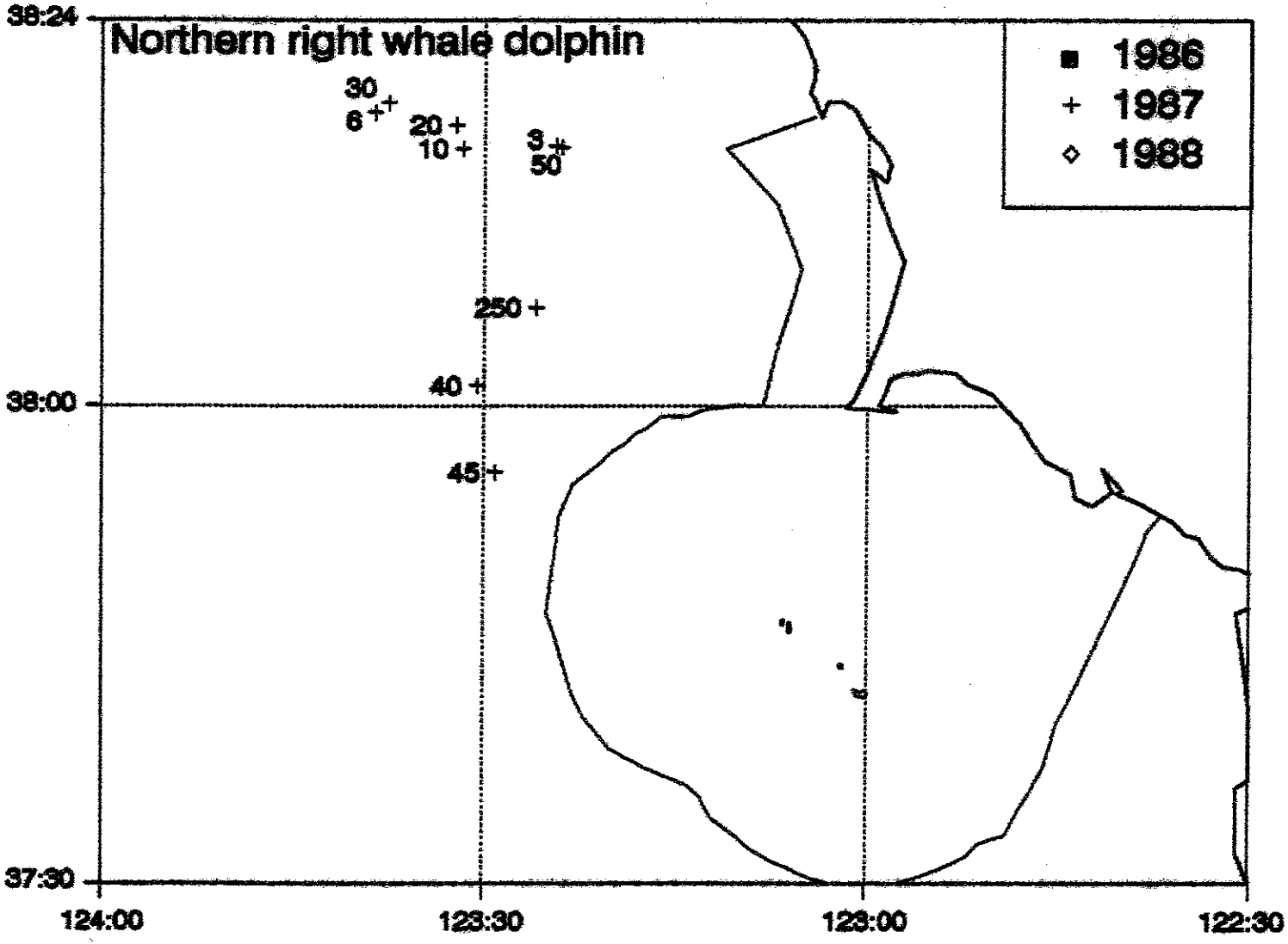


Figure 30. Location of northern right whale dolphin sightings made from vessels and aircraft by year. Group size is indicated.

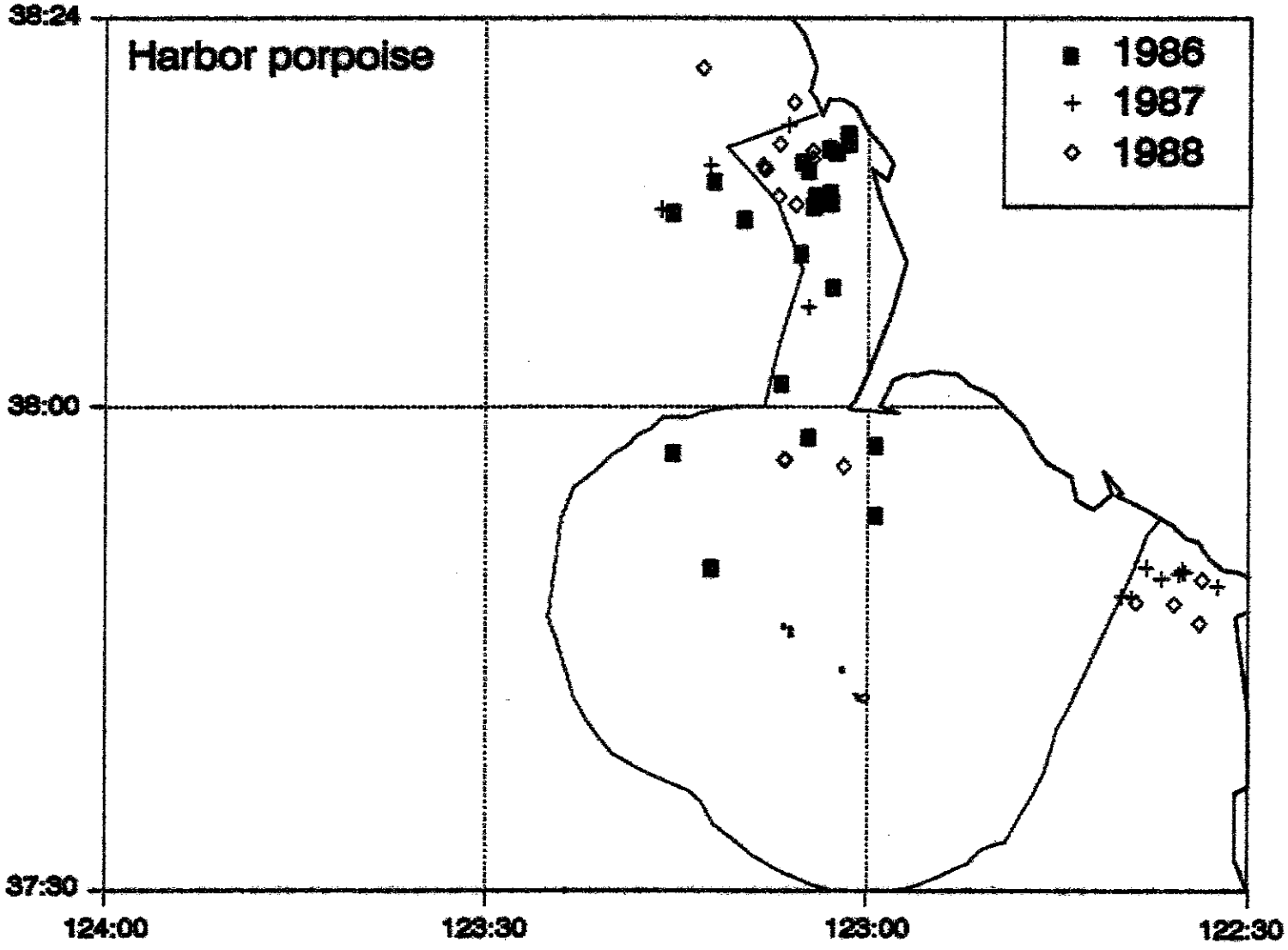


Figure 31. Location of harbor porpoise sightings made from vessels and aircraft by year.

in November (one day of effort). Average water depth of sightings was 430 ft (n=87, s.d.=211). One calf was seen in August 1986.

Sightings were distributed from south of the Farallon Islands to north of Bodega Canyon (Figure 32). Many groups were seen in 1986 and 1987 near Cordell Bank. Similarly, when the sighting density of Dall's porpoise by vessel effort are examined (Figure 33), highest densities of porpoise per hour were seen just west of Cordell Bank, and higher densities seen near Cordell Bank, Bodega Canyon, and west of the Farallon Islands. Average group size was 4 (s.d.=3.9) and ranged from 1 to 30 animals.

Northern sea lion

Fifty-five sightings of 284 northern (or Steller) sea lions (Eumetopias jubatas) were made during vessel and aerial surveys between 1986 and 1988 (Figure 34). Sightings were made throughout the study period, in all months and years. Animals were observed hauled out at Southeast Farallon Island, on Bodega Rock in Bodega Bay, on the Fanny Shoal Buoy, and the NOAA weather buoy 12 nm west-southwest of Bodega Head.

California sea lion

California sea lions were the most commonly seen pinniped in the study region. There were 307 sightings of 5,530 California sea lions (Zalophus californianus) made during vessel and aerial surveys between 1986 and 1988 (Figure 35). Sightings were made throughout the study period, in all months and years. As with Steller sea lions, animals were observed hauled out at Southeast Farallon Island, on Bodega Rock in Bodega Bay, on the Fanny Shoal Buoy, and the NOAA weather buoy 12 nm west-southwest of Bodega Head. In the water, single animals were seen but sometimes they were observed offshore in dense aggregations.

Northern fur seal

Six sightings of 7 northern fur seals (Callorhinus ursinus) were made during vessel and aerial surveys between 1986 and 1988. Most sightings were in 1987 (5 of 6), between 18 August and 10 October in the area between Cordell Bank and Bodega Bay; the one sighting in 1988 was on 21 August was 6 nm west of Point Reyes (Figure 36). Because these small pinnipeds were often alone offshore, many were likely missed and not recorded during surveys.

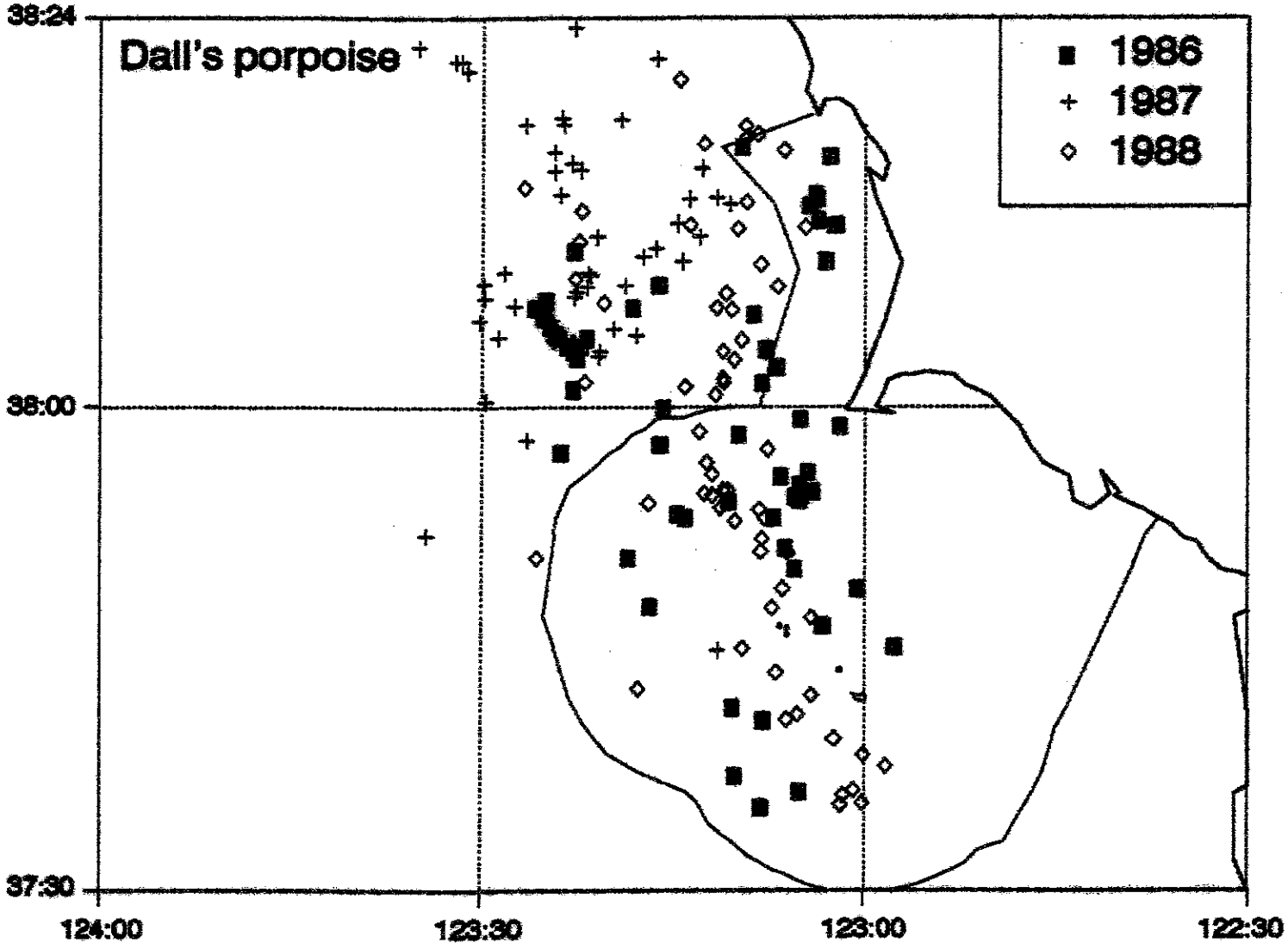


Figure 32. Location of Dall's porpoise sightings made from vessels and aircraft by year.

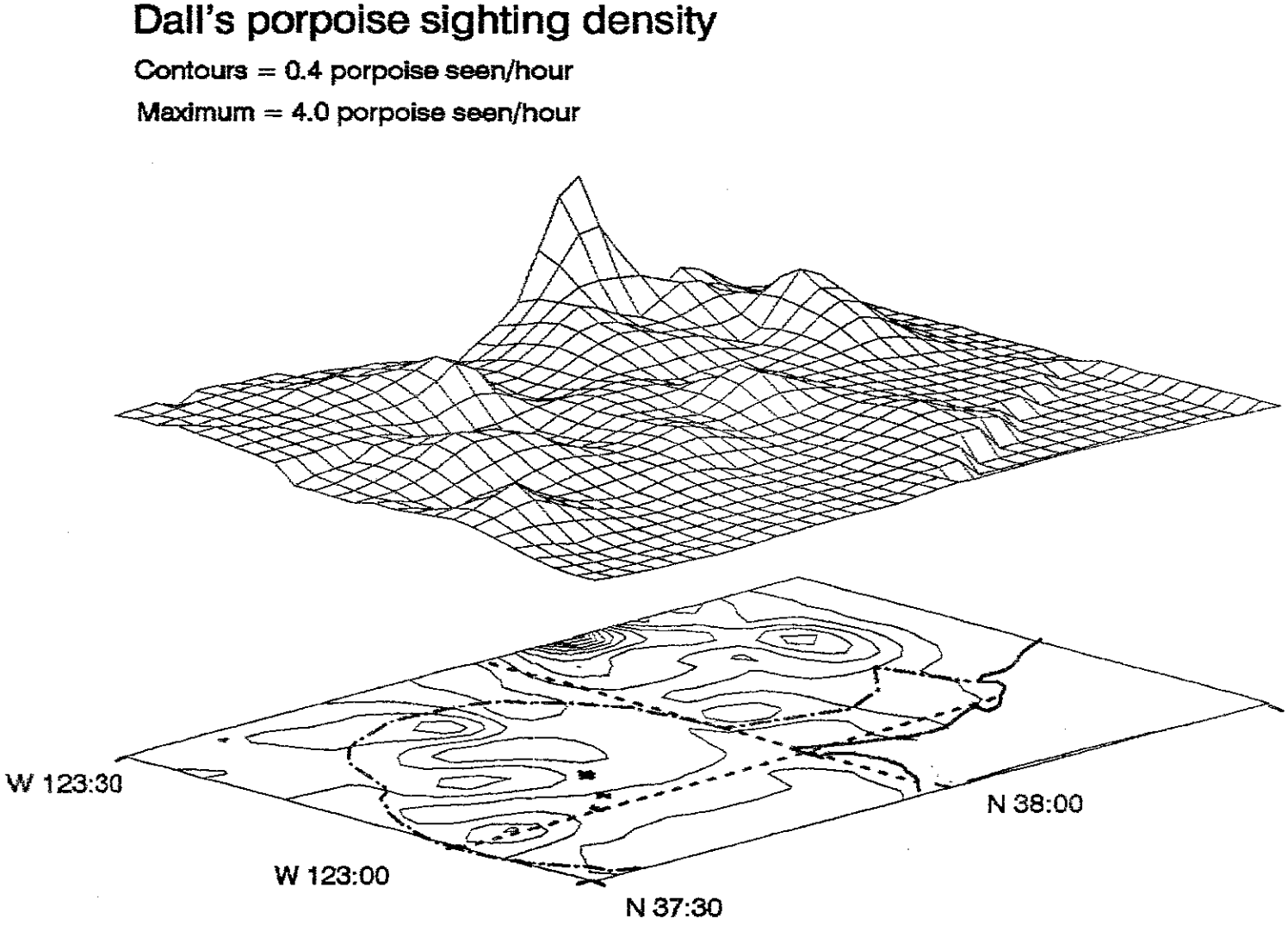


Figure 33. Effort-corrected sighting rate of Dall's porpoise (number per survey hour) seen from vessel surveys for 1986-1988. Data are summarized using cells (5 min latitude by 5 min longitude) with more than three hours of effort. Contours are smoothed by averaging neighboring cells.

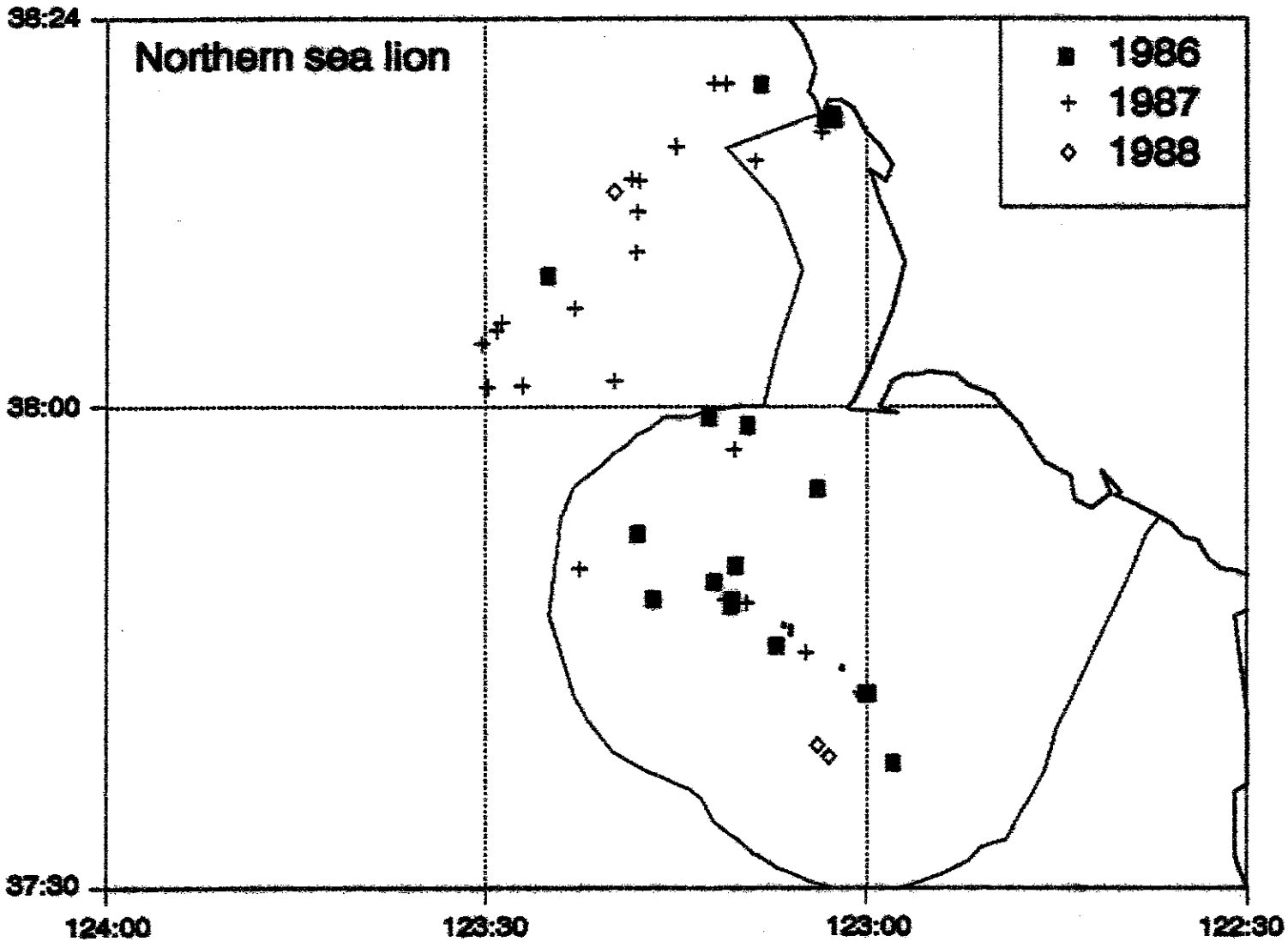


Figure 34. Location of northern (or Steller) sea lion sightings made from vessels and aircraft by year.

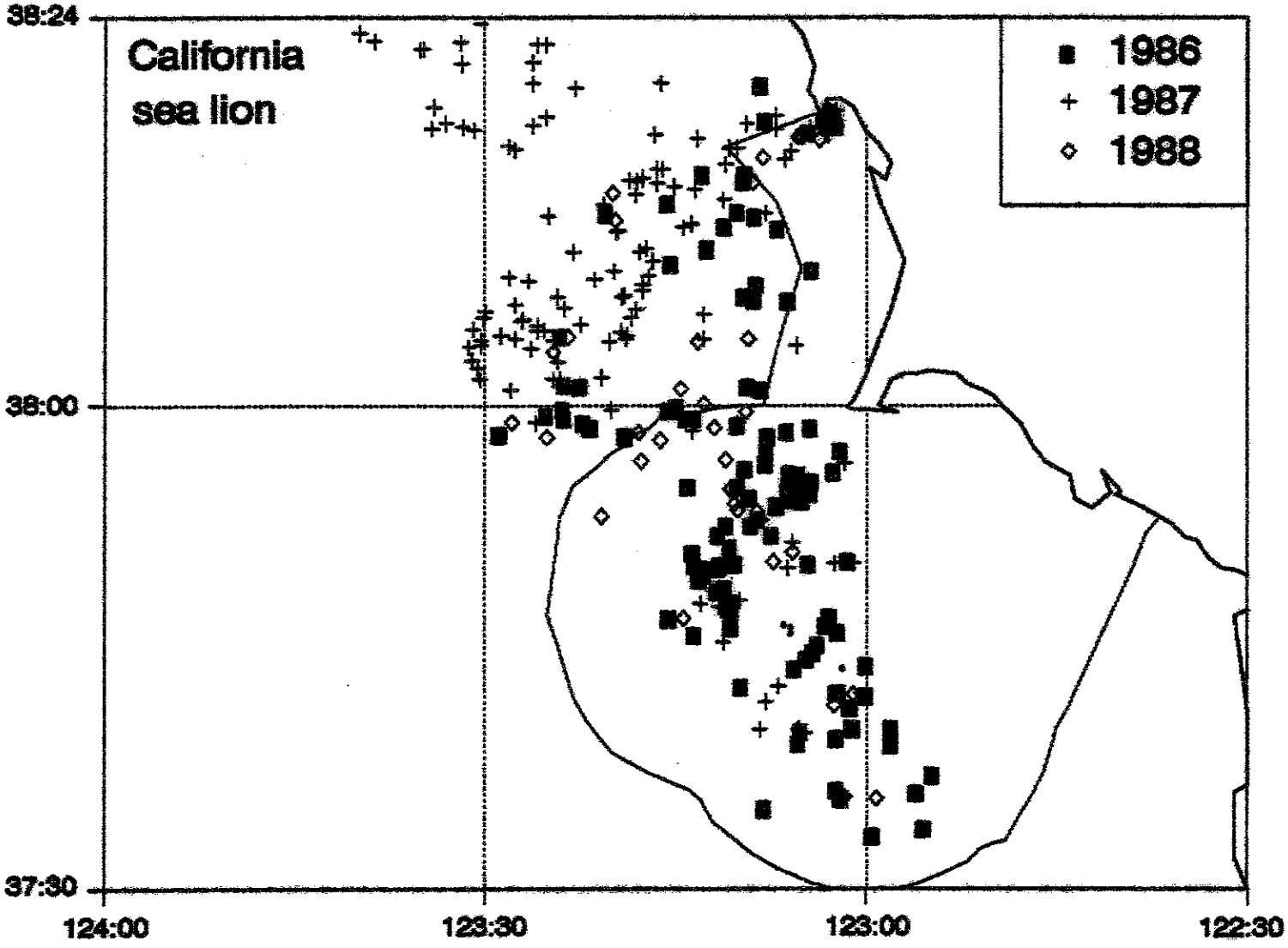


Figure 35. Location of California sea lion sightings made from vessels and aircraft by year.

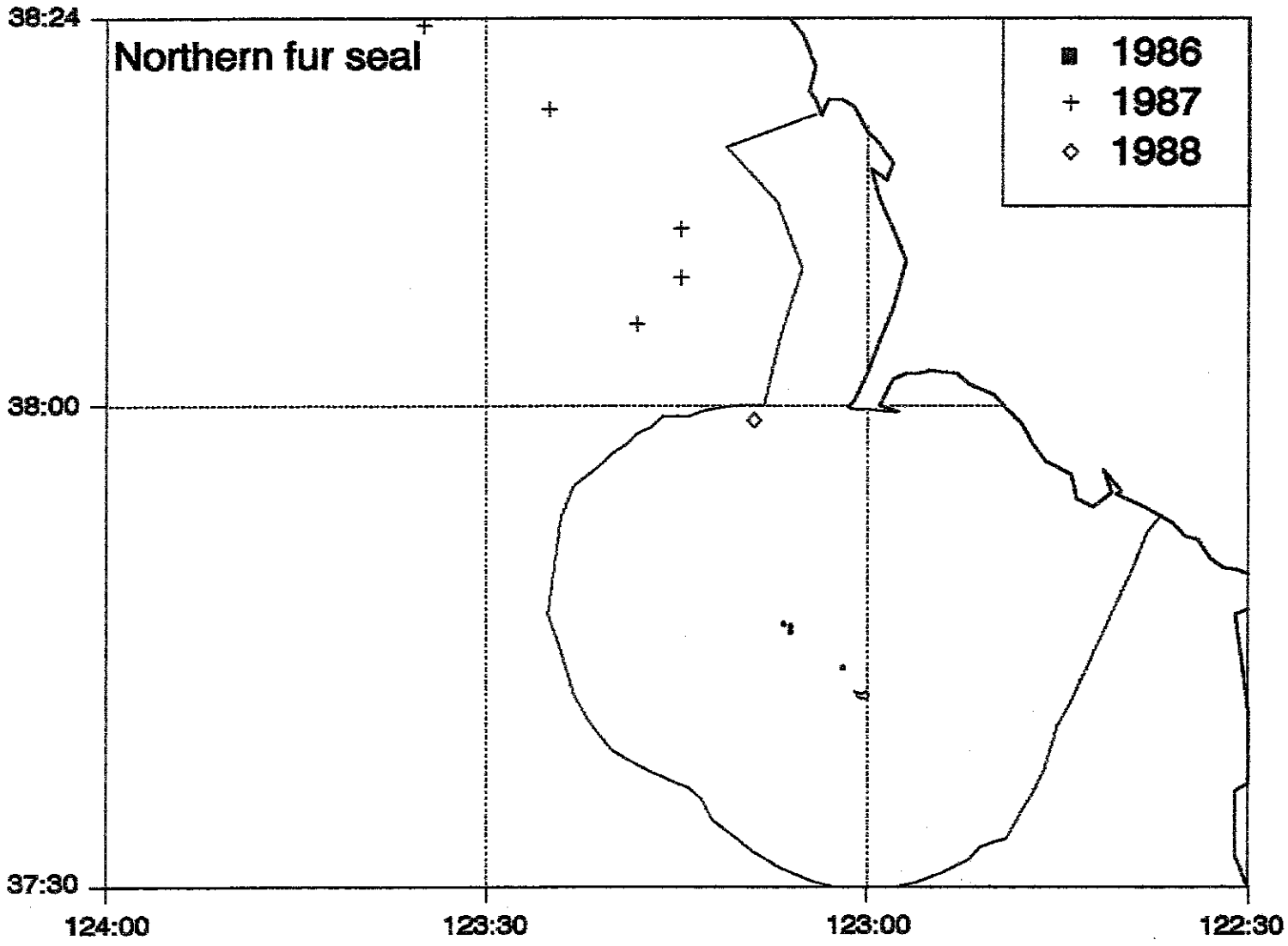


Figure 36. Location of northern fur seal sightings made from vessels and aircraft by year.

Harbor seal

Eighty-one sightings of 1,409 harbor seals (Phoca vitulina) were made during vessel and aerial surveys between 1986 and 1988. Harbor seals were seen throughout the study period, in all months and years. They were observed hauled out in groups of 4 to 200 in Bodega Bay (on Bodega Rock and the rock on the south side of Bodega Head), on Southeast Farallon Island, Bolinas Lagoon, and Drake's Estero. Locations of sightings are shown in Figure 37. Harbor seal occurrence at haul-out sites in the study area have been reported by Allen (1980) and Allen et al. (1980, 1984).

Northern elephant seal

Northern elephant seals (Mirounga angustirostris) were seen hauled on Southeast Farallon Island. We had one sighting of one animals in the water near Bodega Canyon on 22 August 1988. Northern elephant seal occurrence at the Farallon Islands has been described in detail in reports by Huber et al. (1979, 1980, 1981, 1982, 1983, 1985, 1986)

Leatherback turtle

Ten sightings of 10 leatherback turtles (Dermochelys coriacea) were made during vessel and aerial surveys between 1986 and 1988. Six turtles were seen in between July and September 1986 and four were seen in August and September 1988. Locations of sightings are shown in Figure 38. All turtles were seen singly. Average water depth of sighting was 226 ft (n=5, s.d.=26).

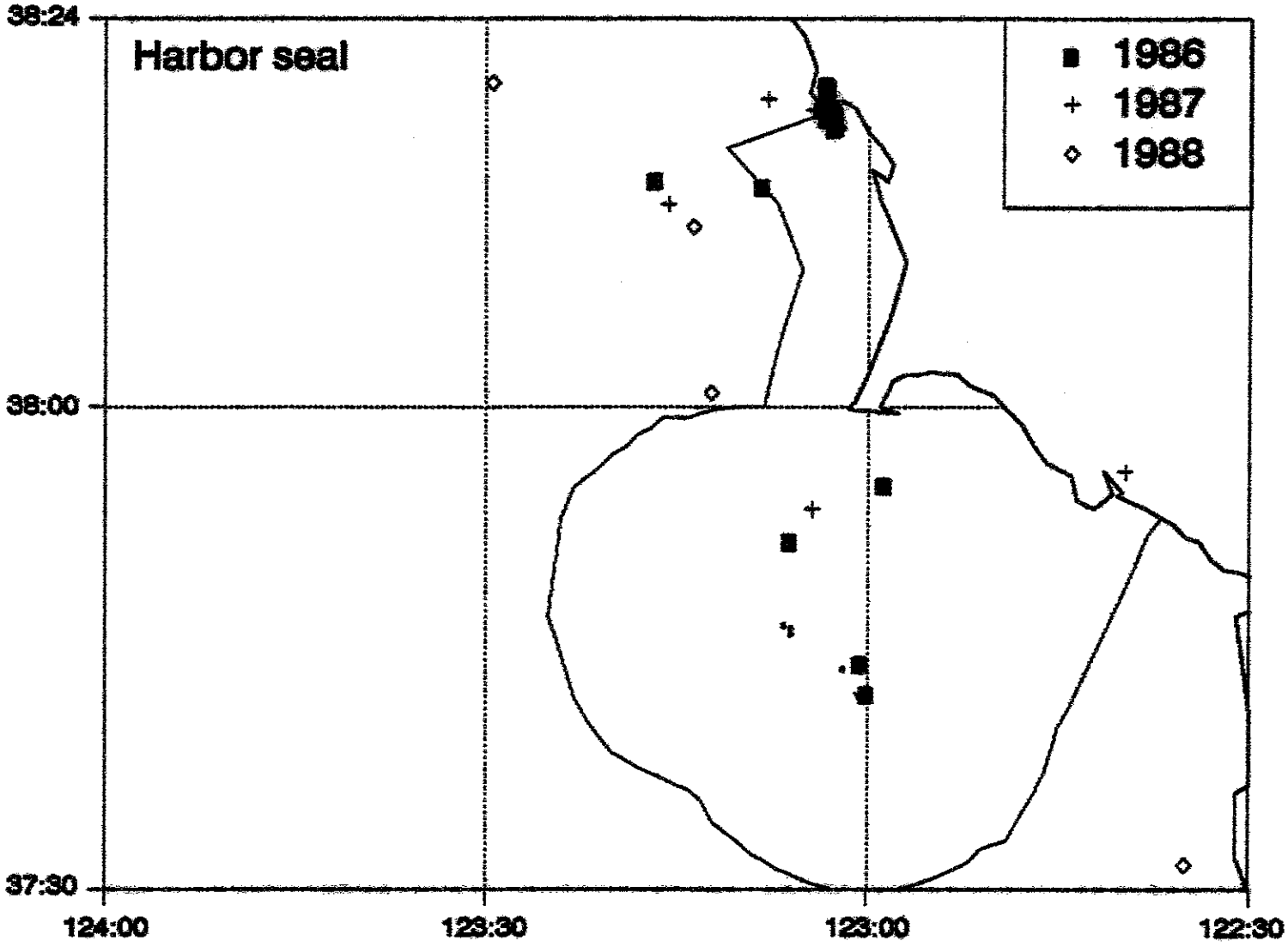


Figure 37. Location of harbor seal sightings made from vessels and aircraft by year.

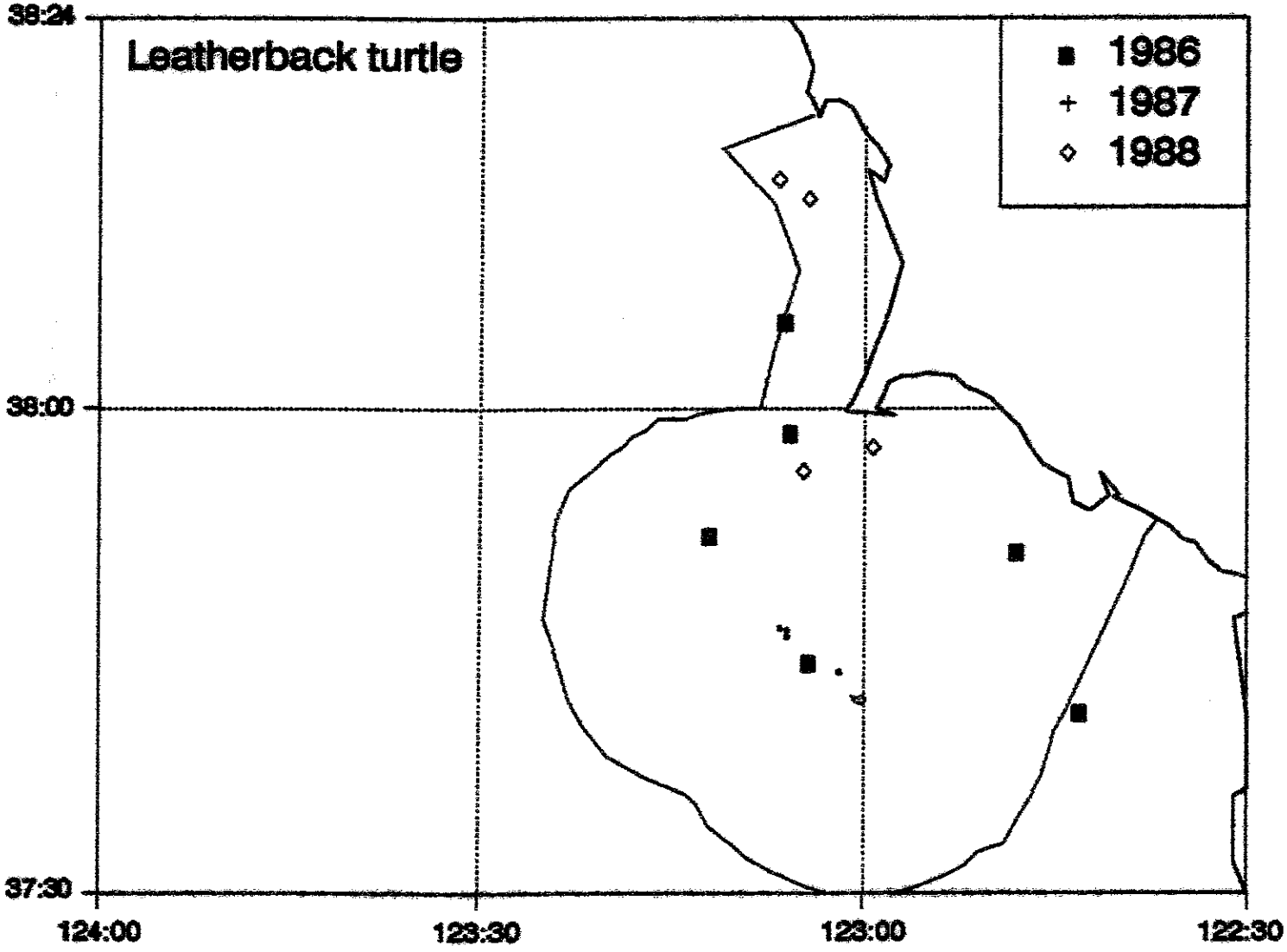


Figure 38. Location of leatherback turtle sightings made from vessels and aircraft by year.

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