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Distribution of cetaceans and sea-surface chlorophyll concentrations in the California Current

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Abstract

A census of marine mammals was conducted off the coast of California (USA) in 1979–1980. The distribution of sea-surface chlorophyll was determined at the same time by onboard fluorometry and by remote sensing using the Coastal Zone Color Scanner on the Nimbus-7 satellite. Comparisons of species and chlorophyll distributions indicate that marine mammals are not randomly distributed with respect to chlorophyll. Cetaceans were more abundant in the productive coastal waters than in the offshore oceanic waters of the California Current. This supports the hypothesis that the distributions of some cetacean species may be related to the mesoscale features that are manifest in the patterns of chlorophyll as revealed in the satellite imagery. It is suggested that oceanic chlorophyll may be used as a habitat descriptor for selected marine mammals, and that remote sensing will provide complementary data useful in the interpretation of observed distribution patterns of marine mammals and in the estimation of their abundance.

Introduction

The rich cetacean fauna off California, first described comprehensively by Scammon (1874), is the subject of increasing interest as human activities continue to intensify in coastal waters. Reviews (Norris *et al.*, 1976; Morejohn, 1977 a) have emphasized both the diversity and mobility of these cetacean populations within the California Current. This marine biome is well known for its rich biological production (Owen, 1974) due to upwelling and the mixing of surface water-masses (Reid *et al.*, 1958). Although one of the most intensively studied marine ecosystems in the world (Hickey, 1979), understanding of the extent and constitution of its cetacean fauna has remained sketchy. This is especially so beyond the continental slope, or off southern California, seaward of the borderland province (Shepard and Emery, 1941).

The work reported here began as two separate research efforts on board the same ship aimed at obtaining a census of marine mammals in the California coastal region and at obtaining surface-validation temperature and chlorophyll data over this broad area in support of satellite sensors. The surface data included the abundance and distribution of marine mammals from sightings and the continuous along-track recordings of near-surface temperature and chlorophyll concentration. The combined data sets allowed a quantitative evaluation of sightings with respect to the temperature and chlorophyll characteristics of the waters surrounding the sites where mammals were observed. The results demonstrate that cetaceans tend to be most abundant where chlorophyll is most concentrated. This is consistent with the hypothesis that cetacean habitats are primarily defined by the coastal, surface water-mass which is rich in chlorophyll, and that the mesoscale dynamics of these waters are important to the different cetaceans. It can further be hypothesized that the distribution of cetaceans is proximally related to the mesoscale distribution of primary productivity through links in the food web.

These ideas are not new. Whalers have long known that whales could be found where their food is plentiful (Foxton, 1956). In the Pacific, studies have shown that areas of mixing, upwelling, and frontogenesis frequently attract whales (Uda, 1954, 1962; Omura and Nemoto, 1955; Uda and Nasu, 1956; Uda and Dairokuno, 1957; Uda and Suzuki, 1958; Nasu, 1957, 1963, 1966; Rovnin, 1969; Volkov and Moroz, 1977; Berzin, 1978; Clarke *et al.*, 1978; Gaskin, 1982). The same appears true for the smaller dolphins and porpoises (Gaskin, 1968; Kasuya, 1971; Evans, 1974, 1975; Miyazaki *et al.*, 1974; Miyazaki, 1977; Miyazaki and Nishiwaki, 1978; Hui, 1979; Au and Perryman, in press). We suggest that if statistical relationships can be found between cetacean habitats, as distinguished by different temperature and/or chlorophyll regimes, then the spatial determination of these variables by remote sensors can quantitatively aid the estimation of abundance and distribution of marine mammals. While the data presented here were not obtained expressly for this purpose, the methodology discussed holds considerable potential for estimation of populations in the sea. Indeed, a main objective of this work is to suggest that combined ship and satellite sampling of the ocean may permit more quantitative assessments of living marine resources.

Both sea-surface temperature (Bernstein *et al.*, 1977; McClain, 1981; Bernstein, 1982; Brown and Evans, 1982) and chlorophyll concentration (Gordon and Morel, 1983) can now be quantitatively determined by satellite sensors. Sea-surface chlorophyll is related to the primary productivity of the water column to the depth of the euphotic zone (Smith, 1981), so that surface chlorophyll measurements may be used to estimate the distribution and amount of oceanic productivity (Smith *et al.*, 1982; Smith, 1984; Brown *et al.*, 1985; Eppley *et al.*, 1985). These data can be obtained from both ships and satellites, providing alternate and complementary sampling schemes. Satellite data are generally less accurate at single station points than those from ships, but provide almost real-time, synoptic coverage of large areas. The combination of ship and satellite sampling techniques permits a calibrated mapping of the regional distribution of sea-surface temperature and chlorophyll concentrations (Smith and Baker, 1982; Smith *et al.*, 1982; Brown *et al.*, 1985).

The purposes of the present work are: (1) to discuss the relative abundances and distributions of cetaceans and their relationships with ocean-water properties in California coastal waters; (2) to suggest methodologies for the utilization of synoptic satellite images (and the statistics derived therefrom) to optimize sampling strategies and improve abundance/distribution estimates of cetaceans.

This study focuses on the California Current, which brings cold subarctic water slowly southward along the California Coast. The current merges with tropical water around Latitude 23°N. Its western boundary, about 700 km from the coast, is the variable transition region between subarctic and Eastern North Pacific Central water. Seasonal coastal upwelling in spring and summer is driven by prevailing northwesterly winds. The major centers of upwelling occur at Latitude 41°N in the vicinity of Cape Mendocino, at Latitude 35°N off Point Conception, and at Latitude 28°N off Point Eugenia. Within the Southern California Bight, islands and irregular bottom topography contribute to locally intense, highly variable mixing and upwelling, which is intensified in the fall months by interaction with the seasonal Davidson Counter Current. Thus, while the California Current may be envisioned as a "wide body of water which moves sluggishly toward the southeast" (Sverdrup *et al.*, 1942), its local structure is characterized by highly variable swirls, eddies, and intermingling of water masses (Bernstein *et al.*, 1977; Hickey, 1979).

Reid *et al.* (1958) and Hickey (1979) have discussed the California Current system, its seasonal variability, and cross-shore structure which can be divided into nearshore (generally < 150 km) and offshore components. The nearshore region is primarily related to the seasonal fluctuation of wind-driven upwelling along the coast. The region offshore from the coast is more associated with the stronger southward flow of the California Current. For convenience, we frequently refer to the inshore component as "coastal" waters and the offshore component as "oceanic", but emphasize that both components are part of the California Current system. The coastal water tends to be chlorophyll-rich and is often differentiated sharply by fronts from the offshore, more oceanic water that grades into the core of the California Current. Both the oceanic boundary of this coastal water and the water mass itself are characterized by dynamic mesoscale features.

Materials and methods

A coastal marine mammal survey (Au and Duffy, 1979; Baker *et al.*, 1984) was conducted from the R. V. "David Starr Jordon" between 27 September and 20 October 1979 between Cape Mendocino and the tip of Baja California (see Fig. 1 for the northern portion of the survey area). A second marine mammal survey (Au, 1980) was made between 17 June and 11 July 1980, following a similar track pattern, but going south only to the latitude of Point Eugenia. There were additional legs on this cruise seaward of the previous September-October coverage, designed to investigate the effects of deep-sea seamounts on cetacean distribution.

Each day, the scientific crew searched continuously for mammals as the ship cruised in an offshore direction. They used 25 × 150 mm Fuji binoculars mounted port and starboard above the flying bridge. At night, the ship sailed to the shoreward start-point of the next day's leg. Along-track temperature and chlorophyll measurements were made continuously, 24 h a day. Vessel speed was between 9 and 10.5 knots (1 knot = 1.85 km h^{-1}). The observer's horizon was approximately 12 km away. Upon sighting a cetacean school, position, distance, and bearing information were recorded. Then the ship usually made a close approach for species identification, determination of school size, and behavioral observations.

Navigation and sighting fixes were provided by a Magnovox Satellite Navigational system with an accuracy of roughly one-half nautical mile. Along-track temperature, salinity and chlorophyll concentration data were recorded continuously on strip-chart recorders and sampled at 1 min intervals with a minicomputer (Hewlett Packard 9845). Temperature and salinity were recorded from the output of the onboard, calibrated thermosalinograph (Ocean Data Equipment TSG-102). Chlorophyll fluorescence was measured with a flow-through fluorometer (Turner Designs) and calibrated periodically with discrete extracts of chlorophyll (Smith *et al.*, 1981).

Satellite imagery from the Coastal Zone Color Scanner aboard the Nimbus 7 satellite (Hovis *et al.*, 1980) was captured at the Scripps Satellite Oceanography Facility. Image

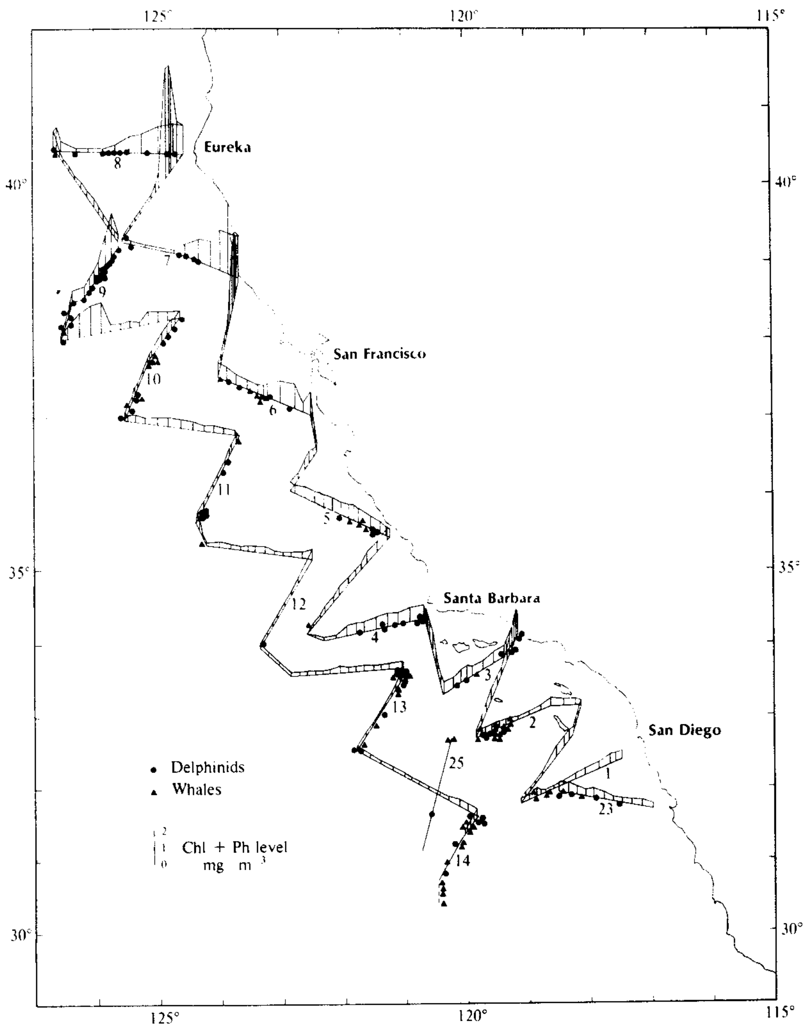

Fig. 1. Northern area of marine mammal survey conducted from the R.V. "David Starr Jordon" between 27 September and 20 October, 1979. Locations of the sighted cetacean schools (delphinids and whales) are indicated by circles and triangles, respectively. The average hourly value of chlorophyll plus pheophytin, in units of mg pigment m^{-3}, is indicated by the along-track histograms. Cruise track is labeled by daily onshore to offshore transects, where "Leg 1" corresponds to 27 September or Julian Day 270. No sightings were made during the "night-time legs" of the cruise

processing and analysis were carried out by means of atmospheric correction and a chlorophyll algorithm (Smith and Wilson, 1980; Gordon and Clark, 1981; Gordon *et al.*, 1983) using software of the RSMAS group at the University of Miami. Statistical analysis of the images was carried out at the UCMBO computer and image processing facility at Santa Barbara. Contemporaneous sea-truth data from the along-track record were used to check the validity of values obtained from the processed satellite images.

The examination of relative abundance of each cetacean species in different parts of the coastal habitat was of primary interest in our work. However, data on relative species-abundance collected from ships are potentially biased, because small schools cannot be seen as far off as can larger schools, and each species has its different characteristic school size and behavior. A correction index was devised to adjust for this undersampling effect among species with small average school sizes (*Phocoenoides dalli*, *Grampus griseus*, *Tursiops truncatus* and *Globicephala* sp.). Adjusted relative abundance was calculated by first taking the mean perpendicular distance from the trackline of the sightings of a given species and dividing by the same for *Delphinus delphis*. The latter is a conspicuous species against which we reference the others. This ratio is a relative sightability correction term which was next divided into the numbers of sightings of the species of interest to obtain an adjusted school abundance. For each species, an adjusted measure of total individuals was then calculated by multiplying the adjusted school abundance by the geometric mean school size (Table 3). The mean perpendicular distance of sightings is widely used to correct for differential sightability, although strictly speaking it is correct only if each species has a negative exponential detection function (Gates *et al.*, 1968; Burnham *et al.*, 1980). Our data were insufficient for rigorous testing of this assumption. The geometric mean school size was used be-

Table 1. Cetacean species sighted in California Current region, between Cape Mendocino and tip of Baja California, during the R. V. "David Starr Jordon" cruise between 27 September and 20 October 1979. The key numbers are used in following tables

Key No.	Specific name	Common name
Dolphins		
1	*Delphinus delphis*	Common dolphin
2	*Phocoenoides dalli*	Dall's porpoise
3	*Grampus griseus*	Grampus
4	*Tursiops truncatus*	Bottle-nosed dolphin
5	*Globicephala* sp.	Pilot whale
6	*Lagenorhynchus obliquidens*	White-sided dolphin
7	*Lissodelphis borealis*	Northern right-whale dolphin
8	*Stenella coeruleoalba*	Striped dolphin
9	*Orsinus orca*	Killer whale
10	Unidentified delphinid	Dolphins and porpoises
Whales/pinnipeds		
1	*Balaenoptera musculus*	Blue whale
2	*Balaenoptera physalus*	Fin whale
3	*Balaenoptera edeni*	Bryde's whale
4	*Megaptera novaeangliae*	Humpback whale
5	Unidentified rorqual	Large whales
6	*Berardius bairdii*	Baird's beaked whale
7	*Mesoplodon* sp.	Beaked whale
8	*Ziphius cavirostris*	Goosebeaked whale
9	Unidentified ziphiid	Beaked whale
10	*Physeter macrocephalus*	Sperm whale
11	*Kogia* sp.	Pygmy or dwarf sperm-whale
12	Other unidentified whale	Whales
13	Pinnipeds	Seals, sea lions

cause it provides a heavier proportional weighting of the presumed undersampled, smaller school sizes. Since school size may be log-normally distributed for reasons given by Williams (1964) and May (1975), the geometric mean should estimate the median, or most typical, value of actual school size.

Twenty identified cetacean species were encountered during the cruises (Table 1). Fig. 1 shows the locations of the sighted schools from the first cruise off southern and central California; the average hourly value of chlorophyll plus pheophytin is indicated by the along-track histograms.

Results

Cetacean population distributions

Cetaceans were most frequent off the California (USA) coast. On the first cruise 87% and on the second cruise 79% of the schools encountered were north of 30.5° North. The most frequently seen delphinid off California was *Delphinus delphis* or common dolphin (38% of all delphinid schools, Table 2) followed by *Phocoenoides dalli* or Dall's porpoise (25%). The latter, however, was a comparatively rare species in terms of total abundance because its average school size was only 5.7 individuals (Table 2). Most schools among species were small (Fig. 2). Even among *D. delphis,* which had a mean school size of 200 individuals, schools smaller than 20 were seen more often than any other size interval. Since sighting conditions during the second cruise were obtained under relatively adverse weather conditions compared to the first cruise, these and the following statistics are based only upon results north of 30.5° North from the first cruise.

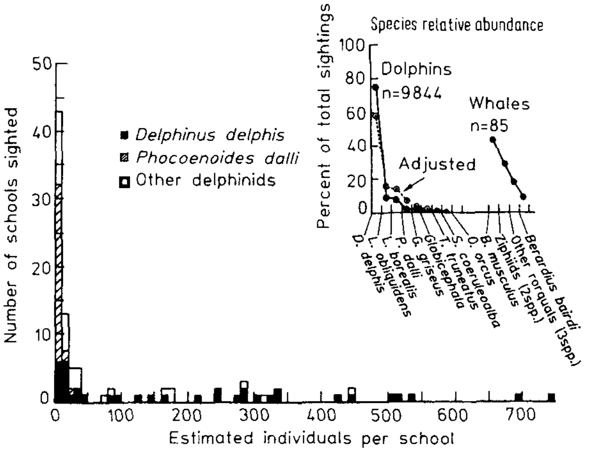

Fig. 2. Number of cetacean schools sighted versus estimated individuals per school. Inset shows species relative abundance. Full specific names are given in Table 1

The adjusted species indexes of total individuals (Table 3) show that the dominant delphinid was *Delphinus delphis* (57%), followed by *Lagenorhynchus obliquidens* or Pacific white-sided dolphin (16%), and *Lissodelphis borealis* or northern right-whale dolphin (14%), all being species with relatively large average school size. The remaining species, including *Phocoenoides dalli,* were relatively rare. These latter species are those that were adjusted for differential sightability. The numerical dominance by *D. delphis* is evident, regardless of whether adjusted or nonadjusted measures are used (Fig. 2).

Among the whales, *Balaenoptera musculus,* the blue whale, was the dominant species with 20 schools and 40 individuals (Table 2, Fig. 2). Next were the ziphiid whales, with 18 schools and 43 individuals (among these were *Berardius bairdii, Mesoplodon* sp. and *Ziphius cavirostris*). The remaining 14 rorqual sightings, including *Balaenoptera physalus, B. edeni* and *Megaptera novaeangliae,* constituted the least abundant grouping. *Physeter macrocephalus,* the sperm whale, with 2 schools and 25 individuals, and *Kogia* sp. (probably the pigmy sperm-whale, *K. breviceps*), with 4 schools and 6 individuals, were two species encountered only on the outer legs.

Fig. 1 summarizes the first-cruise locations of sighted cetacean schools; the average hourly values of along-track chlorophyll plus pheophytin (mg pigment m^{-3}) were only obtained during daylight hours, so that only the numbered

Table 2. Numbers of cetacean schools sighted from R.V. "David Starr Jordon", September–October 1979. Key to species names is in Table 1. Dash indicates no sighting made

Julian Day	Leg	Beaufort sea state	Miles searched	Dolphin species										Whale and pinniped species:												
				1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13
270	1	3–4	88	–	–	–	–	–	–	–	–	–	–	2	–	–	–	1	–	–	–	–	–	–	1	–
271	2	2–3	98	2	–	–	1	–	1	–	–	–	–	4	3	–	–	3	–	–	–	–	–	–	2	7
272	3	2–3	68	3	–	1	2	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	10
273	4	1–4	97	1	1	4	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	11
274	5	2–3	92	1	1	1	–	–	1	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	1	5
275	6	2–3	73	–	–	1	–	–	1	2	–	–	–	4	–	–	1	–	1	–	–	–	–	–	–	1
276	7	1–2	66	1	4	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6
277	8	2–3	96	1	9	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
278	9	1–2	88	10	10	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	7
279	10	1–2	94	2	4	–	–	–	–	1	–	–	2	–	–	–	–	–	–	2	–	1	–	–	2	6
280	11	2–4	94	3	–	–	1	1	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	1	1
281	12	3–4	110	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
282	13	1–2	94	6	–	1	–	–	–	–	1	–	1	3	–	–	–	–	–	–	2	1	–	–	–	9
283	14	1–2	86	3	–	–	–	1	–	–	–	–	2	–	–	–	–	–	–	4	1	–	–	4	2	4
284	15	3–5	101	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
285	16	4–5	109	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
286	17	4	122	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
287	18	4–5	115	1	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
288	19	3–5	93	1	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–
289	20	5–6	105	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
290	21	3–5	86	2	–	–	–	–	4	–	–	–	1	–	–	1	2	–	–	–	–	–	–	–	1	9
291	22	3–4	115	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
292	23	3	74	4	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–
296	25	2–3	92	–	–	–	–	–	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–
Total schools			2 256	43	29	8	6	4	7	5	1	1	10	20	3	2	3	6	2	6	7	3	2	4	10	76
Mean no. of individuals/school				200.4	5.7	21.3	17.2	23.2	150.3	165.0	3.0	2.0	4.8	2.0	2.0	2.0	1.7	1.3	4.0	2.5	2.0	2.0	12.5	1.5	1.3	5.4
No. of schools/100 miles searched				1.6	1.3	0.3	0.3	0.1	0.3	0.2	>0.0	>0.0	0.4	0.9	0.1	0.1	0.1	0.3	0.3	0.1	0.3	0.1	>0.0	0.2	0.4	3.4
No. of individuals/100 miles searched				335.8	7.3	5.7	4.6	3.1	46.6	36.6	0.1	0.1	2.1	1.8	0.3	0.2	0.2	0.4	0.4	0.7	0.6	0.3	0.5	0.3	0.4	18.2
Temperature (°C)				17.48	15.81	17.48	19.07	20.48	17.83	17.14	19.39	–	18.93	18.75	20.28	23.91	17.13	19.64	16.95	19.59	20.54	19.34	19.28	19.79	–	17.81
Salinity (%)				33.42	33.13	33.52	33.48	33.68	33.60	33.25	33.44	–	33.54	33.58	33.65	33.91	33.70	33.53	33.08	33.45	33.64	33.50	33.03	33.48	–	33.47
Pigment (mg chlorophyll m^{-3})				0.52	1.18	0.73	0.71	0.83	1.22	0.43	0.18	–	0.68	0.58	0.49	0.58	2.0	0.43	0.60	0.22	0.43	0.68	0.12	0.22	–	0.78

Table 3. School size and relative abundance of cetacean species off California, September-October 1979. Table entries listed in order from the largest number of total individuals sighted to the smallest number. Data is a subset from Table 2 and is based upon Legs 1–14, 23, and 25 off southern and central California (Fig. 1). "School size" gives arithmetic means ($\bar{x}_A$), logarithmic means ($\bar{x}_L$), standard deviations (std_L) and geometric mean. "Perp. dist." gives perpendicular distance in nautical miles, based upon sightability characteristics of each species and weightings factors. All delphinids except *P. dalli, Grampus griscus, Globicephala* sp. and *T. truncatus* are given the same weighting factor (wt = 1); of the latter group, *Globicepha* sp. and *T. truncatus* are given equivalent weights. The weighting factor for a given species is the mean perpendicular distance, $\bar{d}$, divided by the same for *D. delphis* ($\bar{d}$ = 1.759). "Tot. individs" gives adjusted index of total individuals = (n)(geometric mean) ÷ (wt); whales were not adjusted, as school and sample sizes were small

Species	Sightings (n)	School size				Perp. dist. (nm)		Tot. individs	
		$\bar{x}_A$	$\bar{x}_L$	std_L	Geom. mean	$\bar{d}$	wt	non-adj. (arith.)	adj. (geom.)
Dolphins									
Delphinus delphis	38	201.0	1.89	0.745	77.6	1.759	1.00	7 639	2 950
Lagenorhynchus obliquidens	3	298.3	2.44	0.213	275.4	1.759	1.00	895	826
Lissodelphis borealis	5	165.0	2.15	0.265	141.3	1.759	1.00	825	706
Phocoenoides dalli	29	5.7	0.64	0.325	4.36	0.617	0.35	165	361
Grampus griseus	8	21.3	1.17	0.433	14.8	1.336	0.76	170	156
Globicephala sp.	3	30.0	1.44	0.231	27.5	1.348	0.77	90	107
Tursiops truncatus	4	13.8	0.94	0.489	8.7	1.348	0.77	55	45
Stenella coeruleoalba	1	3.0	0.48	–	3.02	1.759	1.00	3	3
Orsinus orca	1	2.0	0.30	–	1.99	1.759	1.00	2	2
Whales									
Balaenoptera musculus	19	1.95	–	–	–	–	–	37	–
Other rorquals	10	1.50	–	–	–	–	–	15	–
Ziphids except *Berardius bairdii*	12	2.08	–	–	–	–	–	25	–
Berardius bairdii	2	4.00	–	–	–	–	–	26	–
Physeter macrocephalus	3	8.67	–	–	–	–	–	26	–
Kogia sp.	4	1.50	–	–	–	–	–	6	–

daytime legs of the cruise have sightings indicated, whereas chlorophyll measurements were made both day and night. Many of the sightings or groups of sightings (Fig. 1) were in the vicinity of seafloor topographical changes and regions of relatively persistent, high chlorophyll. For instance, the sightings at the ends of Legs 1 and 2 were in the vicinity of the Tanner and Cortez Banks, an area important to fishermen. On Leg 5, the whale sightings occurred near Pioneer Seamount, an area that once supported a nearshore whaling industry (Rice, 1963 b). Sightings along Leg 8 occurred along the topographically complex Mendocino Escarpment. Thus, casual observation would suggest that cetacean schools are concentrated in waters of relatively rich productivity and are not distributed at random among different chlorophyll concentrations.

There is, however, a stochastic element to the shipboard observations, which might explain the above. To test whether cetaceans have a random distribution with respect to chlorophyll in space, all sightings were divided into several chlorophyll concentration intervals. The sightings within chlorophyll concentration intervals were then averaged or normalized by the different number of daylight transect blocks within each concentration interval. Transect blocks are one-minute time intervals of integrated along-track chlorophyll data (including time intervals without cetaceans), each corresponding to a distance of roughly 300 m (at 10 knots). The chlorophyll value used to represent a sighting was the mean of 25 transect blocks, equal to ± 12 min from the actual point of sighting to account for a "nominal sighting radius", which provided values of an average and a variance (see below) of chlorophyll for the vicinity of the sighting location. Fig. 3, using all marine mammal sightings, shows the number of (a) sightings versus chlorophyll concentration in five intervals ($0.01 < 0.03$, $0.03 < 0.1$, $0.1 < 0.3$, $0.3 < 1.0$, $1.0 < 10$) in units of mg pigment m^{-3}, (b) daylight transect blocks for each of these same five chlorophyll intervals, and (c) the corresponding number of sightings normalized by the number of daylight transect blocks.

Also shown in Fig. 3 a, by the dashed histogram values, are the number of sightings that would be expected in each chlorophyll interval if the mammals had been randomly distributed with respect to chlorophyll concentration and would thus have been sighted in proportion to the distance searched (i.e., in proportion to the number of daylight transect blocks in each chlorophyll interval as shown in Fig. 3 b). A chi-square test of the hypothesis that the cetaceans were sighted in proportion to the number of daylight transect blocks in each range led to rejection of the hypothesis of a random distribution of sightings with respect to chlorophyll concentrations at the 99% confidence level (DF = 4, $\chi^2 = 33.6$). The number of sightings per daytime transect block was also regressed against the mean chlorophyll concentration of each interval (Fig. 3 c) and gave a sample correlation coefficient of 0.92. A Student's t-test indicated that the slope of this regression was significantly different than a slope of zero (DF = 3, $0.05 > P > 0.01$), providing further evidence for rejection of

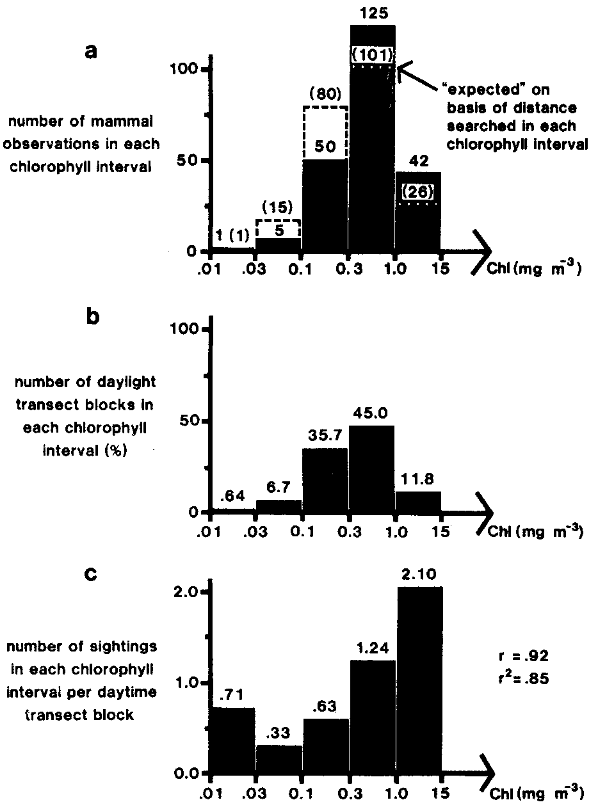

Fig. 3. (a) Number of marine mammal sightings versus chlorophyll concentration divided into five logarithmic intervals ($0.01<0.03$, $0.03<0.1$, $0.1<0.3$, $0.3<1.0$, $1.0<10$, in units of mg pigment m^{-3}); dashed "expected" lines show number of observations based on assumption of a random distribution in proportion to number of daytime transect blocks searched in each interval of chlorophyll concentration. (b) Number of daylight transect blocks (%) in each chlorophyll interval for all mammal sightings; transect blocks are one-minute intervals of shipboard observations. (c) Number of sightings per daytime transect block (arbitrary normalization) versus chlorophyll concentration ($n=223$, $r=0.92$)

the hypothesis of no dependence. This also provides a measure of the degree of correlation between sightings per daytime transect block and chlorophyll concentration, and is consistent with the hypothesis that more sightings occur at higher chlorophyll concentrations.

The robustness of these statistics was tested by distributing the data into several different numbers of equally spaced (on a log scale in order to span three orders of magnitude in chlorophyll concentrations) chlorophyll intervals and also by selecting the chlorophyll intervals with the requirement of obtaining an equal number of transect blocks per chlorophyll interval, again for several different numbers of intervals. In all these cases, chi-square tests of the data and t-tests of the corresponding regression slopes against zero lead to rejection of the hypothesis that the marine mammal sightings were independent of chlorophyll concentration.

Sightings of individual species were too few, once they were divided into appropriate chlorophyll concentration intervals, to allow for meaningful statistical testing of their distributions in space. However, separate tests were done for the combined mysticeti or baleen whales and for the combined odontoceti or toothed whales. There were only 30 observations of the former, and a chi-square test of the hypothesis that they were distributed randomly with respect to the chlorophyll concentration gave a value just below the 90% level of confidence ($\mathrm{DF}=4$, $\chi^2=7.3$). Also, a t-test of the slope of this regression indicated that it was not significantly different from zero ($\mathrm{DF}=3$, $P>0.10$). Thus, at this level of confidence, one could not decisively reject the hypothesis that mysticeti were distributed randomly with respect to chlorophyll concentration. In contrast, a chi-square test of the odontocete sightings led to a rejection of the hypothesis of a random distribution at greater than the 97.5% confidence level ($\mathrm{DF}=4$, $\chi^2=12.6$). The number of sightings of odontocetes per daytime transect block was also regressed against chlorophyll concentration, giving a sample correlation coefficient of 0.81. A t-test of the slope of this regression against zero showed it to be in a borderline area between significance and nonsignificance ($\mathrm{DF}=3$, $0.10>P>0.05$). These results are consistent with the hypothesis that toothed whales are found more frequently at higher chlorophyll concentrations.

Cetaceans and chlorophyll variance

Shipboard observations of along-track chlorophyll concentration and marine mammal schools suggested that some species were not only associated with regions rich in chlorophyll but also with areas where major changes in the surface characteristics occurred, e.g. at interfaces such as drift lines, shear zones, convergences and the coastal-offshore water boundary.

Our along-track data provided a measure not only of the concentration of chlorophyll but also of its variance. Continuously recorded along-track data can, for convenience of analysis, be integrated into 1-min intervals which we refer to as transect blocks. Any number of these transect blocks can be further averaged to obtain a mean and standard deviation of the along-track data for some distance in a given time interval over which the ship has traveled. The mean and standard deviation of all pigment recorded ± 12 min of each sighting was calculated. Twenty-five min is approximately equal to 4 nautical miles of track data and is equivalent to 7 km or 5 satellite pixels (picture elements) at a speed of 10 knots. This provided a "nominal sighting radius" of a circle encompassing the sighted mammals. The radius was chosen small enough so that chlorophyll variance would be sensitive to sharp frontal boundaries yet large enough so that mean chlorophyll would be representative of the region around the sighting. A doubling or halving of the chosen radius did not significantly influence the statistical results. Thus, for each sighting location an average and a coefficient of variation of the

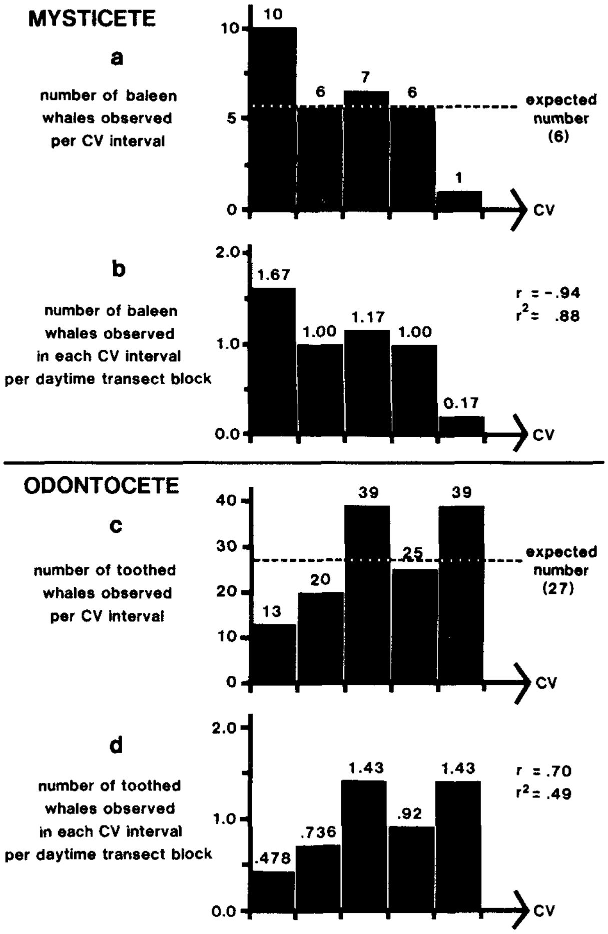

Fig. 4. Number of mysticete (baleen) whale sightings (a) and number of odontocete (toothed) whale sightings (c) versus chlorophyll coefficient of variation (CV) divided into equal frequency intervals. Expected number of observations based on assumption of a random distribution with respect to CV is shown by dashed line. (b) and (d) Number of mysticete ($N=30$, $r=-0.94$) and odontocete ($N=136$, $r=0.70$) whale sightings per daytime transect-block

along-track pigment concentration within this "nominal radius" was calculated. These calculations are both meaningful for sighting statistics and useful in providing a means whereby both ship and satellite data can be directly intercompared (see "Discussion").

We compared the number of schools of Mysticeti and of Odontoceti at five different levels of coefficient of variation (CV) of chlorophyll concentration. The CV will be relatively large in regions of high chlorophyll variability, such as frontal regions, and relatively small in areas where the chlorophyll concentration is homogeneous. Fig. 4 a and b show the data for mysticete whales; Fig. 4a the number of these whales observed as a function of the CV of chlorophyll concentration, Fig. 4 b the number observed per daytime transect block with respect to CV. Fig. 4 c and d show similar data for odontocetes. The CV was subdivided into intervals such that there were an equal number of transect blocks per CV interval, so that if the observations were randomly distributed in space, one would expect an equal number per CV interval. This "expected" number of sightings per CV interval is indicated on Fig. 4 a and c by dashed lines.

For mysticete whales, a chi-square test comparing the observed and expected frequency of sightings for each interval gave a chi-square of 7.10 ($DF=4$, $P=0.14$) so that the hypothesis of a random distribution with respect to chlorophyll variation could not be rejected at the 90% level of confidence. It is still of interest, however, to note that a regression of normalized observations versus CV (Fig. 4 b) gave a correlation coefficient of $r=-0.94$. A t-test of the slope of this regression with that of zero indicated that it is significantly different from zero ($DF=3$, $0.05>P$). If this tendency for mysticete observations to be more numerous in areas of low chlorophyll variation were to be confirmed by further research, it would indicate a sharp contrast in this habitat descriptor as compared to that for odontocetes.

For odontocetes, a chi-square test comparing the observations against the hypothesis of an independent distribution with respect to chlorophyll CV indicated that the null hypothesis could be rejected ($DF=4$, $\chi^2=19.7$, $0.01>P$). In contrast to the baleen whales, the normalized sightings of toothed whales showed a positive correlation ($r=+0.70$) with CV. This suggests that higher numbers of odontocete sightings occurred in regions of relatively high chlorophyll variability.

Cetaceans and physical water types

The above chlorophyll statistics, which may serve as habitat descriptors, are also associated with the conventional physical parameters used to characterize water masses. For example, a major break in surface temperature and salinity often occurred at the coastal-offshore water boundary which also often differentiated regions of low and high chlorophyll concentration (Fig. 5). This boundary tended to correspond to the surface-density isopleth, $\sigma_t=23.8$. Sigma-t is determined from temperature and salinity (see Sverdrup *et al.*, 1942) and, off California, decreases with offshore distance (see Lynn *et al.*, 1982). A classification of the cetacean sighting data as coastal or oceanic, on the basis of interrelationships between temperature, salinity and chlorophyll, and the relationship to fronts, tended to be separable by this sea-surface density interface. Fig. 5 shows that *Delphinus delphis* were encountered in outer coastal and in oceanic waters, while *Phocoenoides dalli* were encountered primarily in coastal waters, as indicated by the dashed envelope lines relative to the $\sigma_t=23.8$ line.

In the satellite imagery a persistent color/temperature front was also recognizable. Water inshore of this color/temperature front (high density, salinity and chlorophyll but low temperature) had characteristics of recently upwelled water. The water offshore this front was characteristic of subarctic water of the California Current system (Hickey, 1979). This break between oceanic and coastal waters was often accompanied by abrupt changes in the encounter rate of birds and mammals. We have therefore used this color/temperature front as the seaward boundary of coastal water. This front is shown in two satellite chlorophyll images in Figs. 6 a and 7. It persisted more or less coincident with the slope break (2 000 m isobath) for the entire period of the cruise.

The ship sampling-intensity by itself was not adequate to give a detailed areal picture of the complexity of the coastal-oceanic boundary. However, mesoscale features were indicated by abrupt changes in the along-track data. From the satellite data, these mesoscale features can be identified (Fig. 6 a). Comparison of the ship and satellite data showed that strong fronts were most apparent in the along-track data where the ship entered or left these mesoscale features and crossed one water type, or habitat, to another.

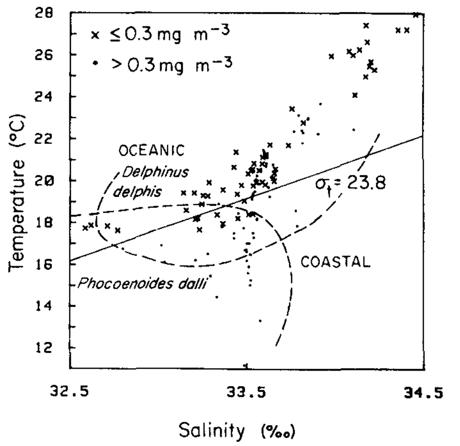

Fig. 5. Temperature–salinity diagram for surface waters in surveyed area. Sightings from areas with greater than 0.3mg pigment m^{-3} are indicated by dots, those from areas with less than 0.3 mg pigment m^{-3} by crosses. Diagram shows relationships between the color/temperature front, the physical properties of the water masses, and cetaceans. *Delphinus delphis* were encountered in outer coastal and in oceanic waters, while *Phocoenoides dalli* were encountered primarily in coastal waters, as indicated by the dashed envelope lines relative to the $\sigma_T = 23.8$ line

The field investigation sampled relatively less of the offshore oceanic water, so there are fewer data concerning the importance of that province as a cetacean habitat. If the coastal water were the major habitat, there would be greater numbers and more species seen in coastal versus oceanic water, relative to the allocation of sampling effort in the two kinds of water. This follows because, as discussed above, most cetaceans were found in higher chlorophyll waters which, in these areas and at this time, were usually coastal waters. Cetacean schools were indeed more frequently encountered in coastal waters than expected on the basis of sampling effort, but the statistical significance of this difference varied according to the stratification of the sample, as shown by several chi-square tests (Table 4). Significantly more cetaceans were sighted in coastal waters than oceanic waters ($P<0.01$) when all schools of cetaceans species were combined, either over the entire area or only off central California. Water types within the Southern California Bight are more complex and do not lend themselves as readily to simple water-mass description; here, the distributions with respect to water masses becomes problematical. Delphinid cetaceans by themselves were significantly more frequent in coastal waters over the entire area and in the Southern California Bight, but not off Central California. In general, a finer stratification of our data led to fewer observations and less significant statistical results.

Individual species and habitat descriptors

Because the relationship between along-track pigment levels to cetacean sighting are significant for the combined populations, it is instructive, in spite of the potential limitations of finer stratification, to consider if water types and/or chlorophyll concentrations may characterize habitat differences among individual cetacean species. To in-

Table 4. Cetacean distribution by water type. Water type was determined by inspection of along-track records of temperature and salinity; chi-square tests were based upon miles sampled in the two kinds of water. Miles searched were along Legs 1–14, 23 and 25

Area	Miles searched			Schools observed											
				All cetaceans				Dolphins only[a]				Whales only			
	Coastal	Oceanic	Total	Coastal	Oceanic	Total	χ^2	Coastal	Oceanic	Total	χ^2	Coastal	Oceanic	Total	χ^2
Southern California Bight	118.6	389.5	508.1	18	32	50	3.799	9	11	20	4.098*	9	21	30	0.419
Central California	659.6	243.6	903.2	82	17	99	4.341*	61	13	74	2.863	21	4	25	1.019
Pooled	778.2	633.1	1 411.3	100	49	149	8.158**	70	24	94	13.43**	30	25	55	1.316

[a] Family Delphinidae * $P<0.05$ ** $P<0.01$

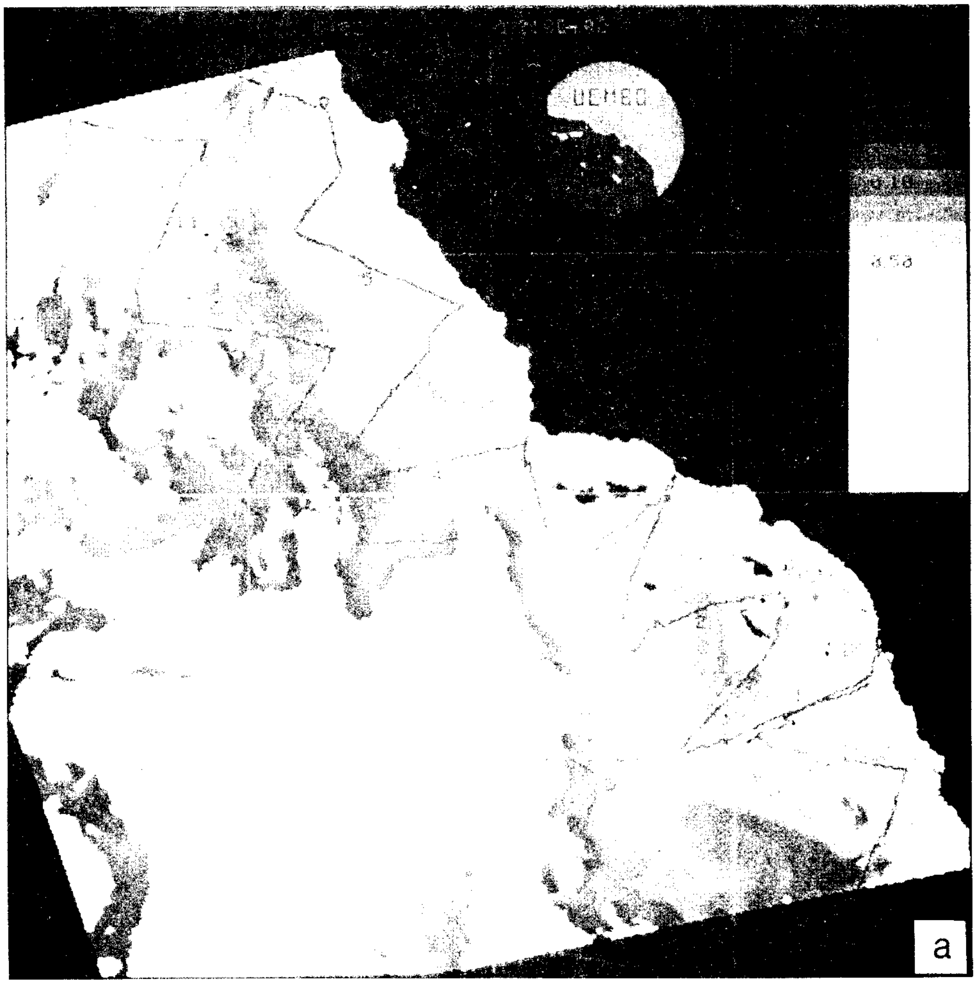

Fig. 6. (a) Processed Coastal Zone Color Scanner image of the California coastal region, Orbit 4749, 2 October 1979; image consists of 512×512 pixels, where one pixel (i.e., one picture element) represents a surface area of roughly 1.5×1.5 km. Phytoplankton pigment concentration (chlorophyll plus pheophytin) ranging from 0.01 to 10 mg pigment m^{-3} is represented by 18 equally-spaced logarithmic steps from low (dark) to high (light) concentration; black areas are land or clouds masked during processing; each leg of cruise track is superimposed on the image and numbered; Leg 1 corresponds to Julian Day 270. Image was obtained during approximately 4-min period near noon on 2 October 1979 (Leg 6, Julian Day 275) while R.V. "David Starr Jordan" was off Monterey Bay (Fig. 1). (b) Variance of chlorophyll image of surveyed area. Orbit 4749, 2 October 1979 (Julian Day 275)

vestigate this hypothesis, we calculated several pigment concentration statistics for each species analogous to those discussed above. First was the pigment concentration measured at the location of the species sighting. Because of small-scale variations in pigment concentrations (Platt and Denman, 1980; Smith and Baker, 1982) we also used the values of pigment recorded ± 12 min of each sighting to obtain the pigment mean as well as the pigment variance within a small distance of the sighting. Second, we determined from the ± 12 min of pigment measurements the "within" sighting variance (Sp^2), and the "between" sighting variance (Sm^2) from all combined sightings of each species. That is, we decomposed the total pigment variance of each species into a portion due to variation within the sighting area and into another portion due to variation between the sightings (Dixon and Massey, 1969; Sokal and Rohlf, 1969). Finally, we recorded the minimum and maximum range of pigment concentrations within which each species was sighted (Table 5). Our objective was to document not only the mean and variance of the chlorophyll within a habitat, but also to investigate whether selected species were sighted from a relatively homogeneous population of chlorophyll concentrations or from areas of widely differing chlorophyll concentrations.

Recognizing that an adequate sample size did not exist for all species sighted, a subset of species was used to test

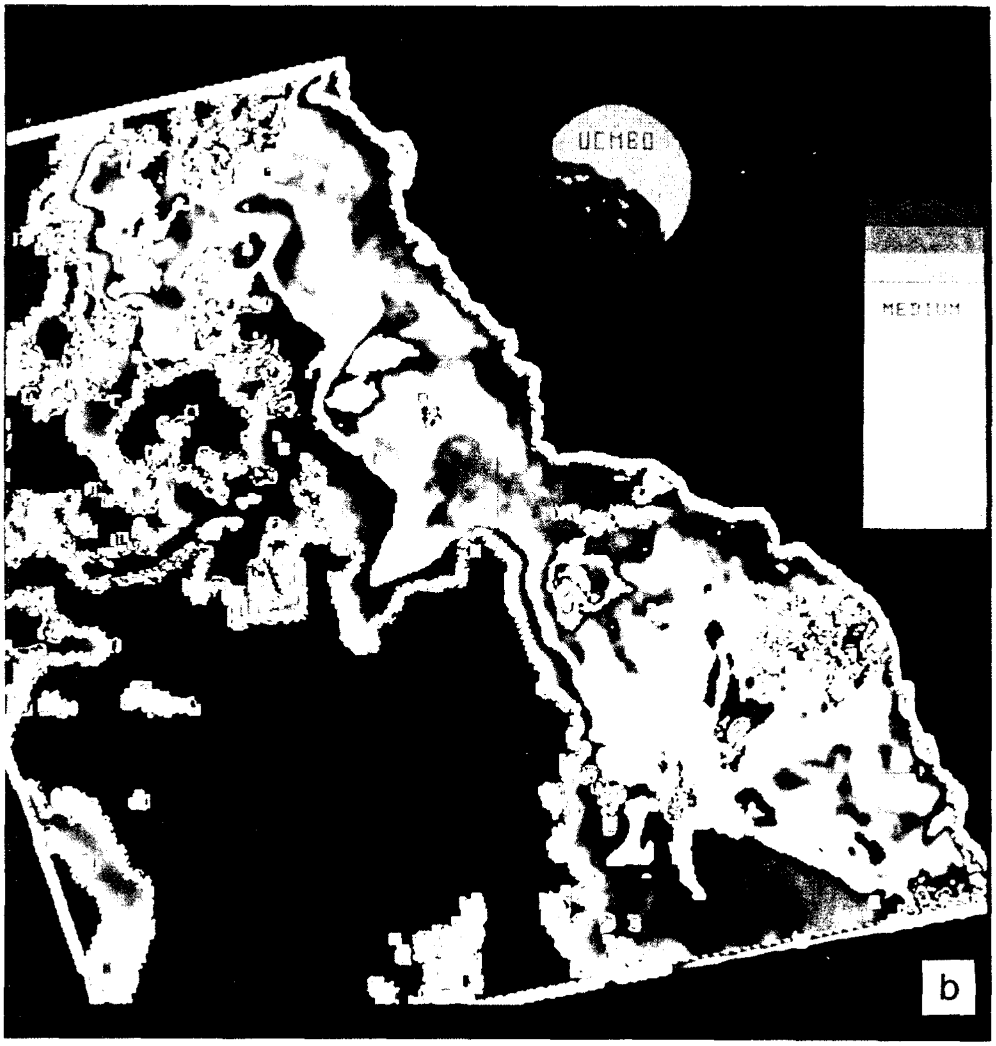

Fig. 6. (continued)

Table 5. Characterization of marine mammal habitats by pigment (chlorophyll) concentration. BCV: between-sighting coefficient of variation; WCV: within-sighting coefficient of variation

Species	Ship data:					Satellite data:				
	Sightings (*n*)	Pigment (mg chl m^{-3})		BCV	WCV	Sightings (*n*)	Pigment (mg chl m^{-3})			
		Range	$\bar{x} \pm Sm$	$Sm/\bar{x}$ (%)	$Sp/\bar{x}$ (%)		Single pixel		Sighting area	
							$\bar{x} \pm \sigma$	CV	$\bar{x} \pm \sigma$	CV
1 *Delphinus delphis*	38	0.014–2.40	0.36±0.40	112	27	9	0.64±0.52	81	0.57±0.29	50
2 *Phocoenoides dalli*	29	0.13–2.80	0.89±0.76	86	28	1	0.50		0.60	
3 *Grampus griseus*	8	0.61–0.83	0.71±0.09	13	11	3	1.21±1.12	93	0.77±0.36	47
4 *Tursiops truncatus*	6	0.12–1.81	0.45±0.47	104	60	1	0.35		0.36	
6 *Lagenorhynchus obliquidens*	7	0.43–2.49	0.92±0.62	68	25	2	0.42±0.04	9	0.51±0.05	9
1 *Balaenoptera musculus*	16	0.16–0.96	0.45±0.26	59	10	14	0.38±0.22	58	0.47±0.17	37
5 Unidentified rorqual	6	0.12–0.86	0.31±0.28	92	13	6	0.83±1.28	154	0.40–0.32	80
8 *Ziphius cavirostris*	7	0.12–0.97	0.31±0.24	79	52	4	0.50±0.19	38	0.60±0.31	52
10 *Physeter macrocephalus*	2	0.12–0.33	0.17±0.09	54		2	0.18±0.04	21	0.16±0.04	25
13 Pinnipeds	56	0.08–1.87	0.60±0.49	82	24	16	0.63±0.46	73	0.55±0.23	42

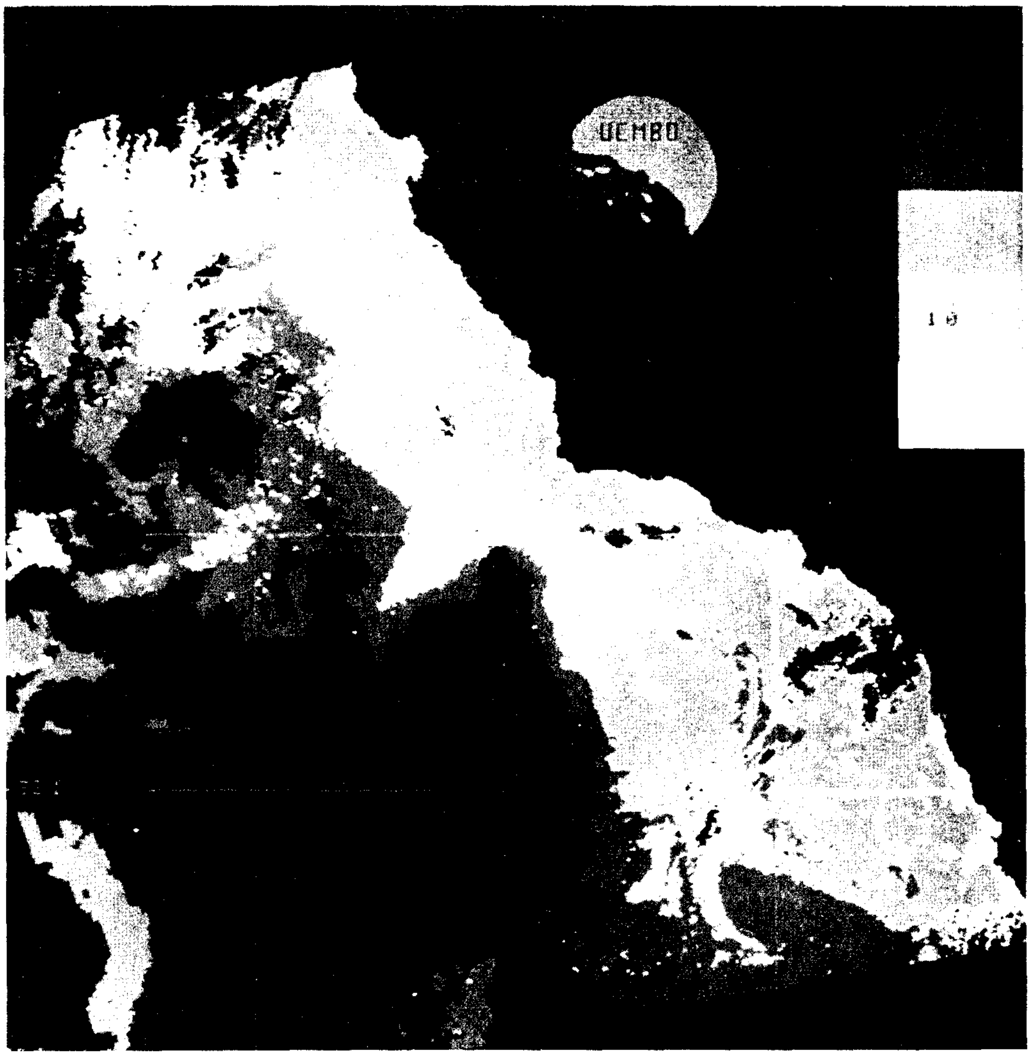

Fig. 7. CZCS image of California coastal region. Orbit 4749, 2 October 1979 (Julian Day 275) processed to show low (<0.3 mg pigment m^{-3}), medium (0.3 to 1.0 mg pigment m^{-3}) and high (>1.0 mg pigment m^{-3}) chlorophyll habitats

whether the sightings for a given species demonstrated statistically significant fidelity to a specific range of chlorophyll concentrations. An analysis of variance *F*-test was used to determine if the average chlorophyll variance from a set of species sightings was significantly larger than the variance of the sighting means. The between and within CVs of pigment level from the ship data are given in Table 5 for each of these species. The between-sighting coefficient of variation, given in Table 5, provides an index of the pigment habitat variability from one sighting to the next for each species (Sm^2). The within-sighting coefficient of variation provides a measure of the pooled variance for all sightings (Sp^2). If the sightings are from populations having unequal means, then (Sm^2) will be considerably larger than (Sp^2). For each species, except *Grampus griseus*, we could reject the hypothesis by *F*-test that its sightings were from areas with the same mean chlorophyll level, i.e., within the chlorophyll range for a species, fidelity to a specific chlorophyll habitat was low.

Estimates of within-habitat heterogeneity (CV of the mean variance of the chlorophyll concentration) showed there were differences between species not correlated with absolute pigment levels. For example, *Delphinus delphis* was widely distributed in heterogeneous, medium-chlorophyll environments, while *Balaenoptera musculus* was sighted predominately in less variable, medium-chlorophyll regions. *Phocoenoides dalli* and *Lagenorhynchus obliquidens* were sighted primarily in medium-to-high chlorophyll waters, whose means exhibited significant chlorophyll differences at each sighting (chlorophyll concentrations ranged from 0.13 to 2.8 and 0.4 to 2.5 mg pigment m^{-3}, respectively; Table 5).

In contrast, pigment differences between *Grampus griseus* sightings suggest that this mammal is attracted to much more constant environments (0.61 to 0.83 mg pigment m^{-3}). Comparison of its between and within sighting CVs supports the hypothesis ($0.05 > P$) that the sightings were in waters with the same mean chlorophyll concentration. However, this result is primarily suggestive since the number of sightings is few.

Interestingly, the more geographically restricted *Phocoenoides dalli* commonly occurred over a wider range of absolute chlorophyll levels within the generally high chlorophyll areas off northern central California than did the widespread *Delphinus delphis*, which tended to occur in offshore waters. Evidently the more productive habitat of *P. dalli* is also characterized by large and changing variations in pigment level. Also, the data suggest that *Lagenorhynchus obliquidens* and *Lissodelphis borealis* are primarily coastal water species. On the other hand, *Physeter macrocephalus* (Rico, 1977) and *Kogia* sp. are clearly oceanic by geography and water type. Other species, especially ones occurring in or near the Southern California Bight (an area of much water-mass mixing), occurred in both kinds of water.

Satellite images

Both qualitative experience and our statistics suggest that oceanic chlorophyll concentrations and sea-surface temperatures, as well as the variance of these properties, can be used as "habitat descriptors" for living marine resources. As a working hypothesis, it could be assumed that habitats of some Cetacea are primarily defined by areas with relatively high chlorophyll concentrations. In California waters at this time of year these are primarily defined by the coastal, high-chlorophyll and low-temperature surface waters. It follows that the mesoscale dynamics of these waters, especially those determining distribution and relative productivity, are important to the different species of Cetacea. Our results indicate that this hypothesis holds when all observations are aggregated; however it is quite likely that this habitat-descriptor hypothesis will also hold at some level of generality for some individual species. We would also emphasize that the data necessary to adequately test, and to optimally use, this hypothesis have not yet been collected.

Table 5 also shows the characterization of marine mammal habitats by pigment concentration as derived from satellite (CZCS) imagery. The table lists sightings for which contemporaneous satellite imagery was available ±6 h of a shipboard sighting. The mean pigment concentration from the satellite picture elements ("sigle pixel") corresponding to the sighting locations are given, along with the standard deviation and coefficient of variation of this pigment concentration from the average of all sighting locations. The "sighting area" data were obtained by first averaging all the pixels within a 7 km × 7 km (5 × 5 pixel) box centered on the sighting location, and then taking a mean of all these data. This area on the satellite image is approximately the area within the "nominal sighting radius" discussed above, and therefore provides an analogous mean, standard deviation and coefficient of variation for comparison with the ship data. Although the satellite data are consistent with the ship data, there are fewer sighting statistics because satellite passes and/or cloud-free imagery did not exist at the time of all shipboard sightings.

Fig. 6 a shows a chlorophyll image of the California coastal region during the period of the cruise. The absolute accuracy of this image is estimated to be (by comparison with ship data) ±40%. Our point of departure for the work reported here is the derived chlorophyll image. The black areas of these images are either land or clouds which have been set to zero value. Landmarks (e.g. Point Conception, Santa Barbara, San Diego, the offshore islands) are easily identifiable by comparing Fig. 1 with the images. Phytoplankton pigment concentrations ranging from 0.01 to 10.0 mg pigment m^{-3} are represented by 18 equally-spaced logarithmic steps from low (dark) to high (light) concentration, corresponding to the grey scale on the images. The ship track (annotated for each leg of the cruise) has been superimposed on the image, and also can be compared with Fig. 1. Note that each processed image not only represents a synoptic view of the relative chlorophyll concentrations in the area observed, but also is a matrix of quantitative information: the chlorophyll concentration at each pixel (each "picture element" corresponds to a surface area of roughly 1.5 km × 1.5 km) location. As a consequence, statistical analyses can be carried out using such images (Smith and Baker, 1982; Smith *et al.*, 1982). The variance based on the image displayed in Fig. 6 a is depicted by Fig. 6 b. This "variance image" clearly demonstrates the area of high chlorophyll variability (lighter) and the area of more constant habitats (darker). Note that the offshore oceanic region is represented as a much more constant environment than many inshore coastal regions. Again, the offshore clouds which have been masked black during processing must be disregarded.

Estimates of the distributions and abundances of cetaceans are usually imprecise owing to the methods of surveying their habitats. Airplane searches provide data from low-flying, fast-moving platforms, while ships allow for more careful observations from a slower-moving platform. Both assume that all animals in the path are seen, while realizing that many of them may avoid the ship or may be underwater at the time of the overflight. In addition, it is known that the time that a cetacean spends at the surface is highly variable and somewhat species-specific. Using current techniques, a species abundance may be estimated from counts of schools per unit area adjusted for detectability (Burnham *et al.*, 1980) and then multiplied by mean school size and the total area searched to obtain an esimate of total abundance. Alternatively, if our habitat-descriptor hypothesis holds and if a cetacean species could be associated with a given range of chlorophyll concentration, then the number of individuals per track-line area of the specific habitat searched (to total track-line area searched) could be normalized by the specific habitat area (to total area searched) for the region under study to obtain an estimate of total abundance.

For example, the image in Fig. 6a has been divided into three grey scale levels (Fig. 7) corresponding to low (<0.3 mg pigment m^{-3}), medium (0.3 to 1.0 mg pigment m^{-3}) and high (> 1.0 mg pigment m^{-3}) chlorophyll concentrations. These habitat divisions are based on the shipboard data as well as upon the clearly delineated color/temperature front as seen in Fig. 6. An immediate result from this habitat image is a quantitative estimate of the three habitat areas. The non-cloudy area shown in this image is approximately 211 000 km^2, and the areas of low, medium and high chlorophyll correspond to 79 000, 114 000, and 18 000 km^2 or 37, 54 and 9% of the total cloudless area, respectively. A second observation from the satellite imagery is that the color/temperature front was relatively persistent (± 10 km of mean position) during the two weeks of the survey in this region off the California coast, indicating that these habitats may be rather persistent.

If shipboard observations can establish characteristics of species habitats, satellite imagery can then be used to estimate habitat areas for calculating species abundances within these areas. For example, *Grampus griseus* was found to be associated with a relatively narrow range of chlorophyll waters (Table 5). If we assume that the habitat for this species is "medium" chlorophyll waters, then its abundance may be more accurately estimated from an expansion of density calculated from the miles searched in that habitat and expanded to the total areal extent of only medium chlorophyll waters. Thus, the total nautical miles (nm) searched within medium chlorophyll waters was 12 465 nm (or 41.3% of the total miles searched). Since the area of this habitat was 54% of the total habitat, we might expect *G. griseus* schools to be 30% (0.54 ÷ 0.41) more abundant than an estimate that assumed the species habitat was the total area.

Other cetaceans seem to be associated with high chlorophyll areas (e.g. *Phoceoenoides dalli* and *Lagenorphynchus obliquidens*). When sightings for these species were superimposed on the satellite imagery, it could be seen that they occurred in near-shore, high-chlorophyll regions or in the high-chlorophyll areas of color fronts. If we were confident of the fidelity of these marine mammals to these habitats, population estimates could be based on the areas of high-chlorophyll water only.

During our survey, *Mesoplodon* sp., *Physeter macrocephalus* and *Kogia* sp. were associated with low-chlorophyll waters on the seaward side of the color/temperature front. This habitat is estimated as 47.5% of the total area, based upon the miles searched in such waters, but only 37% of the area as determined from satellite imagery. We would therefore assume that abundance estimates of these species would be adjusted down by 22% (1.0–0.37 ÷ 0.475).

Discussion

Cetaceans were sighted in coastal water more frequently than expected on the basis of sampling allocation. Our data strongly suggest that in California coastal waters the numerous cetacean sightings were associated with chlorophyll-rich waters which, in turn, are linked to both high primary production (Owen, 1974) and rich and diverse fisheries and ichthyofauna (Horn, 1980). These waters thus appear to be a major habitat of cetaceans. While our work is exploratory, it suggests that more extensive ship/aircraft/satellite stratified sampling will be required for more reliable statistics on cetacean populations. Further, this work indicates that more extensive, quantitative information on ocean water types and possible habitat descriptors should be obtained in conjunction with distribution and abundance surveys. Although the possibility that species aggregate in response to habitat productivity and variability is not the only plausible hypothesis consistent with our observations, the methodology discussed shows the possibility of quantitatively testing this and alternative hypotheses.

Total cetacean sightings per daytime transect block were highly correlated with increasing chlorophyll concentrations ($r=0.92$, Fig. 3c). While a stratification by suborder suggested (the chi-square test was not significant at the 90% level) that mysticete whales are only weakly correlated ($r=0.62$) with surface chlorophyll concentrations, the odontocetes were significantly and positively correlated ($r=0.81$) with chlorophyll concentration. A chi-square test to determine if these whales had a random distribution with respect to chlorophyll allowed rejection of this null hypothesis at the 97.5% confidence level. Although it is clear that a significant correlation exists between cetacean sightings and primary production (as measured by pigment biomass), the degree of "coupling" and the ecological significance of these observations is not obvious. A possible hypothesis is that the distribution and abundance of cetaceans are defined by the coastal surface-water mass, which is rich in chlorophyll, and the link is via the food web. However, these "links" are likely to be species-specific and may be indirect. For example, Evans (1981) suggested that *Delphinus delphis* were concentrated at seamounts and along escarpments, not necessarily because of the high concentrations of chlorophyll there, but because this species was using multisensory environmental cues related to these landmarks to orient during migration.

We have also shown that there is a significant relationship between the sightings of certain cetaceans and the coefficient of variation (CV) of chlorophyll. Further, when stratified to suborder, the toothed whales were significantly correlated with areas of relative high CV, while the baleen whales showed a weak, but non-significant, negative correlation (Fig. 4). The similar results obtained for chlorophyll concentration and CV may be due simply to the fact that chlorophyll is, in many regions, correlated with its own CV.

The cetacean fauna was numerically dominated by *Delphinus delphis* among the delphinid odontocetes and by

Balaenoptera musculus among the whales. *D. delphis* is generally considered the most abundant cetacean off California (Rice, 1963 b; Norris *et al.*, 1976). The abundance of *B. musculus* relative to other whale species was not expected, as the blue whale has been thought to be an infrequent, transient species in California waters (Rice, 1963 b; Norris *et al.*, 1976; Morejohn, 1977 a). The remaining cetacean species showed a tendency for geometric decline in relative abundance among species (Fig. 2). Similar results were obtained during the second coastal cruise, with *D. delphis* and *B. musculus* again dominating the cetacean fauna (Au, 1980). This dominance pattern is a frequent attribute of ecological communities (McNaughton and Wolf, 1970) and may have utility in assessing the status of disturbed biomes. Dominance may arise from "niche preemption" competition in a species guild whose ecology is dominated by some single factor (Whittaker, 1972; May, 1975). For cetaceans off California, this factor may well be the suitability of the physical environment dominated by lateral and vertical mixing processes. Variation in the pigment content of mesoscale water-masses is related to this mixing and may be associated with differences in prey availability.

The contrasts in distribution, morphology and behavior between *Delphinus delphis*, *Phocoenoides dalli* and even *Lagenorhynchus obliquidens* (for which few schools were seen) may be examples of niche separation on the basis of foraging differences. There are large populations of *D. delphis* in the subtropics and large populations of *D. dalli* in the subarctic. California waters represent range extensions where these two populations meet and overlap. *D. delphis* was widespread in the outer coastal and oceanic waters off California. On the second marine mammal cruise, *D. delphis* were encountered on some of the farthest legs offshore (out to 300 km). However, they appeared not to have been attracted by seamounts. Fishing observers aboard albacore boats have also reported this species in offshore oceanic waters, in one case 375 km from the coast (M. Laurs, unpublished data). *D. delphis* feeds opportunistically (Evans, 1975), although with a preference for mesopelagic prey (Fitch and Brownell, 1968). It is diurnally active and may form large schools. *D. delphis* is often associated with other species, notably *Lagenorhynchus obliquidens*, *Lissodelphis borealis* and the pinniped *Zalophus californianus*, which are all species that also form large aggregations (Leatherwood and Walker, 1977). Although the species appears to travel widely, seasonal migration is apparently not pronounced (Norris *et al.*, 1976). On the other hand, the morphologically different *P. dalli*, perhaps the third most abundant cetacean off California (Rice, 1963 a), was abundant only in the northern survey area and apparently prefers the structurally complex coastal water having high and varying chlorophyll levels (Figs. 1 and 6). This species also feeds opportunistically on squids and schooling fish (Kajimura *et al.*, 1980), may be capable of extra deep diving (Ridgeway and Johnston, 1966), and may feed at night (Morejohn, 1977 b). *P. dalli* schools were small (averaging 5 to 6 individuals) in our study (Table 2), and were not with other dolphins. The species may not travel widely in its daily foraging, although its seasonal distributional changes are conspicuous (Brown and Norris, 1956; Brownell, 1971; Norris *et al.*, 1976; Morejohn, 1977 b), and may be determined in part by the seasonal movements of water masses.

The dissimilarities between these delphinids suggest a strong environmental effect upon their ecology, an effect directly related to the contrasting nature of coastal and oceanic waters. The latter is a less productive habitat, where animals may be less specialized (MacArthur, 1972; Pianka, 1976), more far ranging in their foraging, and likely to form larger and more complex social groupings. On the other hand, species of productive habitats can "afford" to be more specialized and some may tend to occur in smaller groupings. These distinctions may explain the differences between *Delphinus delphis* and *Phocoenoides dalli*, and may be analogous to the ecological differences seen between primates (e.g. baboons) from sparse, resource-limited savanna and from productive forest (Crook, 1970).

A similar speculation would be premature for the species of whales, considering the relatively small numbers encountered. We may point out however, that the *Balaenoptera musculus*, a very specialized "swallowing" feeder of krill (Nemoto, 1970) was encountered in greater concentration in two general areas where increased biological production is typical, i.e., the vicinity of Tanner-Cortez Banks and the Pioneer Seamounts. Similarly, humpback whales feed on krill and a variety of small fishes (anchovies, sauries, sardines) and were sighted in green, high-chlorophyll waters. The fin whales also feed on small fishes in addition to krill but tend to be somewhat more cosmopolitan in distribution.

Phytoplankton, as measured by chlorophyll content, and Cetacea represent the opposite ends of the marine food web. Co-occurrence would suggest that the distribution of organisms that comprise the intermediate levels of the food web are also tied closely to the distribution of primary productivity. Our observations suggest that the thin ribbons of increased biomass along fronts or streamline intersections are exploited by foraging cetaceans. Coastal fronts are often characterized by an enrichment of phytoplankton seaward of the front at shallow depths (Mooers, 1978). These features might explain our observation that cetaceans frequently occurred seaward of the first frontal zone between coastal and nearshore waters. Tilting and subsequent shallowing of the mixed-layer near-fronts could also increase the availability of food to foraging mammals.

The general importance of bottom topography to cetaceans is unclear. Most cetaceans encountered in this study were well offshore of the continental slope. In the Southern California Bight, the complex topography makes it difficult to generalize about topographic effects. We suspect that increased turbulence and the extension of coastal water with increased phytoplankton biomass, e.g. as in the Southern California eddy system (Owen, 1980), are the main reasons for reported relationships between cetacean concentrations and topography (Rice, 1963 a; Evans, 1975; Hui, 1979).

The Coastal Zone Color Scanner (CZCS), an instrument aboard the Nimbus 7 satellite, was especially designed to measure oceanic chlorophyll levels, and hence provides information on the mesoscale features of coastal waters. Figs. 6 and 7 are satellite images from the CZCS taken during the cruise period. They show the richness of detail and the spatial complexity of this marine environment, and illustrate the potential of the satellite for studying living marine resources. By conventional methodology, random sampling, irrespective of species subhabitats, produces population estimates. However, the above cetacean-environment associations suggest that the variations in temperature, salinity and chlorophyll-pigment levels can delimit species habitats in order to improve such estimates. For instance, an appropriate sampling strategy could be developed for enumerating species strongly associated with frontal areas. Real-time satellite imagery could direction ship and/or aircraft sampling to these highly productive and highly variable, limited areas, optimizing search patterns and the statistical data therefrom. The upwelling and frontal, high-chlorophyll areas in Fig. 7 comprise less than 10% of the total area, yet between 20 and 30% of the sightings were in, or in close proximity to, these waters. Thus, the satellite images allow these highly dynamic and relatively small areas to be identified and sampled, and their areal extent, as a function of time, to be quantitatively determined.

To the extent that the abundance of selected cetaceans can be shown to have statistically significant associations with habitat descriptors, more reliable estimates of their distribution and abundance can be made using contemporaneous ship and satellite data. The synoptic overview provided by satellites also enhances the understanding of the dynamics and scale of the biological and physical features characterizing the habitats of Cetacea. This may lead to a more fundamental understanding of cetacean ecology and evolution.

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