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Blue whale habitat and prey in the California Channel Islands

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Abstract

Whale Habitat and Prey Studies were conducted off southern California during August 1995 (WHAPS95) and July 1996 (WHAPS96) to (1) study the distribution and activities of blue whales and other large whales, (2) survey the distribution of prey organisms (krill), and (3) measure physical and biological habitat variables that influence the distribution of whales and prey. A total of 1307 cetacean sightings included 460 blue whale, 78 fin whale and 101 humpback whale sightings. Most blue whales were found in cold, well-mixed and productive water that had upwelled along the coast north of Point Conception and then advected south. They were aggregated in this water near San Miguel and Santa Rosa Islands, where they fed on dense, subsurface layers of euphausiids both on the shelf and extending off the shelf edge. Two species of euphausiids were consumed by blue whales, *Thysanoessa spinifera* and *Euphausia pacifica*, with evidence of preference for the former, a larger and more coastal species. These krill patches on the Channel Island feeding grounds are a resource exploited during summer–fall by the world's largest stock of blue whales. © 1998 Elsevier Science Ltd. All rights reserved.

1. Introduction

Blue whales (*Balaenoptera musculus*) are the largest animals to have ever lived on earth, ranging up to 33 m and 172 metric tons (Yochem and Leatherwood, 1985).

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They are selective consumers of massive quantities of krill (a few species of euphausiids), at rates up to 2 metric tons per day (Rice, 1978). When modern whaling methods were developed to capture these large and fast whales in the last half of the nineteenth century, the blue whale became a preferred target of whalers. Stocks in the North Pacific, North Atlantic, and Southern Ocean were severely depleted in the first half of this century. The North Pacific stock was subjected to increasing whaling effort as the Southern Ocean stocks declined (Rice, 1974), until 1966 when the International Whaling Commission listed the blue whale as a protected species and commercial hunting ceased.

Little evidence of recovery has been seen since the end of exploitation for most stocks. However, a large and apparently growing California/Mexico stock of blue whales winters off Mexico and feeds in California waters from June to November. Estimates of stock size are 1723 by line-transect survey (Barlow and Gerrodette, 1996) and 2017 by photographic mark-recapture (Calambokidis and Steiger, 1994). If separated from the former North Pacific stock, the California/Mexico stock is now the largest of eleven putative stocks of blue whales in the world (Best, 1993). It was depleted by whaling, although apparently not as severely as stocks in the central and western North Pacific, North Atlantic, and Southern Ocean (Mizroch et al., 1984). Some California/Mexico whales winter off southern Baja California, in the Gulf of California, or off southern Mexico (Rice, 1974; Calambokidis et al., 1990). Observations off southern California since 1987 have shown that very few blue whales are in these waters during winter and spring, peak abundances are in July through September, and some whales remain into the fall (Larkman and Veit, 1998).

Rice (1974) recorded only 48 blue whales landed at central California shore stations from 1956 to 1965, compared to 900 fin whales. He concluded that blue whales observed to winter off southern Baja California and those caught from Vancouver Island north beginning in June must be migrating past central California far offshore. Although he has since concluded that the California/Mexico stock is separate from the Gulf of Alaska population (Rice, 1992), the fact remains that relatively few blue whales were observed off California prior to 1974. An abundance estimate for California coastal waters in summer–fall 1979/80 was only 470 blue whales, or about one-quarter of the current estimate (Barlow, 1994). The increase is too large to be explained solely by population growth and must, at least partly, result from a change in utilization of California coastal waters for summer feeding.

Large numbers of blue whales have been observed off southern California on the south side of the Santa Barbara Channel, along the northern coasts of three of the Channel Islands (San Miguel, Santa Rosa, and Santa Cruz, Fig. 1) since about 1990 (C. Woodhouse, Santa Barbara Museum of Natural History, pers. comm., 1997). Summer whale-watching trips began to be offered out of Santa Barbara in 1993. The Santa Barbara Channel is a major shipping lane and is frequented by commercial fishermen and recreational boaters. Therefore, it is unlikely that blue whales were aggregating there, either regularly or in large numbers, prior to 1990.

The Whale Habitat and Prey Study (WHAPS) was initiated in 1995 to learn why blue whales were aggregating off the northern Channel Islands. The primary objectives were to (1) study the distribution and activities of blue whales and other large

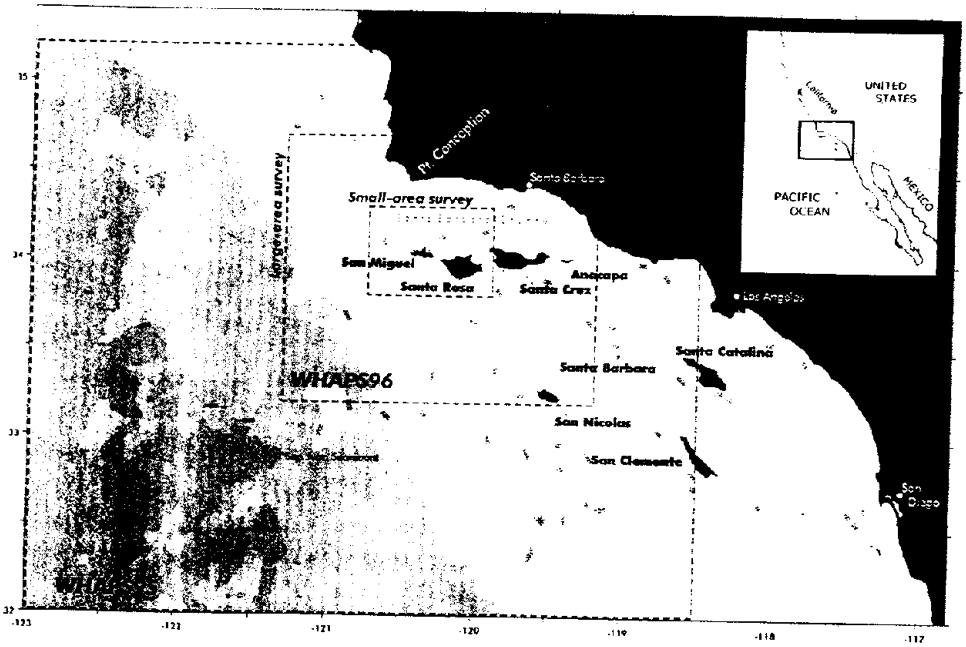

Fig. 1. Whale Habitat and Prey Study area off southern California (inset shows location). Channel Islands, with bold labels, are in the Southern California Bight between Point Conception and San Diego.

whales, (2) survey the distribution of prey organisms (krill), and (3) measure physical and biological habitat variables that influence the distribution of whales and prey. WHAPS95 was an exploratory survey, covering nearshore and offshore waters both north and south of Pt. Conception. WHAPS96 was a more systematic survey, confined to a region around the northern Channel Islands and focusing on the "hot spots" found in 1995 to the west and north of San Miguel and north of Santa Rosa Island. These feeding grounds lie partially within the boundaries of NOAA's Channel Islands National Marine Sanctuary, which is an institution for the management and study of marine life in a 1252 nmi^2 area encompassing San Miguel, Santa Rosa, Santa Cruz, Anacapa, and Santa Barbara Islands.

2. Materials and methods

WHAPS95 was conducted 3 August–1 September 1995 aboard NOAA Ship *McArthur*. WHAPS96 was conducted 10 July–4 August 1996 aboard NOAA Ship *David Starr Jordan*. Procedures were similar on each cruise, but the objectives and survey designs were different.

WHAPS95 explored potential habitat for blue whales and other balaenopterids (fin and humpback whales). Tracklines were not laid out in advance, but three goals governed the survey as it progressed: (1) cover a variety of potential whale habitat types (nearshore and offshore, cold-water and warm-water, productive and unproductive), (2) sample areas with few or no whales, and (3) repeat coverage of areas where whales aggregated. When blue whales were encountered, the ship was often stopped for behavioral observations or moved in a butterfly pattern around the whales to conduct oceanographic, acoustic, and net sampling.

WHAPS96 systematically covered the region where blue whales were most abundant in 1995. A large-area survey was conducted 11–16 July on a grid of stations 43 km apart. Most of the large-area grid was resurveyed 30 July–2 August. A small-area survey of whale "hot spots" near San Miguel and Santa Rosa Islands, with gridlines spaced 2.8 km apart across the shelf break, was conducted 17–29 July. The last two days followed the shelf break around the northern Channel Islands. An additional small-area survey was conducted near San Nicolas Island on 3 August.

2.1. *Whales*

Marine mammal survey effort was conducted using a rotation of five observers. At least one specialist in identifying marine mammals was on watch at all times. A visual watch for marine mammals was maintained during daylight hours (approximately 0700L to 1930L) using 25 × 150 high-powered binoculars mounted on the ship's flying bridge. Binoculars were mounted 10.7 m above the water, giving a maximum ship-to-horizon sighting distance of about six nautical miles. During a watch, observers rotated at 30 min intervals (40 min on WHAPS96) among three positions: at the port binoculars, at data recorder, and at the starboard binoculars. The data recorder searched the full 180° forward of the ship's beam by eye and with 7 × 50-power binoculars (handheld), and recorded sightings, watch effort, and weather information on a laptop computer linked to the vessel's Global Positioning System (GPS).

Each time a marine mammal, or group of marine mammals, was seen, the bearing and distance from the ship were recorded. The bearing was read from an azimuth ring on the binocular mount. An index of distance (angle below the horizon) was read from a reticle printed in the eyepiece.

During WHAPS95 and the WHAPS96 large-area survey, whales were sighted up to 9 km off the trackline when visibility was not limited by fog or haze. In 1995, the ship turned to approach and/or slowed for sightings of whales, or other cetaceans closer than 5 km, so that observers could identify the animals and estimate group size and species composition. During the WHAPS96 small-area survey, schools more than 1.5 km off the trackline were ignored, so identification and size estimates could be made easily without turning on the school. Identification of species sighted was confirmed by the identification specialist. Observers made independent estimates of school size and species composition in 1995 and one consensus estimate in 1996. Independent estimates of whale group size were usually identical, but were averaged if not. Observations of the animals' behavior also were recorded. Black-and-white photographs were taken for identification of individual whales.

Whales were tagged in 1995 and 1996 to study movements of individuals, but a different type of tag was used each year. Blue whales were approached with a small rigid-hulled inflatable boat (RHIB) and tags were affixed by barbs to the skin of the whale with a low-powered crossbow.

Satellite-monitored radio tags were used in 1995 to follow migrations of tens to hundreds of km over several weeks, in collaboration with Bruce Mate at Oregon State University. These tags transmit location and other data through the Argos Location and Data Collection System on NOAA TIROS-N series satellites one to four times daily and are designed to fall off the animals after a few weeks.

Ship-monitored radio tags were used in 1996, from NOAA vessel *Ballena*, to follow dives, searching, and other small-scale movements involved in feeding on observed krill patches. These tags transmitted a signal that was received by a radio direction-finder, giving the whale's location relative to the vessel (Croll et al., 1998). With this information, observers followed the whale and observed its diving behavior. The tags were designed to fall off the animals on radio command, or after 4–24 h by a corrodible link. The whale's time-depth dive information was digitally recorded and downloaded for analysis after tag recovery.

2.2. Krill

Acoustic data were collected to describe the distribution, abundance, and identity of biological sound-scatterers. The acoustic system consisted of a Simrad[1] EK500 multi-frequency echo sounder with downlooking 38, 120, and 200 kHz transducers mounted adjacent to one another in a steel fairing extending 0.5 m from the hull of each ship and located approximately one-third the distance from bow to stern at ~5 m depth. The transducers were narrow beam and circularly symmetrical with 12°, 7°, and 7° between half-power points, respectively. Pulses were transmitted every 2 s at 1 kW for 1 ms duration. Ensonified volumes were approximately conical and sampled every 0.5 m to the bottom or a maximum depth of 200 m. GPS positions were logged every 60 s. System calibrations, using the standard sphere method, were performed before and after the cruises in San Diego Bay.

In 1996, acoustic data were also collected from the NOAA Vessel *Ballena* while tracking radio-tagged whales. The system of two Simrad EY500 single-frequency echo sounders connected to hull-mounted 38 and 200 kHz transducers was similar to the EK500 system on the main research vessel.

Measurements of volume backscattering strength (S_v, dB m^{-3}//1 μPa at 1 m) were adjusted for losses due to spherical spreading and absorption of sound. Echograms were generated from the adjusted S_v; bottom return, surface turbulence and system noise were manually screened. The remaining S_v, attributed to biological scatterers, was thresholded at −81 dB and averaged over horizontal intervals of 185 m (18–30 pings depending on ship speed) and vertical depth bins of 5 m. For presentation, data within pre-defined rectangles were combined to produce a set of average profiles of S_v with depth.

Differences in S_v measured at multiple frequencies have been used to classify acoustic targets (Greenlaw, 1979; Madureira et al., 1993a). The reflection of 38 kHz

[1] Reference to trade names does not imply endorsement by NMFS.

sound by euphausiids of the size collected in this study (10–30 mm) can be characterized as Rayleigh scattering, which is relatively weak. The reflection of 120 and 200 kHz sound from the same animals can be characterized as geometric scattering (or close to the transition from Rayleigh to geometric). Therefore, the relative difference between S_v at 38 kHz and S_v at 120 and 200 kHz should be greater from a krill layer than from animals that would produce Rayleigh scattering at all three frequencies (e.g. copepods) or geometric scattering at all three frequencies (e.g. fish). The acoustic signature of krill in the block-averaged profiles presented here is substantially higher S_v at both 120 and 200 kHz than at 38 kHz.

An index of krill abundance was calculated based on this acoustic signature for each 0.1-km binned profile. First, the difference $\Delta S = 0.5*(S_{v120} + S_{v200}) - S_{v38}$ was calculated for each 5-m depth interval in which both S_{v120} and S_{v200} exceeded S_{v38}. Then, ΔS was averaged from 0 to 200 m or the bottom. ΔS was not converted to krill biomass because net sampling was rarely controlled well enough to precisely match net catches to observed backscatter in targeted patches or layers of high backscatter.

A 2-m Isaacs–Kidd midwater trawl (IKMT) fitted with a 505 μm mesh plankton net was deployed at each station during the WHAPS96 large-area survey to sample zooplankton and micronekton. Volumes filtered were measured with a calibrated General Oceanics model 2030R standard flow meter mounted on the net frame in front of the 2.94 m^2 mouth opening. In 1996, all IKMT tows were oblique from 200 m (or 10–25 m above the bottom in shallower waters). In 1995, IKMT tows were oblique from 100 m or horizontal through scattering layers observed acoustically at depths to 250 m (directed tows, see below); a coarse mesh net (graduated from 390 to 180 to 2 mm from mouth to 505 μm codend) was occasionally used. Tow depths were obtained from a Keller PSI 300DS pressure transducer mounted ~1 m above the roof of the net. Tow speeds ranged between 1.5 and 2.5 knots while attempting to maintain a 45° wire angle.

Directed net tows with a Multiple Opening Closing Net and Environmental Sampling System (MOCNESS) were conducted in 1995 and during the 1996 small-area survey to sample prey patches and layers detected acoustically. Sampling locations were based on type of scattering layer, bathymetry, and the presence/absence of feeding whales. Directed tows were made. The MOCNESS collected vertically stratified samples with four 1 m^2 mouth area, 505 μm mesh nets. These nets were usually towed horizontally through targeted layers, but occasionally obliquely through a depth range if the target layer was thick or was migrating.

All plankton samples were processed within one hour of collection. Wet biomass was measured as displacement volume (Kramer et al., 1972). Whenever possible, all euphausiids (except larval forms) were identified to species and remaining taxa were categorized in major taxonomic groups (Table 2). For each species of euphausiid and major plankton taxonomic group, a volumetric percentage was estimated visually from the total sample or from a representative subsample. These percentages were then converted to estimated species volumes.

Characteristic lengths of dominant species were measured along the longest axis to the nearest mm. For euphausiids, this was from the tip of the rostrum to the tip of the telson. In large samples, subsamples were measured. Selected samples were examined to determine sex and maturity stage. Adult females were identified by the presence of ripe or ripening eggs in the thoracic cavity or by spermatophores attached to the thylecum. Adult males were identified by the presence of fully developed secondary sexual characters (e.g. presence of external or internal spermatophores, fully developed petasma, and modified antennal appendages). Individuals with partially developed sexual characters were classified as subadult or juvenile. Naupliar stages, calyptopes and most early stage furcilia were lumped in one category as "larval euphausiids". After processing, the total sample (or a subsample if the total sample was > 1 l) was preserved for future reference in 10% buffered formalin.

Whale fecal samples were collected opportunistically with a dipnet or bucket and preserved in 10% buffered formalin for subsequent analysis to help determine whale prey preferences. An aliquot was taken from a well-mixed homogeneous sample and all right mandibles and spermatophores of euphausiids were removed and classified as *T. spinifera*, *E. pacifica*, *N. simplex* or unknown, as described in Kieckhefer (1992). Detailed methods and results of WHAPS96 plankton sampling are described in Armstrong and Smith (1997).

2.3. Oceanography

Oceanographic data were collected daily whether or not whales were present. A hull-mounted thermosalinograph collected continuous surface temperature and salinity data. Surface flourescence was measured continuously with a Turner Designs Model 111 flourometer in 1995 only. A CTD with a 12-bottle rosette was used to collect conductivity, temperature, and depth data and water samples for salinity and chlorophyll determinations. A full CTD station with water samples was occupied each day, two hours prior to sunrise. CTD casts were to 1000 m, water depth permitting. Chlorophyll samples, taken to 200 m, and salinity samples, from 0-, 500-, and 1000-m bottles were processed on board the ship.

Every day of the WHAPS95 survey, at two-hour intervals from 0800 to 0000, a mini-CTD/chlorophyll absorption-meter profile was conducted without collection of water samples. If the ship had not moved at least 5 km since the previous station, mini-CTDs were not conducted. During WHAPS96, the mini-CTD/chlorophyll absorption-meter system failed. Instead, additional CTD casts to 300 m were conducted at grid stations during the large-area survey and at the center and endpoint of daily small-area survey grids. Water samples were collected at 11 standard depths (0, 20, 40, 60, 80, 100, 120, 140, 170, 200, and 300 m). CTD casts without bottles were made at corners of each small-area grid where a bottle cast was not made.

In the CTD profiles, mixed layer depth was calculated as the depth at which temperature was 0.5°C less than the surface temperature. Thermocline and pycnocline depths and strengths were calculated as the depths and magnitudes of the maximum 10 m gradients in temperature and sigma-*t*. Stratification was calculated as the stratification parameter, $\bar{U} = 1/h\int_{h}^{0}(\rho - \bar{\rho})gz\,\mathrm{d}z$, representing the energy (joules m^{-3}) required to redistribute the mass of a water column of depth h by complete vertical mixing (Simpson et al., 1977). Here, $\bar{u}$ was integrated either to the bottom or to 200 m and then standardized by h, resulting in units of J m^{-4}.

3. Results

3.1. Oceanography

Maps of 10-m temperature and surface chlorophyll concentration (Fig. 2) show cold, high-chlorophyll water along the coast north of Point Conception and extending to the south and southeast past the westernmost Channel Islands. In the combined CTD station data from 1995 and 1996, 10-m temperature was correlated with pycnocline strength ($r = 0.76$, $n = 290$) and stratification ($r = 0.53$, $n = 252$), i.e. colder surface water was well-mixed. Surface chlorophyll concentration was strongly correlated, after log transformation, with mean euphotic zone chlorophyll concentration

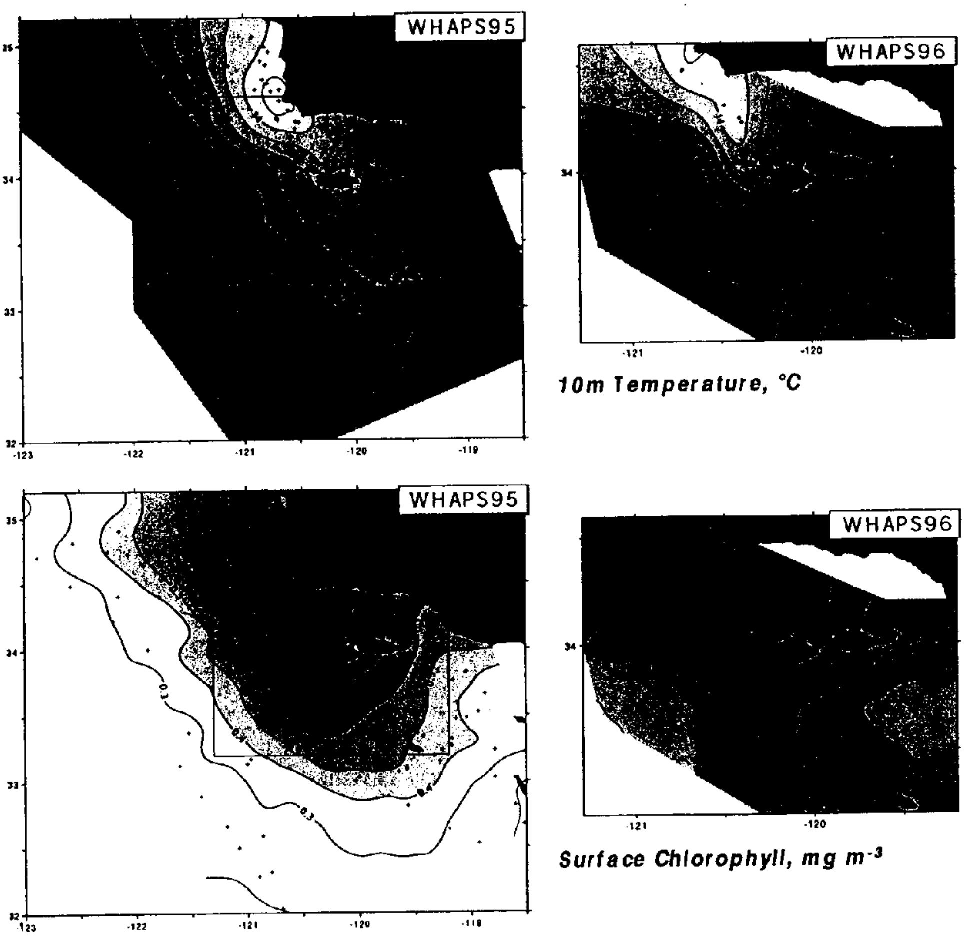

Fig. 2. 10 m temperature (°C) and surface chlorophyll concentration (mg m^{-3}) observed in August 1995 and July 1996.

($r = 0.93$, $n = 53$). In a principal component analysis of 10-m temperature and salinity, pycnocline depth and strength, stratification parameter, and surface chlorophyll concentration, about half the variance is explained by one factor (Table 1). High scores for this factor represent surface water that is relatively cold, well-mixed and productive, i.e. upwelled water. Warm, low-chlorophyll surface water was found to the east and southeast of the cold upwelled water.

3.2. Krill

Plankton species and species groupings are listed Table 2. *Euphausia pacifica* was common (> 5% by volume) in 52%, *Thysanoessa spinifera* in 14%, and *Nematoscelis difficilis* in 27% of 72 oblique IKMT tows in 1995 and 1996. The IKMT results show that *E. pacifica* and *N. difficilis* were more common near or offshore of the 200m shelf edge, while *T. spinifera* was more common in shelf waters < 150 m deep (Armstrong and Smith, 1997).

Distinct krill layers were detected acoustically around the Channel Islands in 1995 and 1996, although only the 1996 small-area survey results are presented here (Fig. 3). Mean profiles of S_v are shown to illustrate both the horizontal and vertical distribution of krill, which is indicated by the shaded occurrence of relatively high backscatter at 120 and 200 kHz. Note the presence of dense krill layers near the shelf edge at 100–200 m depth, and near the bottom on the broad shelf NW of San Miguel. A weak layer was detected off the shelf edge to the west of San Miguel. *Thysanoessa spinifera* and *Euphausia pacifica* were often caught in net tows where these layers were observed (Fig. 3, bottom). The krill layers located along the shelf edge north of the islands were predominantly *Euphausia pacifica*, while the layers on the shelf and to the east of Santa Rosa consist primarily of *Thysanoessa spinifera*. There is overlap in the distribution of these species at the shelf break.

Body lengths of *E. pacifica* ranged from 7.5 to 23.5 mm with a single mode at 16.4 mm for individuals caught both with the IKMT and MOCNESS in 1996. *T. spinifera* ranged in length from 4 to 29.5 mm with a single mode at 16.5 mm. Most of the *E. pacifica* catch were adults, while most of the *T. spinifera* catch were sub-adults and juveniles, based on length-at-maturity studies (Boden *et al.*, 1955). The

Table 1
Factor loadings (unrotated) from principal component analysis of selected oceanographic variables at $n = 242$ stations from WHAPS95 and WHAPS96.

	Factor 1	Factor 2
10 m Temperature	− 0.82	− 0.44
10 m Salinity	0.69	− 0.44
Pycnocline depth	− 0.28	0.77
Pycnocline strength	− 0.50	− 0.77
Stratification	− 0.89	0.28
Log Surface chlorophyll	0.89	0.03
Explained variance (λ)	3.06	1.64

Table 2
Plankton species and species groupings

Diatoms/Radiolaria
Hydrozoa
Scyphozoa
Ctenophora
Polychaeta
Ostracoda
Copepoda
Amphipoda
Euphausiacea
Euphausia pacifica
Thysanoessa spinifera
Nyctiphanes simplex
Nematocelis difficilis
Stylocheiron sp.
Other euphausiids[a]
Larval euphausiids
Decapoda
Gastropoda
Thecosomata/Gymnosomata
Other pelagic molluscs
Chaetognatha
Thaliacea
Larvacea
Larval fish
Adult fish
Fish/invertebrate eggs

[a]All euphausiid species, except larval forms, were identified to species. Incidental species were later lumped in this group.

nets were probably undersampling the larger euphausiids, especially adult *T. spinifera*, which are more adept at escaping the net (Brinton, 1967).

Copepods were often caught in net samples near the surface. Although individual copepods are smaller than euphausiids, patches of closely-spaced individuals can scatter low-frequency sound and are the most likely source of the high backscatter at all three frequencies observed during the day in the upper 50 m throughout much of the study area. Ctenophores and masses of diatoms and radiolarians were also common in some net samples, but are not strong scatterers.

3.3. *Whales*

Blue whales were abundant to the north of San Miguel and Santa Rosa Islands in both 1995 and 1996 (Fig. 4, top). Blue whales were also frequently observed to the west and south of San Miguel Island and on the southwest side of Santa Rosa Island in 1995, but few were seen there in 1996. Behavioral observations were recorded at enough sightings in 1995 to make some generalizations about feeding. Number of

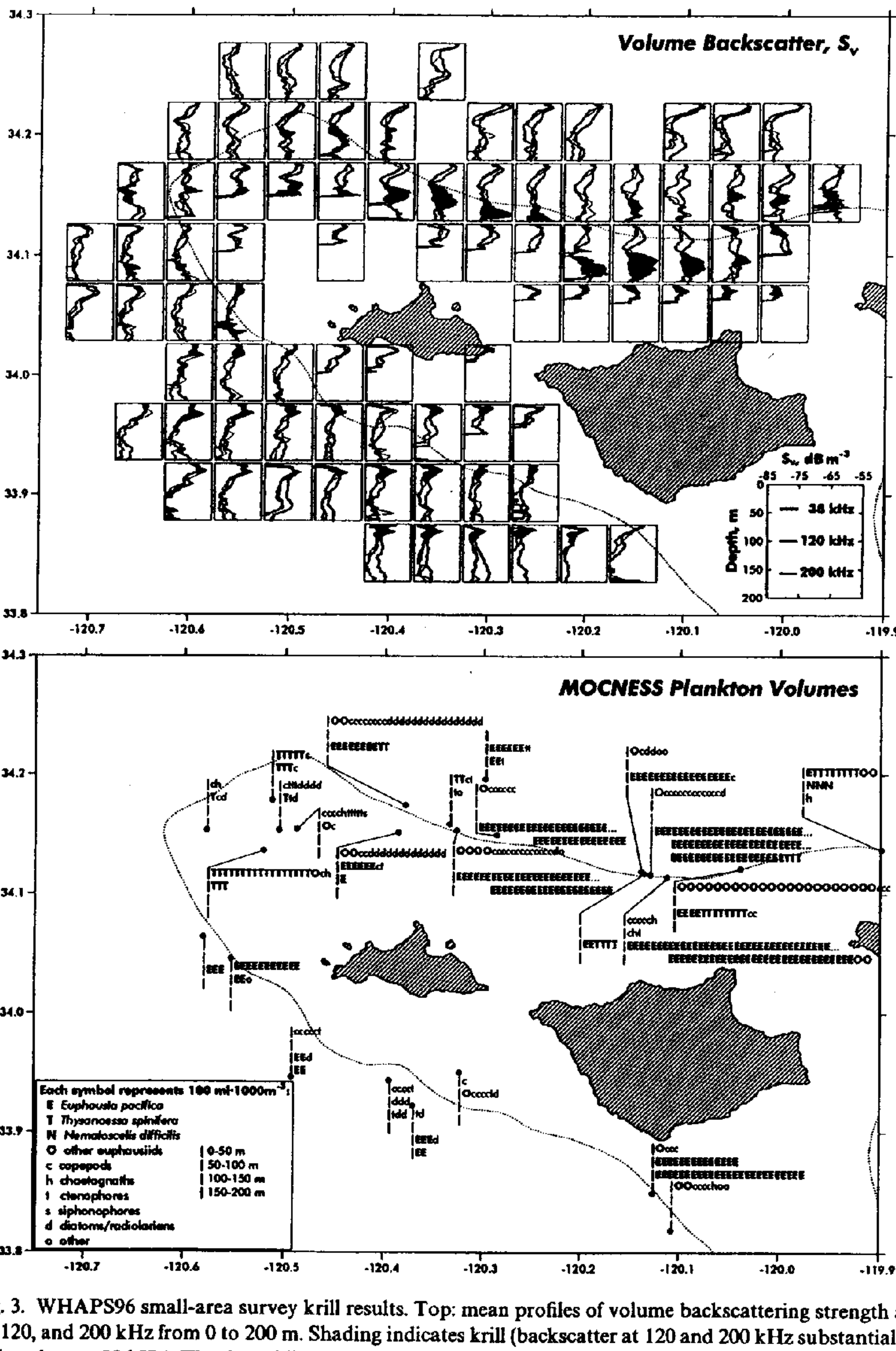

Fig. 3. WHAPS96 small-area survey krill results. Top: mean profiles of volume backscattering strength at 38, 120, and 200 kHz from 0 to 200 m. Shading indicates krill (backscatter at 120 and 200 kHz substantially higher than at 38 kHz). The dotted line is the 200-m isobath. Bottom: plankton volumes by category from MOCNESS tows, usually within a depth interval of a few meters, but displayed here in 50-m intervals.

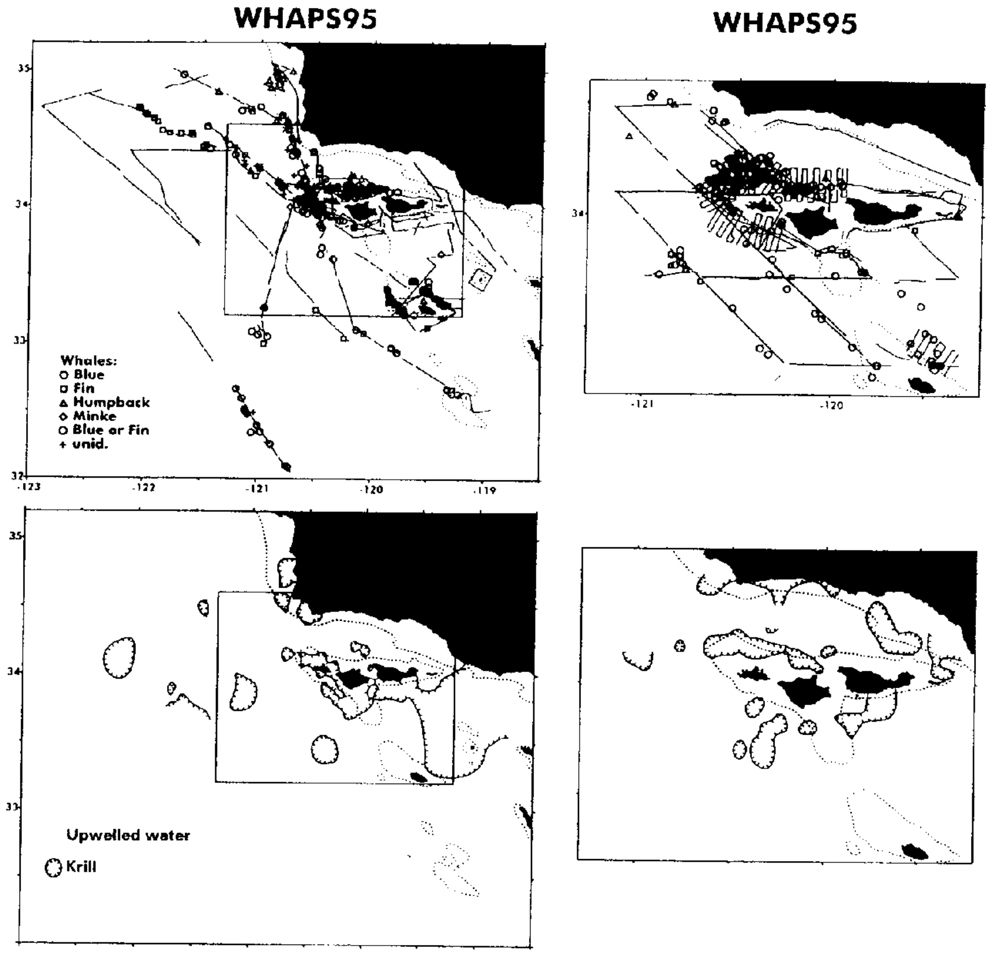

Fig. 4. Top: whale sightings (groups) during WHAPS95 and WHAPS96. Thin line is ship trackline when observers were on effort, dotted line is the 200-m isobath. Bottom: distributions of relatively cold, well-mixed and productive upwelled water (PCA factor 1 score > 0.3, Table 1) and areas of krill abundance ($\Delta S > 7$ dB).

sightings of cetacean species and other categories on WHAPS95 and WHAPS96 are listed in Table 3.

Feeding activity included repeated dives of 3–5 min in the same general area during the day. Towards dusk, when acoustic scattering layers migrated to the surface on the shipboard display, surface feeding behaviors were observed: rolling on the side and making tight circles at the surface with the pectoral fin in the air, and lunging at krill near the surface with mouth open. Feeding was noted at a significant fraction of blue whale sightings over the shelf (out to 3.5 km beyond the 200 m isobath) in three areas: around Santa Rosa and San Miguel Islands (10 of 30 sightings), north of San Nicolas

Table 3
Numbers of sightings of cetacean species and other categories on WHAPS95 and WHAPS96

Scientific name	Common name	WHAPS95	WHAPS96
Balaenoptera musculus	Blue whale	145	314
Balaenoptera physalus	Fin whale	62	16
Megaptera novaeangliae	Humpback whale	80	20
Balaenoptera acutorostrata	Minke whale	5	11
Balaenoptera sp.	Unidentified baleen whale	50	91
Delphinus sp.	Common dolphin	19	55
Delphinus capensis	Common dolphin, long-beaked	18	28
Delphinus delphis	Common dolphin, short-beaked	38	16
Tursiops truncatus	Bottlenose dolphin	13	7
Grampus griseus	Risso's dolphin	28	61
Lagenorhynchus obliquidens	Pacific white-sided dolphin	21	40
Lissodelphis borealis	Northern right whale dolphin	4	1
Phocoenoides dalli	Dall's porpoise	6	21
Orcinus orca	Killer whale	4	0
Mesoplodon sp.	Unidentified beaked whale	2	2
Berardius bairdii	Baird's beaked whale	1	3
	Unidentified dolphin	29	28
	Unidentified small whale	4	4
	Unidentified large whale	73	7

Island (3 of 7 sightings), and along the mainland coast from Pt. Conception north (2 of 4 sightings). In offshore waters, feeding was noted at only 1 of 15 sightings.

Many humpback whales were observed in the same general area as the feeding blue whales in 1995: north and west of San Miguel Island, and off Pt. Conception and along the coast to the north edge of the study area. In contrast to blue whales, no humpbacks were observed south of San Miguel or Santa Rosa Islands, and only one sighting was made in deep water beyond the shelf edge. In some cases, a group of humpback whales was observed feeding within one or two kilometers of a group of feeding blue whales. Feeding humpback whales were observed to surface with mouths open, sometimes in or near a small mass of bubbles. Pink krill escaping from the humpbacks was picked up by phalaropes waiting on the surface. Feeding was noted at a considerable fraction of humpback whale sightings over the shelf (out to 3.5 km beyond the 200-m isobath) in two areas: north of Santa Rosa and north and west of San Miguel Islands (6 of 19 sightings), and from Pt. Conception north (3 of 6 sightings). In other areas north of Pt. Conception and in the Santa Barbara Channel north of the shelf edge, feeding was not noted at 16 humpback sightings. Fin whales were also common in 1995, however they were not aggregated near the islands or coast north of Pt. Conception like blue or humpback whales. Feeding was noted at only 4 of 29 fin whale sightings, all in deep water.

Satellite-monitored radio tags were attached to blue whales by Oregon State University researchers during WHAPS95 and at other times in the Santa Barbara Channel. These tags provided information on the whales" movements and their dive patterns. Tagged blue whales exhibited great variability in their movements. Some whales remained for several weeks in the region of the Channel Island feeding grounds, frequenting the areas where whale aggregations were observed in 1995 (to the north of San Miguel and Santa Rosa Islands and to the west of San Miguel Island). Two whales tagged near San Nicolas Island remained there for several days, apparently feeding on the krill layers detected near the shelf edge on the NE side of the island. Other whales left the Channel Island feeding grounds and moved offshore, to

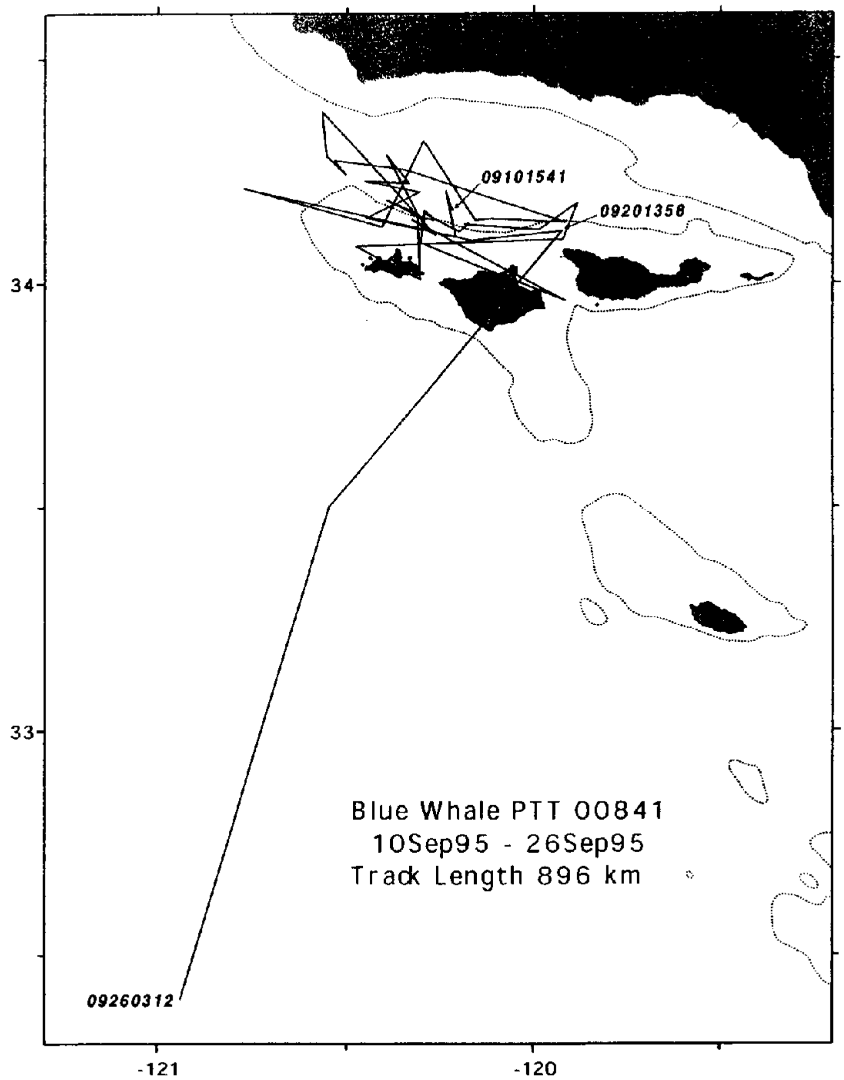

Fig. 5. ARGOS track of a blue whale tagged on 10 September 1995 on the Channel Island feeding grounds. Line segments connect locations obtained at intervals from 1.7 to 18.5 h, except for the last two segments (102.4 and 30.9 h). The dotted line is the 200-m isobath.

the north past San Francisco, or to the south off Baja California. A whale tagged on 11 September 1995, 9 days after WHAPS95, remained on the feeding grounds for at least 10 days after tagging, then moved rapidly to the south, possibly on its way to Baja California (Fig. 5).

Resightings of whales photographically identified during this study provide additional information about the movements of blue whales on and off the feeding grounds. Of 85 resightings of whales photo-identified during WHAPS95 (Calambokidis et al., 1996), most were over short intervals (< 9 km, often same day). Some whales moved between the west end of San Miguel and the north side of Santa Rosa Island. Two whales were resighted in November 1995 far from their original sighting location: one ~ 700 km north off Bodega Bay and one > 1100 km south off southern Baja California. Resightings in 1996 also indicated long movements along the coast both to the north (three whales resighted in the Gulf of the Farallones, off Monterey Bay, and off Morro Bay) and south (one whale to the southern Southern California Bight, Calambokidis et al., 1997).

Ship-monitored radio tags were attached to four blue whales during WHAPS96 and three of the whales were tracked. On 26 July, whale W4 was tagged near the shelf edge about 10 km north of San Miguel Island and tracked for 8 h as it moved 3.6 km north (Fig. 6). A 200 kHz echogram is illustrated: the S_v values range over about 30 dB. From 1400 to 1600, the whale dove on and swam through a krill layer just above the bottom on the shelf. At 1630, the krill layer rose off the bottom and dispersed somewhat, but the whale continued to follow it. At about 1840, the whale swam across the shelf edge and began to dive on a krill layer at about 150 m depth. The whale continued to follow the layer as the sun set and the krill migrated to the surface from 2000 to 2040.

A comparison of blue whale diet composition and krill availability on the Channel Island feeding grounds in 1996 shows a clear preference for adult *Thysanoessa spinifera* (Table 4). Krill caught in IKMT tows at two large-area survey stations north of San Miguel and Santa Rosa Islands was dominated by larval and juvenile euphausiids (from a very large catch in one tow) and *Euphausia pacifica*. Krill caught in MOCNESS tows on the shelf and near the shelf edge in this region was dominated by *E. pacifica*. These samples were often, but not always, targeted on strong acoustic scatterers. Identifiable remains in fecal samples were about half *T. spinifera* and half *E. pacifca*. These results indicate preference by blue whales for larger (adult) euphausiids and, among the adults, a preference for *T. spinifera* over *E. pacifica*.

4. Discussion and conclusions

The results of the Whale Habitat and Prey Studies show that blue whales aggregated near the Channel Islands during the summer, where they feed on dense patches of krill associated with the island shelf. Krill were most abundant along the shelf on the north and west sides of San Miguel Island and the north side of Santa Rosa Island. WHAPS was not designed to explain the aggregation of krill at this time and place, but some important factors are suggested by other studies.

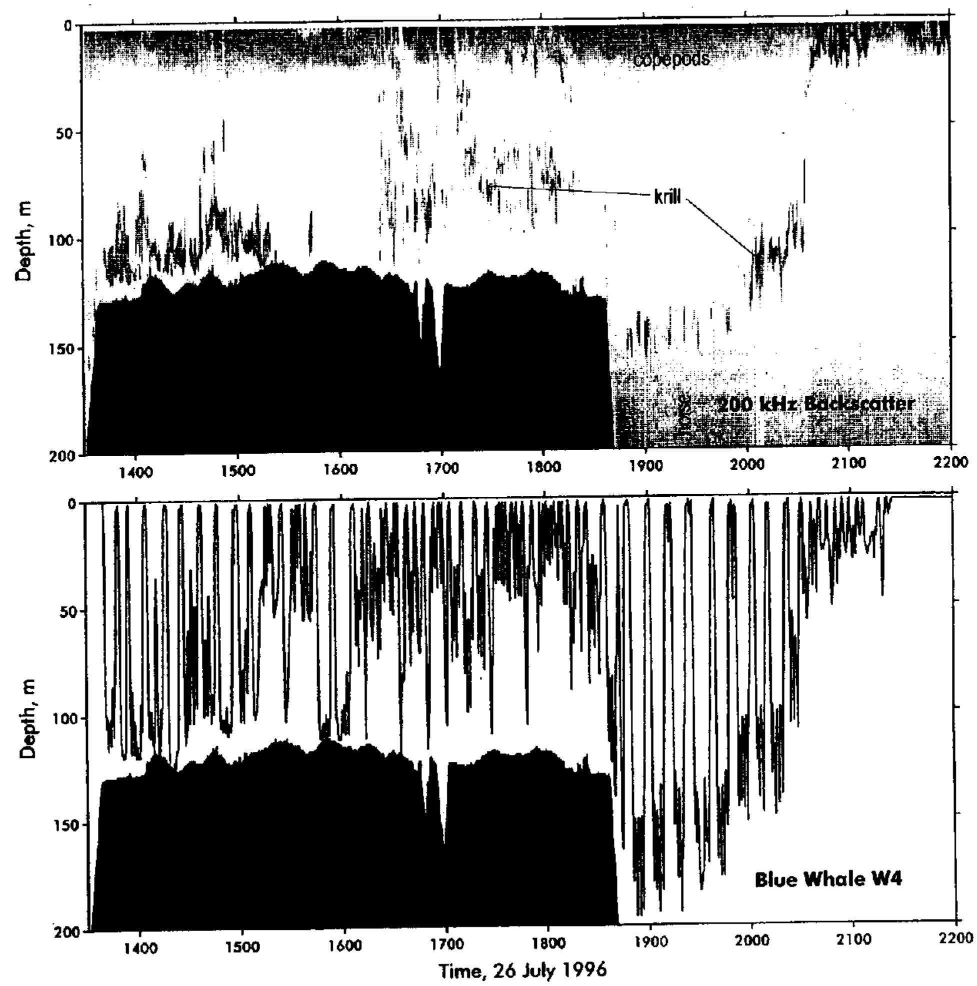

Fig. 6. Echogram (top) illustrating 200 kHz backscatter observed from NOAA Vessel Ballena while tracking radio-tagged blue whale W4 (time-depth record below).

Table 4
Euphausiid krill availability (from oblique IKMT and directed MOCNESS tows, percent by volume) and blue whale diet composition (from 13 fecal samples, percent by number) on the north sides of San Miguel and Santa Rosa Islands in July 1996

	T. spinifera	*E. pacifica*	*N. simplex*	Others
IKMT ($n = 8$)	2.4	41.5	0.0	56.1
MOCNESS ($n = 67$ in 18 tows)	19.2	73.5	0.8	6.5
Diet ($n = 13$)	44.8	48.6	0.7	5.9

Euatorward alongshore winds driving coastal upwelling are strongest in May–June along the California coast just north of Pt. Conception (35–37°N, Schwing and Mendelssohn, 1997). The upwelled water is moved offshore by Ekman transport and then entrained in the slow, southward flow of the California Current: the core of the current is about 200 km offshore at Point Conception in July, with flow at the surface of 9 cm s^{-1} (Lynn et al., 1982; Lynn and Simpson, 1987). Detailed studies of the new production cycle in the upwelling center at Point Conception have shown that nitrate in the cold, salty water upwelled to the surface results in moderate levels of new production (Dugdale and Wilkerson, 1989). Peak nitrate uptake and production of phytoplankton biomass occurs with a time delay of about 10 days. This translates to a spatial displacement on the order of 100 km as the upwelled water advects offshore and to the south. The local abundance of euphausiids, which consume phytoplankton and small zooplankton, may thus be explained by high primary (and secondary) production in the upwelled water advected south to the Channel Island feeding grounds.

Circulation in the Santa Barbara Channel may support retention of krill aggregations along the north side of San Miguel and Santa Rosa Islands: except during strong upwelling events, circulation during the summer is dominated by a cyclonic eddy in the western channel (Hendershott and Winant, 1996). Euphausiids were also abundant at shelf edge locations on the south side of the islands (Fig. 3) and along the mainland, and at offshore deep-water locations (Fig. 4). Bathymetry and the distribution of upwelled water (Fig. 4) suggest that an island shelf or shelf edge overlain by cool, unstratified water is necessary for krill patches to be exploited by blue whales.

The most abundant and common euphausiids in this region were *Euphausia pacifica*, *Nematoscelis difficilis* and *Thysanoessa spinifera*. All are are cold-water, northern species of the California Current (Brinton, 1981) although their vertical and horizontal distributions differ somewhat. *E. pacifica* ranges throughout the subarctic Pacific, including the Gulf of Alaska to as far south as 25°N. It performs extensive vertical migrations, off California the adults live at a daytime depth of 200–400 m rising to near the surface at night (Brinton, 1976). *N. difficilis* is predominant somewhat seaward and to the south of *E. pacifica* (Brinton, 1981) with adults occuring primarily below 200 m both night and day (Boden et al., 1955). *T. spinifera* is the most coastal species of the three, occurring in neritic waters mostly less than 100 m deep (Brinton, 1962). It occurs from the southeastern Bering sea south to northern Baja California, with regions of high density associated with centers of upwelling (Boden et al. 1955; Brinton, 1962). *E. pacifica* has continous recruitment year round with peaks associated with upwelling periods (Brinton, 1976). The larger *T. spinifera* has a discrete spawning season that extends from May to July off California, also coincident with strongest upwelling (Brinton, 1981).

Blue whales are the most selective feeders of the baleen whales and are known to consume *E. pacifica* and *T. spinifera*, but not *N. difficilis*, in the North Pacific (Yochem and Leatherwood, 1985). Although *Nyctiphanes simplex* is heavily preyed upon by blue whales in Mexican waters, it occurred in only small numbers in our samples. This is a southerly neritic species usually found south of Point Conception to Mexico, with a complementary distribution to *T. spinifera* and common in the Southern California

Bight only during warm years (Brinton, 1981). Like *T. spinifera*, it is found above 200-m and associated with areas of upwelling (Gendron, 1992; Brinton and Townsend, 1980). It is particularly abundant and consumed by blue whales in the Gulf of California during March and April (Gendron, 1992), but was not an important krill species in the Channel Islands.

The two most common krill species on the Channel Island feeding grounds were found in different locations. *E. pacifica* was more abundant at the shelf edge and extending off the edge of the shelf in dense layers at 150–200-m depth during the day. The coastal species *T. spinifera* was most abundant on the shelf, especially the broad shelf extending NW from San Miguel Island, at 50–150-m depth during the day. Analysis of diet composition, based on a few fecal samples, suggests a preference for *T. spinifera*. This preference may be related to the larger size of adults and to the availability of dense patches on the shelf. During the course of WHAPS96, when two research vessels visited the feeding grounds repeatedly during the month of July, blue whales seemed to become less abundant north of Santa Rosa Island, where they were feeding on *E. pacifica* at the shelf edge, as they became more abundant north of San Miguel Island, where they fed on *T. spinifera* on the shelf.

Blue whales may be taking advantage of the seasonal swarming behavior of *Thysanoessa spinifera* in relatively shallow water. This swarming appears to be related to sexual development (Brinton, 1981; Smith and Adams, 1988). From May to July, it forms extensive inshore surface swarms as fully mature adults (females 25 mm, males 21 mm mean TL) during the peak of the upwelling season (Smith and Adams, 1988). These reproductive adults are thought to swarm, breed and then presumably die at the end of their three-year life cycle (Nemoto, 1957). Indeed, swarms of spent females have washed up on beaches at La Jolla, California (Brinton, 1962) and at Bandon, Oregon (Pearcy and Hosie, 1985). These spring breeding swarms may be spared whale predation from April to June when blue whales of this population are still at lower latitude winter feeding grounds, but the new cohort beginning sexual development mid-summer to fall is obviously vulnerable and accessible to feeding whales. Those we sampled from dense swarms were generally sub-adults just beginning sexual development, similar to *T. spinifera* whale-associated swarms sampled by others in late summer and fall further north off central California (Kieckhefer, 1992; Schoenherr, 1991; Smith, unpublished data). These authors also found surface and subsurface *T. spinifera* swarms to be composed primarily of sexually developing females and males (15–18 mm TL). Thus, it appears that summer feeding whales exploit large aggregations of sub-adult *T. spinifera* just beginning their sexual development in the upwelling-rich neritic waters surrounding the northern Channel Islands.

The environmental characteristics that make the northern Channel Islands a good site for summer feeding by blue whales may apply to other locations in the California Current system. Blue whales also feed on surface swarms and subsurface layers of *T. spinifera* along the edge of the Monterey Submarine Canyon (Schoenherr, 1991). *T. spinifera* swarms have also been observed over the broad continental shelf in the Gulf of the Farallones, around the Farallon Islands off San Francisco Bay (Smith and

Adams, 1988), where blue whales are abundant during the summer (Calambokidis et al., 1997). Individual blue whales photographically identified near the Channel Islands have been resighted both within and between years at these central California sites, as well as off northern California and off southern Baja California and in the southern Gulf of California (Calambokidis et al., 1996).

Blue whale feeding aggregations are dynamic: whales move onto and perhaps between feeding grounds during summer, but on the feeding grounds they aggregate, move, and disperse from day to day. The dynamics of prey aggregations may be a very important factor affecting whale distribution and activity during their stay on the feeding grounds and merit further study.

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