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An integrated approch to the foraging ecology of marine birds and mammals

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Abstract

Birds and mammals are important components of pelagic marine ecosystems, but our knowledge of their foraging ecology is limited. We distinguish six distinct types of data that can be used in various combinations to understand their foraging behavior and ecology. We describe methods that combine concurrent dive recorder deployment, oceanographic sampling, and hydroacoustic surveys to generate hypotheses about interactions between the physical environment and the distribution, abundance, and behavior of pelagic predators and their prey. Our approach is to (1) map the distribution of whales in relation to the distribution of their prey and the physical features of the study area (bottom topography, temperature, and salinity); and (2) measure the foraging behavior and diet of instrumented whales in the context of the fine-scale distribution and composition of their prey and the physical environment. We use this approach to demonstrate a relationship between blue whale distribution, sea surface temperature, and concentrations of their euphausiid prey at different spatial scales offshore of the Channel Islands, California. Blue whale horizontal spatial distribution was correlated with regions of high acoustic backscatter. Blue whale dive depths closely tracked the depth distribution of krill. Net sampling and whale diet revealed that whales fed exclusively upon dense schools of *Euphausia pacifica* (between 100 and 200 m) and *Thysanoessa spinifera* (from the surface to 100 m). Whales concentrated foraging efforts upon those dense euphausiid schools

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that form downstream from an upwelling center in close proximity to regions of steep topographic relief. We propose that (1) the distribution of *Balaenoptera* whales in the coastal California Current region is defined by their attraction to areas of predictably high prey density; (2) the preferred prey of these whales are several species of euphausiids (*E. pacifica*, *T. spinifera*, *and N. simplex*) that are abundant in the California Current region; (3) blue whales concentrate their foraging efforts on dense aggregations of euphausiids found at discrete depths in the water column; (4) these localized areas of high euphausiid densities are predictable and sustained by enhanced levels of primary productivity in regions which are located downstream from coastal upwelling centers (indicated by sea surface temperature); (5) topographic breaks in the continental shelf located downstream from these upwelling centers work in concert with euphausiid behavior to collect and maintain large concentrations of euphausiids swarms, and (6) despite seasonal and inter-annual variability, these processes are sufficiently consistent that the distribution of *Balaenoptera* whales can be predicted.

1. Introduction

Birds and mammals are important top-level predators in marine ecosystems. They can consume significant quantities of prey (Furness and Cooper, 1982; Duffy and Schneider, 1994; Croll and Tershy, 1988), affect the distribution and abundance of prey species (Birt et al., 1987), and may serve to structure marine communities (Estes and Palmisano, 1974; Oliver and Slattery, 1985; Oliver et al., 1985; VanBlaricom and Estes, 1987). However, most detailed studies of marine birds and mammals have focused on their breeding activities on land or in calving areas where little feeding occurs (see papers in Burger et al., 1980; Payne, 1983; Jones et al., 1984; Ainley and Boekelheide, 1990). Consequently, the behavior and ecology of marine birds and mammals at sea have, until recently, been poorly understood (Costa, 1993). This has been especially true for pelagic marine mammals and diving seabirds since little is known about their behavior below the water surface, where they spend up to 95% of their time (Costa, 1993).

Six distinct types of data can be used in various combinations to understand the foraging behavior and ecology of marine birds and mammals: (1) the distribution and abundance of the predators at large and small spatial scales; (2) the horizontal and vertical movements of individuals at large and small temporal scales; (3) the physical oceanography of the region from the literature, concurrent remote sampling, and/or on-board data collection; (4) measures of prey availability (abundance and distribution) based on fisheries data, hydroacoustic sampling, or net hauls; (5) predator diet; and (6) fitness measures of foraging success such as growth, survival, and reproductive success. Individually, each of these are important in understanding the foraging ecology and behavior of marine predators. However, we believe that the most significant gains can be made by combining multiple data sets (see also Costa, 1993), especially when data are collected concurrently.

In the last 15 years, the development and widespread application of recoverable data loggers and satellite tags have revolutionized our understanding of the diving behavior of pelagic marine mammals and diving birds (Costa, 1993). Gains have been most impressive with pinnipeds and penguins (e.g. Leboeuf et al., 1983; Gentry and Kooyman 1986; Kooyman, 1989; Hindell et al., 1991; Delong et al., 1992), due to the relative ease with which they can be instrumented. These descriptive studies have helped set the stage for more theoretical or hypothesis-driven studies (e.g. Costa, 1991; Houston and Carbone, 1992; Arnould et al., 1996; Boyd, 1996; Carbone and Houston, 1996) which attempt to test hypotheses about foraging strategies in diving animals. At the same time, the development of hydroacoustic prey sampling technology has significantly expanded our knowledge of the distribution and abundance of schooling fishes and invertebrates. However, these technologies rarely have been combined to examine interactions between pelagic endothermic predators and their prey.

The combination of these two techniques with the addition of concurrently collected data on the physical environment allow, for the first time, a detailed examination of how biotic and abiotic environmental parameters can be used to predict the temporal and spatial distribution of pelagic predators. Coastally feeding blue whales from the southeastern North Pacific are ideal organisms for such a combined approach for several reasons: (1) in this region, they feed almost exclusively on euphausiid crustaceans (Schoenherr, 1991; Tershy et al., 1993; Croll et al., 1998); (2) they feed by engulfing schools of prey, rather than capturing individuals (Lambertson, 1983; Würsig, 1990), and these schools of prey are amenable to net sampling and hydroacoustic estimates of distribution and abundance; and (3) their distribution and movements should be closely related to the distribution and behavior of their prey since, unlike most breeding seabirds and pinnipeds, they are not central place foragers. In addition, due to their large size they are also less likely to be influenced by the distribution of predators, suitable breeding sites, and water temperature. Unfortunately, unlike colonially breeding pinnipeds or seabirds, it is not possible to quantify ultimate measures of foraging success such as changes in offspring weight and number or adult body weight in *Balaenoptera* whales.

We have combined radio tracking, deployment of time-depth recorders, active hydroacoustic prey sampling, and oceanographic sampling techniques to study, within an ecological context, the foraging behavior of *Balaenoptera* whales at several locations along the coast of North America (Gulf of California, Channel Islands, Monterey Bay). In this paper we describe our approach and review results from a study of blue whales in the vicinity of the Channel Islands, California (Whale Habitat and Prey Study, 1995–1996; Fiedler et al., 1998) to examine interactions between the physical environment, and the distribution, abundance, and behavior of blue whales and their primary prey, euphausiids.

2. Methods

2.1. Integrated approach

The study was conducted in the vicinity of the Channel Islands off Southern California (Fig. 1). In general, our approach was to: (1) map whale distribution in relation to the large-area (1000s of km^2) distribution of their prey and the physical features of the study area (bottom topography, temperature, and salinity); (2) measure the small-area (100s of km^2) distribution of whales, distribution and composition of schooling zooplankton, and above physical features of the study area; and (3) measure the foraging behavior and diet of the whale in the context of krill distribution and composition.

2.2. *Large-area surveys*

Large-area surveys ($\sim 1000\ km^2$) were conducted between July 11–16, 1996 on board the NOAA ship *David Starr Jordan* in a regular grid pattern at a ship speed of ~ 20 km/h to document large scale patterns in cetacean and prey distributions, hydrography, and bathymetry (Fig. 1). Methods for marine mammal surveys are detailed in Fiedler et al. (1998). Briefly, three marine mammal observers surveyed from the track line out 90° abeam using 25 × 150 high-powered binoculars mounted on the ship's flying bridge. Species, number of individuals, sighting cue, behavior, location, time, and weather conditions are recorded at the time of each marine mammal sighting. Angle and distance of sighting are estimated using an azimuth ring and reticle line incorporated into the binoculars. Conductivity, temperature and depth (CTD) casts were made at regular station intervals within the study grid. Continuous underway measurements of temperature, salinity and light transmission also were recorded while underway.

2.3. *Small-area surveys*

Small-area surveys were conducted between July 17–21, 1996 in areas identified during our large area surveys as having relatively dense concentrations of marine mammals or prey. The area covered was on the order of 100 km^2 with transect spacing 2.8 km. Observations of marine mammals and prey were made in the same manner as described above for large area surveys.

2.4. *Hydroacoustic sampling*

The vertical and horizontal distributions of prey were measured along survey track-lines using a Simrad EK-500 (Simrad, Redmond, WA) echosounder system operating at 38, 120, and 200 kHz. The transducers were mounted on a fairing that extended approximately 50 cm from the hull of the ship. The systems were calibrated before and after each study period using the standard sphere method (Johannesson and Mitson, 1983). At each frequency, echo-power was sampled every 10, 3, and 2 cm, for the 38, 120, and 200 kHz echosounders, respectively. Adjustments were made for spherical spreading and absorption losses. These values were averaged in range so as to produce a set of 250 or 500 recorded values (indexed by date, time, and geographic position) for each ping (typically 2 s^{-1}). The vertical distribution of prey was illustrated by rendering these volume backscattering strength measurements (SV) as echograms.

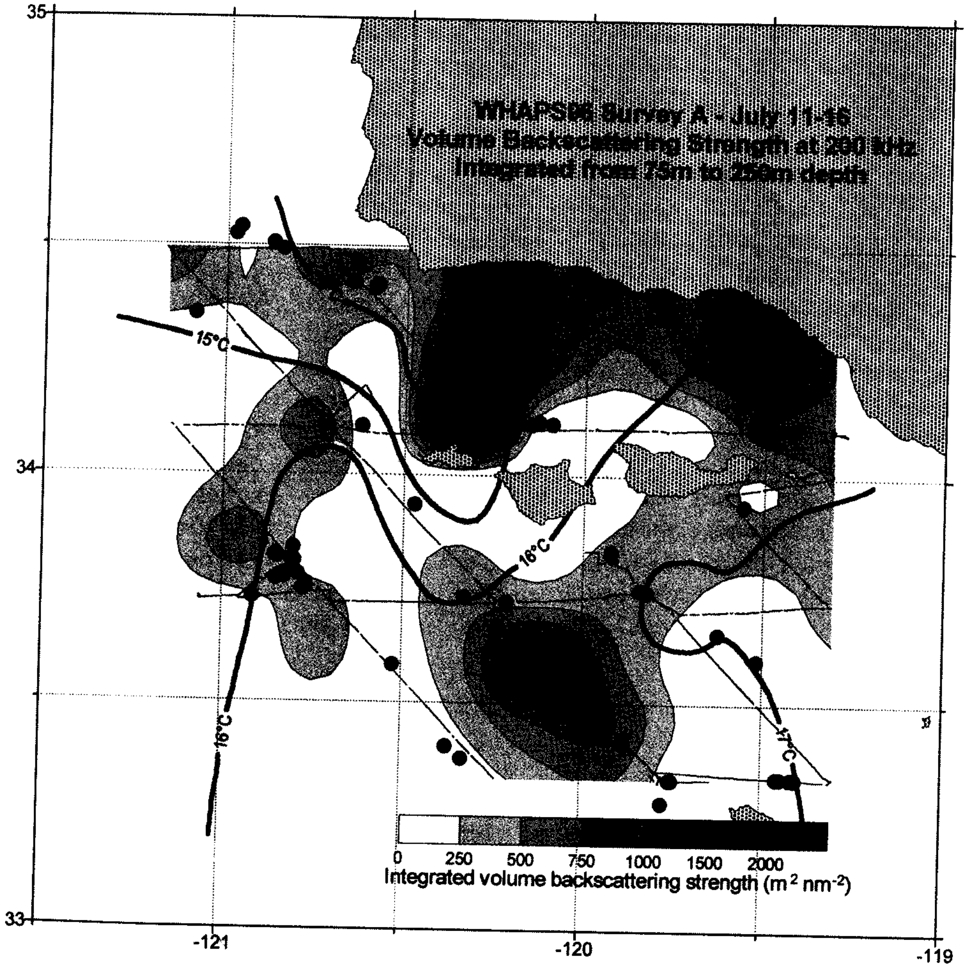


Fig. 1. Large-area survey conducted in the vicinity of the Santa Barbara Channel Islands July, 1996. Isotherms (drawn from 10 m temperature data collected during CTD casts) indicate cold upwelled water extending south from Point Conception into the Channel Islands. Within the upwelled water is an area of high volume backscattering strength integrated from 75 to 200 m depth, the daytime depth range of euphausiids targeted by foraging whales. Dotted lines indicate ship tracklines during the survey, circles indicate surface sightings of rorqual whales.

To elucidate the horizontal distribution of prey, SV thresholded at -81 dB was filtered to exclude non-biological sources (i.e. bottom and bubble echoes), integrated vertically over the depth range of interest, and averaged over horizontal intervals of 185 m (18–30 pings depending on vessel speed). These integrated volume backscattering strengths (Sa) were gridded (spacing equals approximately 1/3 transect spacing), using kriging methods (Surfer, Golden Software, Colorado), and contoured.

2.5. Net sampling

Acoustically detected aggregations and layers of prey were sampled with a Multiple Opening-Closing Net and Environmental Sampling System (MOCNESS) with 505 μm mesh nets. The MOCNESS collected vertically stratified samples with four nets, each with a $1\ m^2$ opening. Nets were usually towed horizontally through targeted layers, but occasionally were towed obliquely through a depth range if the targeted layer was thick or migrating.

Samples were processed within one hour of tow completion. Wet biomass (displacement volume) (Kramer et al., 1972) and volumetric percentage of major planktonic taxa (from total sample or representative subsample) were measured. Characteristic length measurements (along longest axis) were taken for dominant species. Large samples were subsampled for measurement. Euphausiid samples were identified to sex where sexual characters were discernable (females determined by presence of ripening eggs or spermatophores attached to thylecum, males determined by secondary sex characteristics and fully developed petasma); the remainder were classified as larval/juvenile euphausiids. Processed samples were archived in 10% buffered formalin.

2.6. Whale diet

The diet of blue whales was determined through analysis of fecal samples opportunistically collected from whales as they surfaced. Surface defecations of whales encountered during all operations were collected with a 167 μm mesh plankton net and preserved in 10% formalin. Samples were later analyzed for whale diet composition based upon identifiable prey remains (Kieckhefer, 1992). Briefly, 2.5 ml aliquots were randomly subsampled, and all euphausiid right mandibles and spermatophores were identified to species and counted. In order to convert mandible lengths to standard body lengths (tip of rostrum to tip of telson), a sample of euphausiids from California waters was collected with a standard, vertically towed, plankton net (0.75 m diameter, 505 μm mesh). Standard body lengths (to the nearest 1 mm) of *T. spinifera* ($n = 169$) and *E. pacifica* ($n = 144$) taken from plankton samples were correlated with dissected right mandible lengths (tip of incisors to tip of mandibular insertion) measured to the nearest 0.1 mm with an image analyzer (Javelin Color Video Microscope Camera) and NIH Image software. The resulting relationship was applied to right mandible lengths measured in fecal samples to estimate euphausiid standard body lengths for *T. spinifera* and *E. pacifica*.

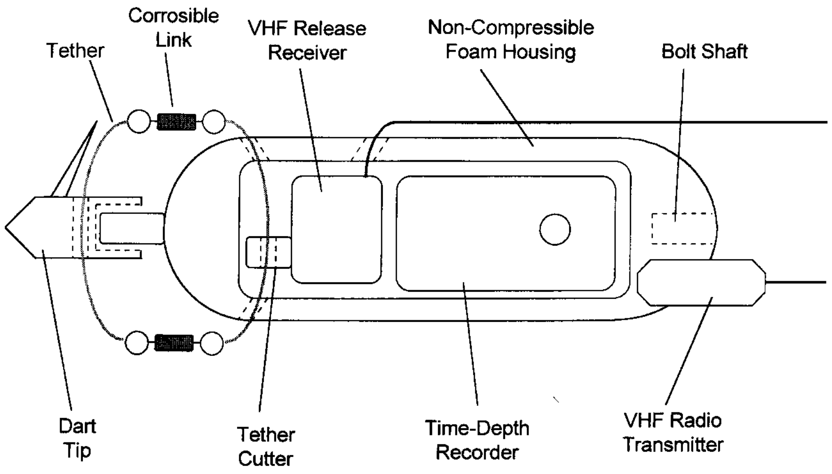
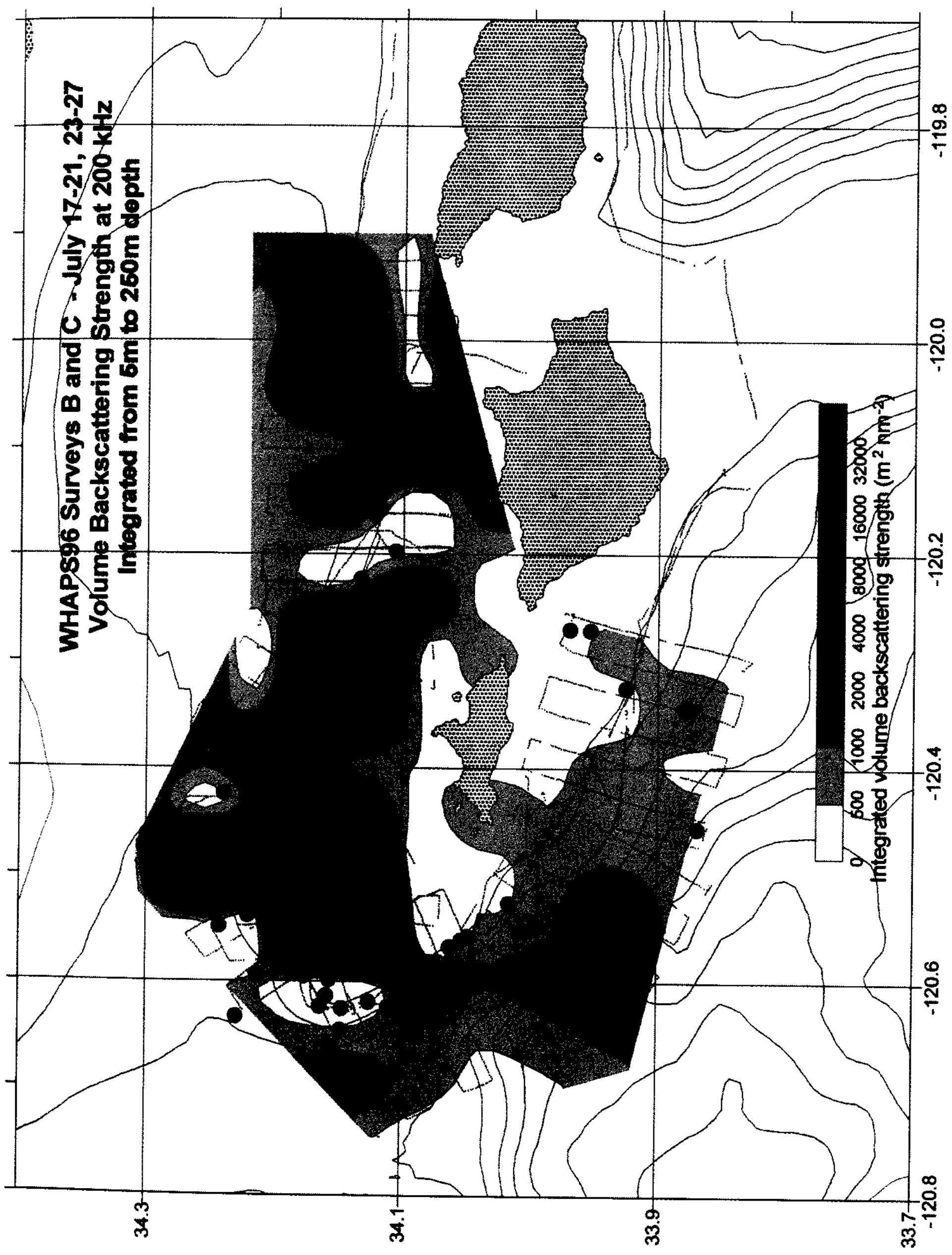


Fig. 2. Design of time-depth recorder package for study of foraging behavior of *Balaenoptera* whales.

2.7. Foraging behavior of whales

During small area surveys, recoverable electronic devices (Figure 2) were attached to blue whales foraging in the vicinity of prey patches identified during small-area surveys from a small rigid-hulled inflatable boat. The tag was attached, using a compound crossbow, to the dorsal surface of the whale 2–3 m caudal of the blowhole. Attempts were made to tag during a non-terminal portion of a surface respiration sequence. The tags consisted of a syntactic foam housing which contained: (1) a Wildlife Computers (Redmond, Wa.) Mk 5 time/depth/temperature recording device (TDR) potted in syntactic (noncompressible) foam, (2) a VHF radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota) to permit tracking of the tagged whale; and (3) a radio activated release mechanism (Jamie Stamps, Livermore, Ca.) (Fig. 2). Corrosible links were placed in-line on the tether to provide a secondary electro-chemical release. The package was released from the animal via a signal from the release transmitter which activated an on-board line cutter (Quantic Industries, Hollister, CA). Once released, the package was designed to float with the VHF antenna above the water surface to allow localization for recovery. Time, depth, and temperature were logged at 1-sec intervals. Tagged whales were tracked from a separate vessel (R/V Ballena) which contained on board a directional VHF radio tracking system, Simrad EY-500 38 and 200 kHz echosounder systems, and a package release

Fig. 3. Small-area survey conducted in the vicinity of the shelf break around the western end of the Santa Barbara Islands. Two hundred meter depth contours are shown. Areas of high volume backscattering strength integrated from the transducer to 250 m or to the bottom if shallower were mapped along the shelf break north of the islands. Dotted lines indicate ship tracklines during the survey, circles indicate surface sightings of rorqual whales.



radio transmitter. While tracking the whale, the vertical distribution of prey were continuously logged.

Visual observations of the behavior of the tagged animal (speed and direction of movement and proximity of conspecifics) were noted at each surface interval. Once released from the whale, the floating package was localized and recovered using the directional VHF system for data download.

3. Results

3.1. Distribution and abundance of euphausiids and blue whales

High hydroacoustic volume backscatter strength at 200 kHz and high whale densities were encountered during large-area surveys in the Santa Barbara Channel area north of San Miguel/Santa Rosa Islands (Fig. 1). Sea surface temperature data show that this area was located in a mass of cold, well mixed water extending south from an upwelling center off Pt. Conception (Fig. 1). Small-area surveys of the detailed structure of these backscatter concentrations demonstrate that highest backscatter was encountered along the shelf break north of the islands, and whale concentrations were tightly linked to these concentrations (Fig. 3).

Daytime hydroacoustic backscatter concentrations at 200 kHz were found on the north sides of San Miguel and Santa Rosa islands between the surface and 50 m over the shelf and between 100 and 175 m off the shelf break (Figs. 4 and 5).

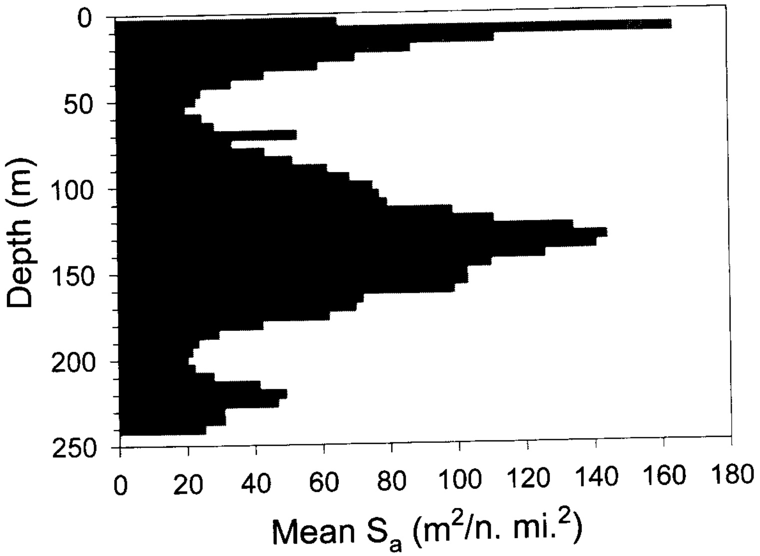


Fig. 4. Acoustic backscatter by depth from 200 kHz echosounder small-area surveys in the vicinity of San Miguel and Santa Rosa Islands, Channel Islands, California.

3.2. Net samples and whale diet

Thysanoessa spinifera and *Euphausia pacifica* were the dominant species of krill sampled by the MOCNESS nets in hydroacoustically identified layers (Table 1). During the day, *T. spinifera* (juvenile and sub adults, mean body length 17.5 mm, range 6–30.5 mm) was the dominant species found in euphausiid layers located over the shelf from the surface down to 50 m. *E. pacifica* (adults, mean body length 15.7 mm, range 7.0–22.5 mm) dominated krill layers sampled off the shelf from 100 to 175 m.

Whale fecal material sampled in the study area consisted exclusively of *T. spinifera* (mean calculated body length 18.3 mm, range 10.8–27.8 mm) and *E. pacifica* (mean calculated body length 15.3 mm, range 10.0–23.9 mm) and reflected the composition of net samples taken in the same area (Table 1).

3.3. Whale foraging behavior

A total of 200 foraging dives were sampled for four blue whales. Dive depth averaged 68.1 m (± S.D. 57.5 m), dive duration averaged 4.3 min (± S.D. 2.9 min). Blue whale dive effort was concentrated on dense euphausiid schools indicated by high acoustic volume backscatter at 200 kHz (Fig. 4), and whale dive depth tracked the vertical migration of the backscatter layer towards the surface at sunset (Fig. 5).

4. Discussion

Oceanographic heterogeneity leads to patchiness of prey, temporal changes in prey distribution and abundance, and short term changes in prey behavior. These in turn are fundamentally important in determining the distribution, abundance, behavior, reproduction, and foraging success of marine mammals. Pinniped, cetacean, and seabird distribution patterns have been shown to be closely correlated with a number of oceanographic phenomena: thermoclines, fronts, upwelling plumes, Langmuir cells, and large scale patterns in temperature, productivity, and prey (e.g. Whitehead and Glass, 1985; Payne et al., 1986, 1990; Boyd and Arnbom, 1991; Piatt and Methaven, 1992; Kenney et al., 1995; Winn et al., 1995). Fewer studies have examined the correlation between diving predator foraging behavior and the distribution of prey (e.g. Antarctic fur seal dive patterns and the vertical distribution of krill (Croxall et al.,

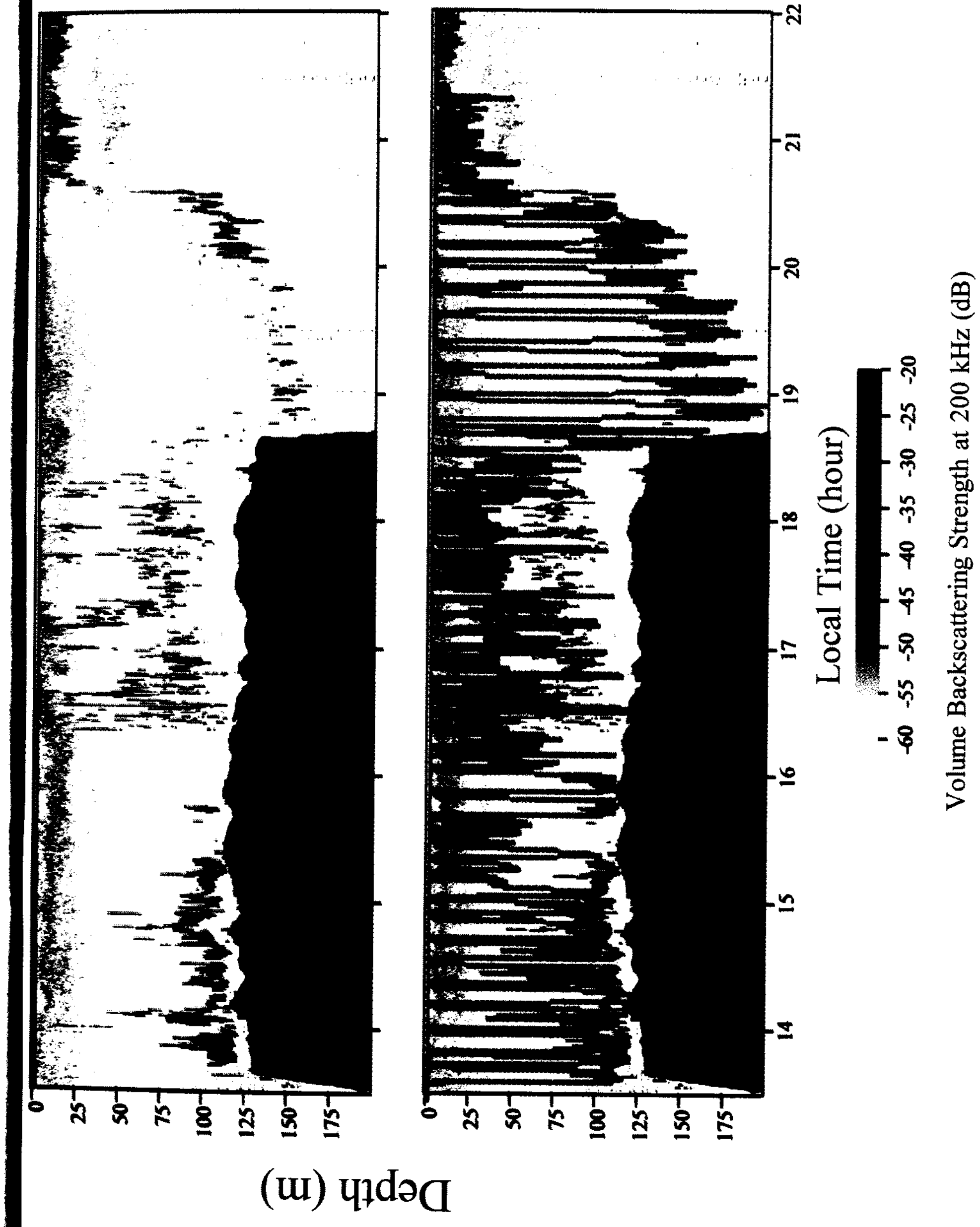


Fig. 5. Top panel: echogram recorded from 200 kHz echosounder on the *R/V Ballena* while tracking foraging blue whale with attached TDR North of San Miguel Island, Channel Islands. Bottom Panel: dive record of foraging blue whale superimposed on echogram. Whale initially fed on aggregations of *T. spinifera* over the shelf, and subsequently switched to feeding on aggregations of *E. pacifica* adjacent to the shelf break (Modified from Fiedler et al., in press).

Table 1
Percent composition of diet of blue whales (by number) and MOCNESS net samples (by volume) and MOCNESS sampling depth taken in the Channel Islands, California during the Whale Habitat and Prey Study July 1996

	T. spinifera	*E. pacifica*	*N. simplex*	Larval Euphausiid	Copepod	Unknown Euphausiid
Whale diet	48.2	45.5	0.2	0	0	6.1
Net samples						
50 m	49.5	0.2	0.4	9.1	40.8	0
100 m	16.6	81.5	0.2	0.2	1.5	0
150 m	17.1	78.2	0	0.8	3.9	0
200 m	4.0	95.9	0	0	0.1	0
250 m	0	98.1	0	0	1.9	0
Mean	17.4	70.8	0.1	2.0	9.6	0

1985); pinniped haulout patterns and the diel behavior of krill (Fraser et al., 1989); right whale dive patterns and zooplankton distribution (Winn et al., 1995); and baleen whale occurrence and schooling fish density (Piatt and Methaven, 1992).

Since at least 1986, the California population of blue whales has been observed to forage consistently in specific regions of the California coast between June and October (Gulf of the Farallones/Cordell Bank, Monterey Bay, and Channel Islands) (Schoenherr, 1991; Fiedler et al., 1998, J. Calambokidus, pers. comm.; R. Ternullo and N. Black, pers. comm.; D.A. Croll and B.R. Tershy, pers. obs.). While Shoenherr (1991) documented blue whales in the Monterey Bay region feeding upon surface swarms of *Thysanoessa spinifera*, the linkage between seasonal foraging blue whales, prey abundance, and the physical dynamics have not been well understood. Through our integrated approach, we found that blue whales concentrate their foraging efforts on euphausiids aggregated on the shelf break of the Santa Barbara Channel downstream from an upwelling center off of Point Conception. Fiedler et al. (1998) found that upwelled water, characterized by low temperature and high chlorophyll concentration, was advected south across the Santa Barbara Channel towards San Miguel and Western Santa Rosa Islands. It is likely that this productive water supports the aggregations of *Euphausia pacifica* and *Thysanoessa spinifera* we found aggregated over and adjacent to the shelf break north of San Miguel and Santa Rosa islands. The topographic break in the shelf beneath the upwelled water provides water depths in excess of 200 m, which allows euphausiids to undergo their characteristic diel migration behavior. This feature also may serve to concentrate both euphausiids and phytoplankton through currents or internal waves (Genin et al., 1988). Thus, these dynamics result in large aggregations of *T. spinifera* from the surface to 50 m over the shelf and *E. pacifica* between 100 and 175 m adjacent to the shelf break. Blue whales forage almost exclusively on these species (Table 1), and whale foraging depth corresponds to the densest vertical layers of euphausiids (Fig. 5). In addition, the dive depths of the whales track the diel migration of the euphausiids as they rise to the surface at night (Fig. 5). The lengths of both *E. pacifica* and *T. spinifera* found in whale feces were longer than those measured in net samples. This may have resulted from size selection by the whales (through passive selection by the baleen of the whale) or net avoidance by larger euphausiids (Fiedler et al., 1998).

Our data support the following hypotheses:

(1) the distribution of *Balaenoptera* whales in the coastal California Current region is determined by their attraction to areas of predictably high prey density,
(2) the preferred prey of these whales are two species of euphausiids (*E. pacifica* and *T. spinifera*) that are abundant in the California Current region,
(3) blue whales concentrate their foraging efforts on dense aggregations of euphausiids found at discrete depths in the water column,
(4) these localized areas of high euphausiid densities are predictable and sustained by enhanced levels of primary productivity in regions which are located downstream from coastal upwelling centers,
(5) topographic breaks in the continental shelf located downstream from these upwelling centers work in concert with euphausiid behavior to collect and maintain large concentrations of euphausiids swarms.

We further speculate that, despite seasonal and interannual variability, these processes are of sufficient consistency that the distribution of *Balaenoptera* whales can be predicted.

Progress in our understanding of the ecology of pelagic species has been limited by the ability to concurrently measure diving behavior within the context of appropriate environmental parameters (Costa, 1993). Recent developments in the fields of hydroacoustics, time-depth recorders, and satellite navigation have enabled us to combine these technologies to enhance our understanding of the foraging ecology of marine birds and mammals (Fiedler et al., 1998). This has allowed us to examine the relationship between the horizontal distribution of fin and blue whales, sea surface temperature, and euphausiid concentrations at different spatial scales (Figs. 1 and 2); the relationship between the structure of euphausiid prey schools and the geomorphology of the foraging area (Figs. 1 and 2), whale diet in relation to prey availability (Table 1), and whale foraging behavior within the context of prey distribution and the geomorphology of the study area (Fig. 5). We feel that the most important contribution of this study is to demonstrate an integrated approach to examine the temporal and spatial relationship of marine birds and mammals to the structure and variability of their habitat. Ultimately, this will allow us to test hypotheses about how the biotic and abiotic environment can be used to predict pelagic predator distribution, movement, and foraging behavior.

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References

Ainley, D.G., Boekelheide, R., 1990. Seabirds of the Farallon Islands. Stanford University Press, Stanford.

Arnould, J.P., Boyd, I.L., Speakman, Y. Jr., 1996. The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. Journal of Zoology 239, 769–782.

Birt, V.L., Birt, T.P., Gulet, D., Cairns, D.K., Montevecchi, W.A., 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Marine Ecology Progress Series 40, 205–208.

Boyd, I.L., Arnbom, T., 1991. Diving behavior in relation to water temperature in the southern elephant seal: foraging implications. Polar Biology 11, 259–266.

Boyd, I.L., 1996. Temporal scales of foraging in a marine predator. Ecology 77, 426–434.

Burger, A.E., Wilson, R.P., Garnier, D., Wilson, M.-P.T., 1993. Diving depths, diet, and underwater foraging of Rhinoceros Auklets in British Columbia. Canadian Journal of Zoology 71, 2528–2540.

Carbone, C., Houston, A.I., 1996. The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. Animal Behavior 51, 1247–1255.

Costa, D.P., 1991. Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. American Zoologist 31, 111–130.

Costa, D.P., 1993. The secret life of marine mammals. Oceanography 6, 120–127.

Croll, D.A., Tershy, B.R., 1998. Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica, Polar Biology 19, 365–374.

Croxall, J.P., Everson, I., Kooyman, G.L., Ricketts, C., Davis, R.W., 1985. Fur seal diving behavior in relation to vertical distribution of krill. Journal of Animal Ecology 54, 1–8.

DeLong, R.L., Stewart, B.S., Hill, R.D., 1992. Documenting migrations of northern elephant seals using day length. Marine Mammology Science 8, 155–159.

Duffy, D.C., Schneider, D.C., 1994. Seabird Fishery interactions: a manager's guide. In: Nettleship, D.N., Burger, J., Gochfeld, M. (Eds), Seabirds on Islands, Birdlife Conservation Series, 1, 26–38. Birdlife International, Cambridge.

Estes, J.A., Palmisano, J.F., 1974. Sea otters: their role in structuring nearshore communities. Science 185, 1058–1060.

Fiedler P., Reilly, S., Hewitt, R., Demer, D., Philbrick, V., Smith, S., Armstrong, W., Croll, D., Tershy, B., Mate, B., 1998. Blue whale habitat and prey in the Channel Islands. Deep-Sea Research II (in press).

Fraser, W.R., Pitman, R.L., Ainley, D.G., 1989. Seabird and fur seal responses to winter krill swarms in Antarctica. Polar Biology 10, 37–41.

Furness, R.W., Cooper, J., 1982. Interactions between breeding seabird and pelagic fish populations in southern Benguela region. Marine Ecology Progress Series 8, 243–250.

Gentry, R.L., Kooyman, G.L., 1986. Fur seals: Maternal Strategies on Land and at Sea. Princeton University Press, Princeton, NJ.

Harvey, J.T., Benson, S.R., 1997. Marine bird and mammal distribution and abundance in Monterey Bay during 1996, Moss Landing Marine Laboratories Technical Publication 97-02.

Hindell, M.A., Slip, D.J., Burton, H.R., 1991. The diving behavior of adult male and females southern elephant seals (Mirounga leonina). Australian Journal of Zoology 39, 595-619.

Houston, A.I., Carbone, C., 1992. The optimal allocation of time during the dive cycle. Behavioral Ecology 3, 255–265.

Johannesson, K.A., Mitson, R.B., 1983. Fisheries acoustics: a practical manual for aquatic biomass estimation. FAO Fisheries Technical Paper 240, 249 pp.

Jones, M.L., Swartz, S.L., Leatherwood, S. (Ed.), 1984. The Gray Whale. Academic Press, New York.

Kenney, R.D., Winn, H.E., Macaulay, M.C., 1995. Cetaceans of the Great South Channel, 1979–1989: right whale (Eubalaena glacialis). In: Kenney, R.D., Wishner, K.F. (Eds.), Continental Shelf Research, The South Channel Ocean Productivity Experiment: SCOPEX, Vol. 15, pp 385–414. Pergamon Press, Oxford.

Kieckhefer, T.R., 1992. Feeding ecology of humpback whales in contintal shelf waters near Cordell Bank, California. MS Thesis, Moss Landing Marine Labs, CA.

Kooyman, G.L., 1989. Diverse Divers: Physiology and Behavior. Springer, New York.

Lambertson, R.H., 1983. Internal mechanism of rorqual feeding. Journal of Mammalogy 64, 76–88.

Le Boeuf, B.J., Costa, D.P., Huntley, A.C., Feldkamp, S.D., 1988. Continuous, deep diving in female Northern elephant seals. Canadian Journal of Zoology 66, 446–458.

National Research Council, 1994. Low Frequency Sound and Marine Mammals. National Academy Press, Washington, DC.

Oliver, J.S., Slattery, P.N., 1985. Destruction and opportunity on the sea floor: effects of gray whale feeding. Ecology 66, 1965–1975.

Oliver, J.S., Kvitek, R.G., Slattery, P.N., 1985. Walrus disturbance: scavenging habits and recolonizations of the Bering Sea benthos. Journal of Experimental Marine Biology and Ecology 91, 233–246.

Payne, P.M., Wiley, D.N., Young, S.B., Pittman, S., Clapham, P.J., Jossi, J.W., 1990. Recent fluctuations in the abundance of Baleen whales in the Southern Gulf of Maine in relation to changes in selected prey. Fishery Bulletin 88, 687–696.

Payne, P.M., Nicolas, J.R., O'Brien, L., Powers, K.D., 1986. The distribution of the humpback whale, Megaptera novaeangliae, on George Bank and in the Gulf of Maine, USA in relation to densities of the sand eel, Imitates Americans. National Marine Fisheries Service Fisheries Bulletin 84(2), 271–278.

Payne, R., 1983. Communication and behavior of whales. AAAS Selected Symposium 76. West view Press, Boulder, Colorado.

Piatt, J.F., Methven, D.A., 1992. Threshold foraging behavior of baleen whales. Marine Ecology Progress Series 84, 205–210.

Richardson, W.J., Greene, C.R., Jr., Malme, C.I., Thomson, D.H., 1991. Effects of noise on marine mammals. OCS Study MMS 90-0093; LGL Report TA834-1. Report from LGS Ecological Research Associates Inc. Bryan, Texas.

Schoenherr, J.R., 1991. Blue whales feeding on high concentrations of euphausiids around Monterey Bay submarine canyon. Canadian Journal of Zoology 69, 583–594.

Tershy, B.T, Acevedo, A., Breese, D., Strong, C.S., 1993. Diet and feeding behavior of fin and Bryde's whales in the Central Gulf of California, Mexico Revista de Investigacion Cientifica 1(1), 31–38.

VanBlaricom, G.R., Estes, J.A. (Ed.), 1988. The Community Ecology of Sea Otters, Springer, Berlin.

Watkins, W.A., Wartzok, D., 1985. Sensory biophysics of marine mammals. Marine Mammal Science 3, 219–260.

Whitehead, H., Glass, C., 1985. The significance of the Southeast Shoal of the Grand Bank to humpback whales and other cetacean species. Canadian Journal of Zoology 63(11), 2617–2625.

Winn, H.E., Goodyear, J.D., Kenney, R.D., Petricig, R.O., 1995. Dive patterns of tagged right whales in the Great South Channel. In: Kenney, R.D., Wishner, K.F. (Eds.), Continental Shelf Research, The South Channel Ocean Productivity EXperiment: SCOPEX, Vol. 15, pp 593–611. Pergamon Press, Oxford.

Würsig, B., 1989. Cetaceans. Science 244, 1550–1557.