Abstract.—Acoustic backscatter data from a 38-kHz echo sounder and a 150-kHz acoustic Doppler current profiler (ADCP) were collected during Southwest Fisheries Science Center marine mammal surveys in the eastern Pacific aboard the NOAA ship David Starr Jordan in 1992 and 1993. These data were processed to give profiles of volume scattering strength. A deep scattering layer dominated the time-depth patterns of backscatter. This layer migrated from a depth of 300-400 m during the day to 0-100 m at night, when it was located just above the thermocline. The source of backscatter was primarily small fish and squid, which are dolphin prey. Dolphin sighting rates were correlated positively with nighttime volume scattering strength above the thermocline. Spatial and temporal variability of prey biomass in the surface layer, as indexed by volume scattering strength, may have important consequences for dolphin feeding, as well as for distributional responses to habitat variability by dolphins.

Dolphin prey abundance determined from acoustic backscatter data in eastern Pacific surveys

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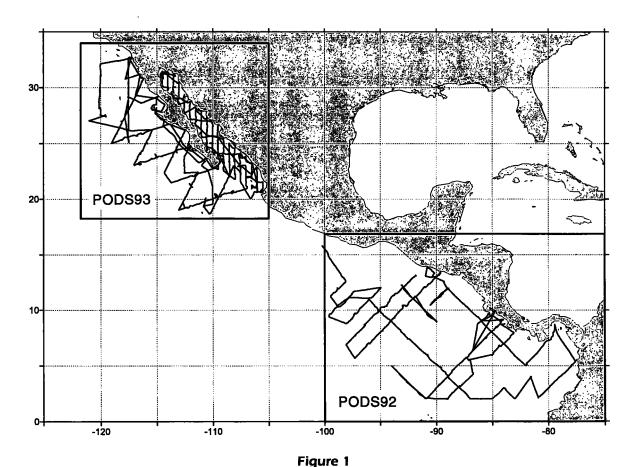
Acoustic data, consisting of the returns of pulses of sound from targets in the water column, are routinely used to assess fish distribution and abundance (Forbes and Nakken, 1972; Johannesson and Mitson, 1983; MacLennan and Simmonds, 1992). Such data are now also being used to quantify the biomass and distribution of zooplankton and micronekton (Greene and Wiebe, 1990; Hewitt and Demer, 1993). Innovative techniques using multifrequency amplitude and phase information can give estimates of size, movement, and acoustic properties of individual planktonic organisms (Farmer and Huston, 1988; Holliday et al., 1989). Another approach in acoustic studies of zooplankton and micronekton has been to employ instrumentation that is used routinely, notably the acoustic Doppler current profiler (ADCP, Roe and Griffiths, 1993). Several studies have used uncalibrated ADCP echo intensity data, with various levels of processing, to estimate relative patterns of plankton biomass distribution in space and time (Flagg and Smith, 1989; Plueddemann and Pinkel, 1989; Smith et al., 1989; Heywood et al., 1991).

We have been collecting echo intensity data from a 38-kHz echo sounder since 1986 and from a 150kHz ADCP since 1992 on Southwest Fisheries Science Center marine mammal surveys. This report describes data collection and processing and presents results from two cruises during which nearly complete data sets were obtained (population of Delphinus stocks 1992 [PODS92] and 1993 [PODS93]) (Fig. 1). Other data collected on these surveys provide a context for these results in terms of predators and habitat. Line-transect data were collected for dolphin abundance estimates (Mangels and Gerrodette, 1994a, 1994b). We use sighting rate here as an index of dolphin abundance. Physical and biological oceanographic data were also collected to characterize habitat variability (Philbrick et al., 1993).

Materials and methods

A 38-kHz Simrad EK-400 scientific sounder was used on NOAA ship David Starr Jordan beginning in 1986. Rather than a commercial echo integrator, we used an acoustic data acquisition (ADA) system, consisting of an analog-to-digital converter and a personal computer. A 150-kHz ADCP was installed on the Jordan in 1991. We collected nearly complete sets of 38- and 150-kHz acoustic data in 1992 and 1993.

A sonar equation relating volume backscattering strength per m^3 (S_{y} ,



Cruise tracks of NOAA ship David Starr Jordan during Population of Delphinus Stocks (PODS) cruises (28 July-2 November 1992) and (28 July-6 November 1993).

 $dB // 1\mu Pa$ at 1 m) to the echo level (EL), integrated and recorded after 20logR TVG amplification in the transceiver, was formulated as follows (Simmonds, 1990):

$$S_v = EL - (SL + RR) - 10 \log \psi - 10 \log c\tau/2,$$
 (1)

where $EL = 20 \log V_o$ (dB) (V_o ="gain-controlled envelope" signal, volts);

SL =source level (dB);

RR = receiver response (including receiver gain and transducer on-axis voltage response), dB;

 $10 \log \psi = \text{equivalent beam angle};$

c = speed of sound (m/s);

 τ = pulse length (1 × 1/1,000 per millisecond).

Transmission loss does not appear in this equation because it was corrected by a $20\log R$ time-varied gain (TVG) function applied to V_o in the transceiver. The TVG was checked with a transceiver test mode that input a constant voltage signal. The recorded $20\log R$ TVG output did not differ significantly

from the theoretical function ($TVG = 20 \log R + 2\alpha R$, where α is the nominal sound absorption coefficient of 0.008 dB/m and R is range in meters). The range (R) was based on a sound velocity entered into the control unit at the start of the cruise.

On-axis sensitivity (SL+RR) was estimated by measuring the system response (EL) to a standard calibration sphere (38.1-mm diameter tungsten carbide with 6% cobalt binder, target strength $TS=-42.3\,\mathrm{dB}$; Foote, 1990) suspended 7 m below the transducer. In this case, Equation 1 reduces to

$$EL = TS + (SL + RR), \tag{2}$$

where $EL = 20 \log V_o + 20 \log R$.

The "gain-controlled envelope" signal (V_o) represents a peak voltage and was converted to a root-mean-square (rms) voltage by multiplying by $1/\sqrt{2}$. The additional $20\log R$ term was added to the system's $20\log R$ TVG, used during the echo-integration surveys, to correct for the spherical spreading of the return from the point calibration target. Solving Equa-

tion 2 for the on-axis sensitivity gave (SL+RR) = 74.2 dB.

Operationally, the ADA program squared V_o , which is proportional to pressure at the face of the transducer, to give an echo intensity value (Eq. 1) proportional to power or energy flux per unit of area. The intensity values were then binned in 50 10-m bins between 10-m and 510-m depth. The binned intensities were averaged at 10-sec intervals over ten minutes (60 pings), equivalent to an interval of 3 km at the typical ship speed of 18 km/h. Recorded intensities were converted to units of decibels (dB=10 $\log I$ / I_{-} , where I_{-} represents the standard reference of 1μ Pa at a 1-m distance from the face of the transducer). Then, a correction to the TVG function was formulated by using depth-dependent sound velocities and attenuation coefficients calculated from CTD data taken once or twice daily with the algorithms of François and Garrison (1982). Finally, a constant 53.4 dB was subtracted to account for the combined source level, transducer response, receiver gain, and beam pattern terms $(-SL - RR - 10 \log \psi - 10 \log \tau)$ 2) in Equation 1. The equivalent beam angle is very difficult to measure directly without special apparatus; therefore we used the manufacturer's nominal value (10 log ψ =-19.6 dB; Simrad EK400 Scientific Sounder Instruction Manual).

Acoustic Doppler current profilers have been used since the early 1980's to estimate current velocity from the Doppler shift of acoustic signals backscattered from suspended matter (plankton and sediments) in the water column. Echo intensity is calculated and recorded during data-processing. RD Instruments has developed instrument modifications and an algorithm to calibrate these values and to estimate volume backscattering strength (S_{ν}, dB) . The algorithm is based on the following working version of a sonar equation (RD Instruments, 1990):

$$S_{v} = 10 \log \begin{bmatrix} 4.47 \times 10^{-20} K_{2} K_{s} (T_{t} + 273) \\ (10^{k(E-E_{r})/10} - 1) R^{2} / \\ (c P K_{1} 10^{-2\alpha R/10}) \end{bmatrix},$$
(3)

where K_2 = system noise factor = 4.3;

 K_s^{5} = system constant = 4.17 × 10⁵; T_t = transducer temperature (°C);

k = conversion factor = 0.435 dB/count;

E =echo intensity (counts);

 E_r = reference level for echo intensity (counts);

R =slant range (m);

c =sound velocity (m/s);

P = transmit pulse length = 8 m;

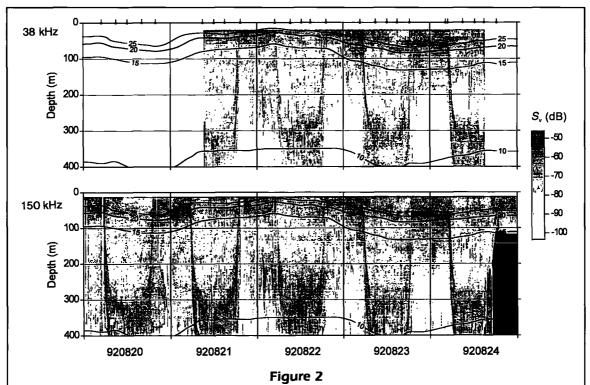
 K_1 = power into the water, W; α = sound absorption coefficient (dB/m).

Although this equation was formulated to be applied to individual beams of the ADCP, we used average amplitude data for E because we were using an empirical reference level (E_{x}) . The reference level for echo intensity, E_r , represents thermal noise in the system electronics plus ship noise. E_r was assumed equal to the minimum value of E (<40 counts) observed in each average profile or ensemble (~740 pings in 10 minutes). The manufacturer states that this in-situ method of estimating E_r is preferable to calculating E_r from measured system temperatures. Because ship temperature was relatively constant and water temperature ranged over only 4°C in 1992 and 10°C in 1993, E_r varied by only ($\pm 7-8$ counts. Values of E < 10 counts were not used (RD Instruments, 1990) and appear as blank areas at depth in 150 kHz time-depth sections (Fig. 2).

Values for c and α were calculated from CTD data taken once or twice daily according to Francois and Garrison (1982). Transducer temperature, T_{i} , was assumed equal to observed surface temperature. Slant range, R, was corrected for estimated sound velocity in relation to the value assumed by the ADCP software (1,475 m/s). The conversion factor, k (dB/ count), depends on the temperature of the system electronics. However, the deck unit was located in a temperature-controlled room (18-21°C) so that the range of k was 0.433 to 0.437 (<1 dB). Power into the water, K_1 , was assumed constant and estimated to be 53.4 \overline{W} (RD Instruments, 1990). The ADCP was set up with 50 bins of length 8 m, starting at 4 m from the transducers.

In both the 38- and 150-kHz data sets, the depth bin representing the bottom was identified initially by an algorithm searching for strong gradients of $S_{\mu}(z)$. These results were modified by visual inspection of time-depth sections. Data from the bottom depth bin and below were excluded from subsequent analysis. Some 1992 and 1993 profiles of S, appeared to be biased low on account of sound attenuation due to bubbles beneath the ship during stationkeeping and during very rough weather (cf. Fig. 2, 20 August, at the first tick marking the morning CTD station). We identified biased profiles from anomalously low S_{ij} in bins below the top depth bin. The problem was more prevalent in the 150-kHz data (2.5% of 1992 profiles and 1.0% of 1993 profiles) than in the 38kHz data (0.5% of 1992 profiles and 0.1% of 1993 profiles). We excluded the biased profiles from statistical analyses.

Dolphin sightings were recorded during daylight hours from the flying bridge of the vessel by a team



Time-depth sections of 38-kHz and 150-kHz volume scattering strength (S_{ν} , dB) and temperature during five days of PODS92 surveys. Contour lines are isotherms (°C), from XBT (expendable bathythermograph) profiles at tick marks along top of section.

of three observers using 25-power binoculars (Mangels and Gerrodette, 1994a, 1994b). Local dolphin abundance was indexed by the number of sightings of spotted (Stenella attenuata), spinner (S. longirostris), striped (S. coeruleoalba), common (Delphinus delphis and D. capensis), bottlenose (Tursiops truncatus), Risso's (Grampus griseus), rough-toothed (Steno bredanensis), Fraser's (Lagenodelphis hosei), Pacific white-sided (Lagenorhynchus obliquidens), and unidentified dolphins. Daily numbers of sightings were standardized to sighting rates of schools or individuals per 100 km in optimum sea-state conditions (Gerrodette¹). Sighting rates were log-transformed to normalize distributions before testing correlation with various time and depth means of $S_{\alpha}(z,t)$. We report correlations with 150 kHz S_{ν} here because data were collected on about 25% more days than those for $38kHz\bar{S}_{...}$

Acoustic and other data were gridded by kriging with the software SURFER (Golden Software, 1995). Variogram models were fitted to the data and the best fit was selected by using the original code based

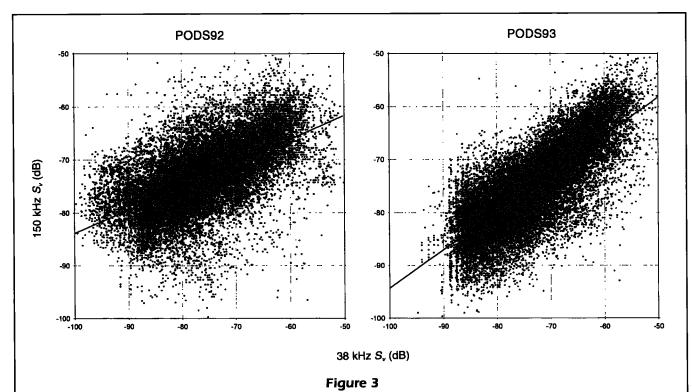
on Pannatier (1996). Contour maps were also generated with SURFER.

Results

The five-day time-depth sections in Figure 2 illustrate features observed in all sections: 1) data at one or both frequencies were occasionally missing; 2) the 150-kHz signal was lost in the noise at depths >200 m; and 3) bottom depth was <400 m as on 24 August after about 1700 hours. All time-depth sections of S_{ν} were dominated by a deep-scattering layer (DSL) at 300–400 m depth during daylight hours and 0–100 m during the night. The DSL migrated about 200 m in 1–2 hours near dawn and dusk. Morning descent was generally more rapid than evening ascent. During some days, the DSL was split into two distinct layers at depth, separated by up to 100 m (cf. Fig. 2, 38 kHz section on 22 and 23 August).

The DSL was detected at both 38 and 150 kHz. However, the 150-kHz return from the DSL at its daytime depth was barely above background noise levels. The smaller effective depth range of the ADCP was due to 1) greater attenuation of sound at the higher frequency (α =0.039 dB/m at 150 kHz com-

¹ Gerrodette, T. 1996. On estimating relative abundance. Unpubl. manuscript.



Relationships between 38-kHz and 150-kHz volume scattering strength (S_n, dB) in corresponding 10-and 8-m depth bins (centered at 25, 65, 105, 145, 185, 225, 265, and 305 m) at all times of day or night during PODS92 (n=24,193) and PODS93 (n=26,963) surveys.

pared with 0.008 dB/m at 38 kHz) and 2) transducer orientation 30° off the vertical, resulting in a slant range 15% greater than depth.

Volume scattering strengths at 38 and 150 kHz were significantly correlated (Fig. 3, r=0.58 in 1992 and r=0.77 in 1993). Some error in this relation is due to the different sizes and inexact depth matching of bins between frequencies. The ADCP samples echo intensity only in the last quarter of each depth bin, so that scattering is averaged over only 2 m,

compared with 10 m for the 38-kHz echo sounder. Correlation decreased at depth (e.g. in 1993, r=0.83 at 25 m and r=0.53 at 185 m). This could have been due simply to the low signal to noise ratio at depth in the 150-kHz data. However, it probably also reflects changes in species and size composition, and thus spectral response, of scatterers at depth. The mean difference between 38- and 150-kHz volume scattering strength in Figure 3 was -2.9 dB in 1992 and 0.0 dB in 1993.

Spatial patterns of mean day and night volume scattering strength (\overline{S}_{ν}) in the surface layer (0–100 m) were very similar at the two frequencies; therefore

Table 1

Mean day (0800–1600) and night (2000–0400) volume scattering strengths (S_n, dB) in the surface layer (0–100 m) in 1992 and 1993. Values are cruise means, with range in parentheses. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

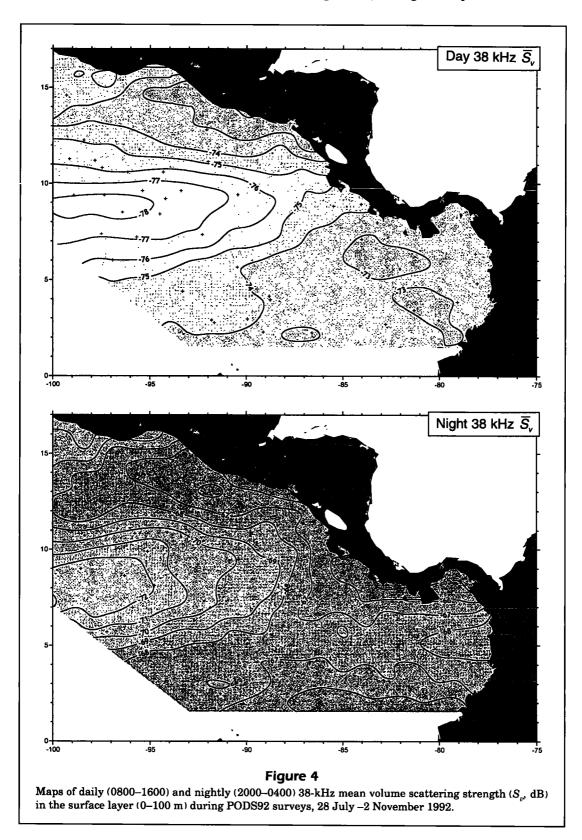
		Day	Night
PODS92	38 kHz	-75.1 (-82.2 to -70.7)	-68.6 (-77.1 to -62.0)
	150 kHz	-73.9 (-83.7 to -69.0)	-67.5 (-76.8 to -57.3)
PODS93	38 kHz	-76.3 (-85.8 to -69.4)	-65.3 (-73.5 to -60.2)
	150 kHz	-79.2 (-90.2 to -70.1)	-68.2 (-80.3 to -59.7)

only the 38-kHz patterns are illustrated here (Figs. 4 and 5). On average, night values exceeded day values by 6.4 dB in 1992 and 11.0 dB in 1993 (Table 1). Thus, near-surface \overline{S}_{ν} was 4 and 13 times greater at night than during the day, indicating that 77–92% of the scatterers left the surface layer during the day. Mean surface \overline{S}_{ν} values (daily or nightly, 38 or 150 kHz) varied by 11.5 to 20.6 dB during the cruises, representing ranges of 14 to 115 times.

In 1992, low \overline{S}_{ν} was observed along 8–9°N both night and day (Fig. 4). \overline{S}_{ν} increased to the south towards the equator and to the north and east towards

the coast. The highest \overline{S}_{ν} values were observed along the coast of Costa Rica and the coast of Mexico south of the Gulf of Tehuantepec (16°N, 95°W).

In 1993, \overline{S}_{ν} was high in the Gulf of California and along the Pacific coast of southern Baja California (Fig. 5). \overline{S}_{ν} was generally low in the northern and



offshore part of the study area and increased towards the southeast corner near Cabo Corrientes (20°N, 105°W).

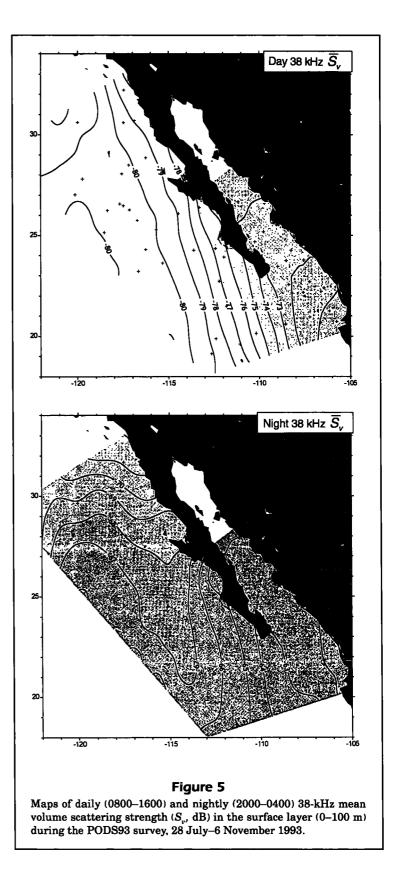
Time-depth sections (Fig. 2) show a close relation between the deep scattering layer and the thermocline at night. The DSL ascended through the thermocline in the evening, then remained just above the thermocline until it descended in the early morning. The DSL followed changes in the depth of the thermocline during some nights (cf. 22-23 August, Fig. 2). Where the thermocline is deep, S_{ij} is maximum at 10-20 m above the thermocline and then declines closer to the surface. Where the thermocline is shallow, S_{ij} is maximum at, or very close to, the surface. The nighttime depth of the DSL was significantly correlated with thermocline depth, except for the 38-kHz DSL in 1993 (Table 2). Mean S_{ν} above the thermocline was slightly, but not significantly, greater above more shallow thermoclines 1992.

Dolphin abundance, as indexed by sighting rates of schools or individuals per 100 km, was significantly correlated with nighttime mean \overline{S}_{ν} above the thermocline in 1992 and with 0–400 m mean \overline{S}_{ν} in 1993 (Table 3, the 150-kHz results are shown here owing to larger sample sizes but the 38-kHz results were similar). In 1992, both mean \overline{S}_{ν} above the thermocline and dolphin abundance were high near the countercurrent thermocline ridge along 9°N (Fig. 6). In 1993, mean \overline{S}_{ν} above the thermocline and dolphin abundance were relatively high near the mouth of the Gulf of California, at intermediate thermocline depths.

Discussion

Deep scattering layers have been observed throughout the Pacific with low-frequency depth sounders (<30 kHz). Tont (1976) reported mean daytime depths of 319 m in the eastern tropical Pacific and 282 m in the California Current, similar to the depths observed here (Fig. 2). Small mesopelagic fish with gasfilled swimbladders are now recognized to be the most important low-frequency back-scatterers in the open ocean (Chapman, 1947; Marshall, 1951; Brooks, 1977), although early reports attributed DSL's to cephalopods (Lyman, 1948) or euphausiids (Hersey and Moore, 1948).

What do our acoustic observations represent? Volume scattering strength (dB) represents a sum of in-



dividual target strengths (TS), except at very high target densities where shadowing and multiple scattering occur (MacLennan and Simmonds, 1992). Target strength is a nonlinear function of sound frequency and the cross-sectional area of the target (Demer and Martin, 1995) and TS per unit of area is typically expressed as a function of the dimensionless number (ka), where k is the acoustic wavenumber $(k=2\pi/\lambda)$ and a is a characteristic dimension of the target (Chu et al., 1992). At low sound frequencies (ka<1, "Rayleigh" scattering), TS drops off rapidly. Thus, scattering of relatively low frequency sound by small targets is weak. At high frequencies (ka>1, "geometric" scattering), early models predicted TS to be approximately con-

stant (Love, 1977). Most other models of geometric scattering are highly nonlinear, with deep nulls in individual TS versus (ka) curves. However, Chu et al. (1992) suggested that averaging over pings and individuals in field studies of volume backscattering should "smear out" these nonlinearities.

The wavelengths of 38-and 150-kHz sound correspond to target dimensions of approximately 4 and 1 cm, respectively. This is the effective size of macrozooplankton and micronekton organisms, such as euphausiids, siphonophores, small fish, and squid. Targets <4 cm, such as copepods, will scatter sound strongly at 150 kHz. Scattering of 38-kHz sound will be relatively weak Rayleigh scattering and may be undetectable over system noise. These smaller targets may have weakened the correlation between backscattering at the two frequencies (Fig. 3).

We were unable to make net tows to identify acoustic targets, owing to time constraints on the cetacean survey cruises. Therefore, we can make only an educated guess about the composition of the observed deep-scattering layers. Roe et al. (1984), in a uniquely comprehensive study of a community of vertically migrating organisms in the temperate northeast Atlantic, considered fish, decapod crustaceans, mysids, euphausiids, amphipods, copepods, ostracods, siphonophores, medusae, ctenophores, and chaetognaths. Ignoring small or weak scatterers, we must consider fish, crustaceans (decapods, mysids, and euphausiids), and siphonophores, as well as cephalopods, as possible components of the observed DSL's.

Average biomass densities of mesopelagic fish (primarily myctophids) and cephalopods are equal to, or slightly greater than, those of crustaceans in the eastern tropical Pacific (Blackburn, 1968; Blackburn et al., 1970) and subtropical Pacific (Maynard et al., 1975). Target strength depends on the composition,

Table 2

Pearson product-moment correlations between properties of the nighttime (2000–0400) deep-scattering layer and the thermocline depth observed in 1992 and 1993. S_v = volume scattering strength (dB). Thermocline depth = depth of maximum 10-m temperature gradient. ***=P<0.001, **=P<0.01. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

		Correlations with thermocline depth		
		Depth of maximum $S_{_{ m c}}$	Mean $S_{\scriptscriptstyle (\!ert)}$ above thermocline	
PODS92	38 kHz	+0.86***	-0.15	
	150 kHz	+0.84***	-0.23	
PODS93	38 kHz	+0.25	-0.01	
	150 kHz	+0.43**	+0.15	

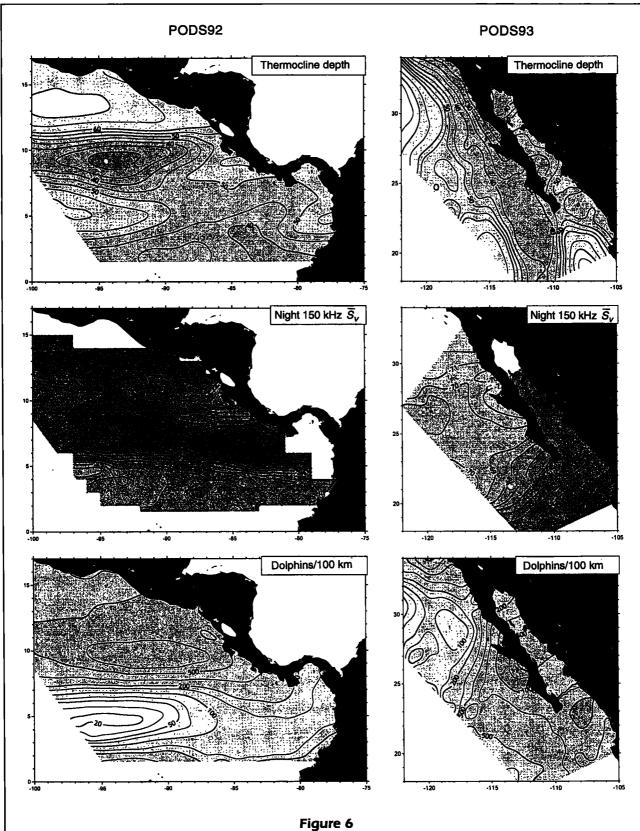
Table 3

Correlations between dolphin sighting rates (schools and individuals per 100 nautical miles of effort, log-transformed) and mean 150-kHz volume scattering strength (S_v , dB) above the thermocline at night (2000–0400), and 0 to 400 m night and day (0800–1600). *** = P<0.001, ** = P<0.01, * = P<0.05. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

	Dolphin sighting rates		
	Schools	Individuals	
PODS92			
Night $S_{_{\scriptscriptstyle \mathrm{U}}}$ above thermocline	+0.35*	+0.38**	
Night S 0-400m	+0.05	+0.02	
$\operatorname{Day} S_{\nu} \stackrel{\circ}{0}$ -400m	-0.01	-0.02	
PODS93			
Night S_{ν} above thermocline	+0.27	+0.15	
Night S, 0-400m	+0.36**	+0.20	
$Day S_v 0-400m$	+0.38**	+0.18	
·			

shape, and orientation of the target, as well as on relative size. At 38–120 kHz, small fish with gas-filled swim bladders (e.g. clupeoids) and squid have target strengths 5–10 dB greater than those for crustaceans of the same size (Tables 6.3 and 6.4 in MacLennan and Simmonds, 1992; Marchal et al., 1993). Siphonophores have a gas bladder that scatters sound and have been observed migrating with myctophids in a DSL off Baja California (Barham, 1966). However, myctophids, flying fish, and squid were much more abundant than siphonophores at night dipnet stations on our cruises.² Therefore, mesopelagic fish and

² Pitman, R. 1996. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Box 271, La Jolla, CA 92038. Personal commun.



Thermocline depth (m), average nighttime backscatter above the thermocline (dB), and dolphin sighting rate observed in 1992 and 1993.

squid were most likely the major component of the observed DSL's, although a variety of crustaceans were undoubtedly present in the survey areas. Nonmigrating, epipelagic fish and squid are likely represented by near-surface backscattering during the day.

The small fish and squid that we argue were detected by our acoustic systems are dolphin prey (Fitch and Brownell, 1968; Miyazaki et al., 1973; Perrin et al., 1973; Robison and Craddock, 1983; Robertson and Chivers, 1997). The ranges of volume scattering strength we observed—more than three orders of magnitude among bins (Fig. 2), up to 10× variation between night and day and 500× variation among daily means—must be important factors in dolphin feeding strategies and habitat choices. Thermocline depth, which influences prey distribution, is an important component in dolphin habitat variability (Reilly and Fiedler, 1994).

We observed a positive correlation between the abundance of dolphins (observed during daylight) and the abundance of prey at night, when spotted and spinner dolphins are known to feed on mesopelagic prey near the surface (Perrin et al., 1973; Robertson and Chivers, 1997). Over 90% of the dolphins identified in both surveys were common, spotted, spinner, and striped dolphins. In the eastern tropical Pacific (PODS92), a region characterized by a strong and shallow thermocline (Wyrtki, 1967), nighttime prey abundance was more closely related to thermocline depth. Off Baja California (PODS93), the thermocline had less influence on distribution of prey. Dolphin community structure was also different: common dolphins represented 61% of the identified dolphins in this region, compared with only 37% in the PODS92 survey area.

Our results indicate that dolphin distribution can be related to prey abundance measured acoustically and that the physical environment influences the abundance of dolphin prey. Marchal et al. (1993) observed a similar DSL in the eastern tropical Atlantic that was related both to thermal structure and to tuna abundance. Simple and readily available sonar systems can yield useful results when survey time or resources are limited. Monitoring long-term changes in zooplankton or micronekton biomass, as Roemmich and McGowan (1995) did with net samples off southern California, could be facilitated by the application of such acoustic methods. However, in present and future studies of cetacean feeding and cetacean responses to habitat variability, we will use multispectral acoustic systems and validation by net samples to quantify availability and distribution of specific prey types.

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Literature cited

Barham, E. G.

1966. Deep scattering layer migration and composition: observations from a diving saucer. Science (Wash. D.C.) 151:1399-1403.

Blackburn, M. R.

1968. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance, and relations to tuna. Fish. Bull. 67(1):71-115.

Blackburn, M. R., M. Laurs, R. W. Owen, and B. Zeitschel. 1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. 7:14-31.

Brooks, A. L.

1977. A study of the swimbladders of selected mesopelagic fish species. In N. R. Andersen and B. J. Zahuranec (eds.), Oceanic sound scattering prediction, p. 565–590. Plenum Press. New York, NY.

Chapman, W. M.

1947. The wealth of the ocean. Sci. Monthly (NY). 64:192– 197.

Chu, D., T. K. Stanton, and P. H. Wiebe.

1992. Frequency dependence of sound backscattering from live individual zooplankton. ICES J. Mar. Sci. 49:97-106.

Demer, D. A., and L. V. Martin.

1995. Zooplankton target strength: volumetric or areal dependence? J. Acoust. Soc. Am. 98(2):1111-1118

Farmer, D. M., and R. D. Huston.

1988. Novel applications of acoustic backscatter to biological measurements. In B. J. Rothschild (ed.), Toward a theory on biological-physical interactions in the world oceans, p. 599-614. Kluwer, Dordrecht.

Fitch, J. E., and R. L. Brownell Jr.

1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Canada 25(12):2561-2574.

Flagg, C. N., and S. L. Smith.

1989. On the use of the acoustic Doppler current profiler to measure zooplankton abundance. Deep-Sea Res. 36:455– 474.

Foote, K. G.

1990. Spheres for calibrating an eleven-frequency acoustic measurement system. J. Cons. Int. Explor. Mer 46:284–286.

Forbes, S. T., and O. Nakken (eds.).

1972. Manual of methods for fisheries resource survey and appraisal. Part 2: The use of acoustic instruments for fish detection and abundance estimation. FAO Man. Fish. Sci. 5:138 p.

Francois, R. E., and G. R. Garrison.

1982. Sound absorption in sea water: Part II: Boric acid contribution and equation for total absorption. J. Acoust. Soc. Am. 72:1879-1890.

Golden Software.

1995. SURFER for Windows, version 6. Golden Software, Inc., Golden, CO, 483 p.

Greene, C. H., and P. H. Wiebe.

1990. Bioacoustical oceanography: new tools for zooplankton and micronekton research in the 1990's. Oceanography 3:12-17.

Hersey. J. B., and H. B. Moore.

1948. Progress report on scattering layer observations in the Atlantic Ocean. Trans. Am. Geophys. Union 29:341– 354.

Hewitt, R. P., and D. A. Demer.

1993. Dispersion and abundance of Antarctic krill in the vicinity of Elephant Island in the 1992 austral summer. Mar. Ecol. Prog. Ser. 99:29-39.

Heywood, K. J., S. Scrope-Howe, and E. D. Barton.

1991. Estimation of zooplankton abundance from shipborne ADCP backscatter. Deep-Sea Res. 38:677-691.

Holliday, D. V., R. E. Pieper, and G. S. Kleppel.

1989. Determination of zooplankton size and distribution with multifrequency acoustic technology. J. Cons. Int. Explor. Mer 46:52-61.

Johannesson, K. A., and R. B. Mitson.

1983. Fisheries acoustics: a practical manual for aquatic biomass estimation. FAO Fish. Tech. Paper 240, 249 p.

Love, R. H.

1977. Target srength of an individual fish at any aspect. J. Acoust. Soc. Am. 62:1397-1403.

Lyman, J.

1948. The sea's phantom bottom. Sci. Monthly (NY) 66: 87-88

MacLennan, D. N., and E. J. Simmonds.

1992. Fisheries acoustics. Chapman and Hall, London, 325 p.

Mangels, K. F., and T. Gerrodette.

1994a. Report on cetacean sightings during a marine mammal survey in the eastern tropical Pacific Ocean aboard the NOAA ships *McArthur* and *David Starr Jordan*, July 28-November 2, 1992. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-200, 74 p.

1994b. Report on cetacean sightings during a marine mammal survey in the eastern Pacific Ocean and the Gulf of California aboard the NOAA ships McArthur and David Starr Jordan, July 28-November 6, 1993. U.S. Dep. Commer., NOAA Tech. Memo. NMFS- SWFSC-211, 88 p.

Marchal, E., F. Gerlotto, and B. Stequert.

1993. On the relationship between scattering layer, thermal structure and tuna abundance in the Eastern Atlantic equatorial current system. Oceanol. Acta 16(3):261–273.

Marshall, N. B.

1951. Bathypelagic fishes as sound scatterers in the ocean. J. Mar. Res. 11:1-17.

Maynard, S. D., F. V. Riggs, and J. F. Walters.

1975. Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. Fish. Bull. 73:726-736.

Miyazaki, N., T. Kusaka, and M. Nishiwaki.

1973. Food of Stenella coeruleoalba. Sci. Rep. Whales Res. Inst., Tokyo, 25:265–275.

Pannatier, Y.

1996. VARIOWIN: software for spatial data analysis in 2D. Springer-Verlag, New York, NY, 91 p.

Perrin, W. F., R. R. Warner, C. H. Fiscus, and D. B. Holts.

1973. Stomach contents of porpoise, Stenella spp., and yellowfin tuna, Thunnus albacares, in mixed-species aggregations. Fish. Bull. 71:1077-1091.

Philbrick, V. A., P. C. Fiedler, S. B. Reilly, R. L. Pitman, and L. T. Ballance.

1993. Report of ecosystem studies conducted during the 1992 eastern tropical Pacific common dolphin survey on research vessels *David Starr Jordan* and *McArthur*. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-180, 74 p.

Plueddemann, A. J., and R. Pinkel.

1989. Characterisation of the patterns of diel migration using a Doppler sonar. Deep-Sea Res. 36:509-530.

RD Instruments.

1990. Calculating absolute backscatter. Tech. Bull. ADCP-90-04, San Diego, CA, 24 p.

Reilly, S. B., and P. C. Fiedler.

1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986–1990. Fish. Bull. 92:434–450.

Robertson, K., and S. J. Chivers.

1997. Prey occurrence in pantropical spotted dolphins, Stenella attenuata, from the eastern tropical Pacific. Fish. Bull. 95(2):334-348.

Robison, B. H., and J. E. Craddock.

1983. Mesopelagic fishes eaten by Fraser's dolphin, Lagenodelphis hosei. Fish. Bull. 81(2):283-289.

Roe, H. S. J., M. V. Angel, J. Badcock, P. Domanski,

P. T. James, P. R. Pugh, and M. H. Thurston.

1984. The diel migrations and distributions within a mesopelagic community in the northeast Atlantic. 1. Introduction and sampling procedures. Prog. Oceanogr.13: 245-268.

Roe, H. S. J., and G. Griffiths.

1993. Biological information from an Acoustic Doppler Current Profiler. Mar. Biol. 115:339–346.

Roemmich, D., and J. McGowan.

1995. Climatic warming and the decline of zooplankton in the California Current. Science (Wash. D.C.) 267:1324– 1326.

Simmonds, E. J.

1990. Very accurate calibration of a vertical echo sounder: a five-year assessment of performance and accuracy. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 189:183-191.

Smith, P. E., M. D. Ohman, and L. E. Eber.

1989. Analysis of the patterns of distribution of zooplankton aggregations from an Acoustic Doppler Current Profiler. Rep. Calif. Coop. Ocean. Fish. Invest. 30:88-103.

Tont, S. A.

1976. Deep scattering layers: patterns in the Pacific. Rep. Calif. Coop. Ocean. Fish. Invest. 18:112-117.

Wyrtki, K.

1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1:117-147.