Pergamon

Deep-Sea Research I, Vol. 44, No. 4, pp. 627–645, 1997
Published by Elsevier Science Ltd
Printed in Great Britain
0967-0637/97 $17.00 + 0.00

PII: S0967–0637(96)00098–2

Abyssopelagic grenadiers: the probable cause of low frequency sound scattering at great depths off the Oregon and California coasts

REDWOOD W. NERO,* CHARLES H. THOMPSON* and RICHARD H. LOVE*

(*Received* 6 *February* 1995; *in revised form* 11 *October* 1995; *accepted* 21 *May* 1996)

Abstract—Volume reverberation measurements from the slope base and abyssal plain along the coasts of Oregon and northern California show an unexpected scattering layer peaking around 2000 Hz at depths greater than 1000 m. A model of swimbladder resonance applied to published records of bottom-dwelling grenadier size and abundance provided a good fit to the data, suggesting the widespread pelagic occurrence of grenadiers, *Coryphaenoides* spp., of 20–68 cm length at densities near 0.004 ind. m^{-2} over the slope base and abyssal plain. Published by Elsevier Science Ltd

INTRODUCTION

During a volume scattering measurement cruise off the Oregon and California coasts in August 1992, a thick, weak, low-frequency sound scattering layer was consistently observed at depths greater than 1000 m. This layer was unexpected: a study of pertinent literature prior to the experiment had given no indication of its existence (Nero, 1992). Shallower, stronger layers were also found. These layers are well documented and are dominated by Pacific whiting and mesopelagic fishes (Dark *et al.*, 1980; Kalish *et al.*, 1986).

Identification of the scatterers in the deep layer was based on the plausible assumption that they were swimbladder-bearing fishes. Fish swimbladders have an acoustical response that is very similar to that of air bubbles in water; when insonified at the proper frequency they resonate. This resonance frequency is dependent on swimbladder size and depth and, to a lesser extent, on fish behavior (Weston, 1967). This acoustic resonance can provide useful quantitative information about fish populations, since swimbladder size can be related to fish size and the strength of scattering depends on their numbers. Because of this usefulness, a variety of acoustic models have been developed for the study of various aspects of swimbladder resonance (Andreeva, 1964; McCartney and Stubbs, 1970; Love, 1978; Hall, 1981; Stanton, 1989; Clay, 1991; Feuillade and Werby, 1994).

These models have been used a number of times to calculate scattering strengths from net catches of fishes for comparison to acoustic data collected at the same time. Brown and Brooks (1974), Batzler *et al.* (1975), Love (1975), Hall and Quill (1983), and Kalish *et al.* (1986) employed this method with mesopelagic fishes while studying the "deep scattering layer". Holliday (1972, 1977a) used it in studies of scattering from schools of anchovy, jack mackerel, and rockfish. The models have also been used to estimate fish sizes when no

* Naval Research Laboratory, Stennis Space Center, MS 39529–5004, U.S.A.

biological data were available (Chapman *et al.*, 1974; Akal *et al.*, 1993). In an experimental study of low frequency scattering in the Norwegian Sea, Love (1993) used variations of the above techniques. Concurrently collected fisheries data were modeled to identify a layer of blue whiting, which had been expected, and historical data were modeled to identify a layer of redfish, which had not been expected.

The approach used in this paper is a modification of that used to identify redfish in the Norwegian Sea. First, an examination of deep water trawl data was conducted. This examination indicated that adult deep water grenadiers, *Coryphaenoides* spp., usually considered to be benthic, had been found in very small numbers at depths well above bottom (Pearcy, 1976). Using grenadier characteristics in the swimbladder scattering model produced results that compared very favorably to the volume reverberation measurements. This result, combined with the fact that no other species of the proper size has been known to inhabit these waters, led to the conclusion that this widespread deep layer is caused by abyssopelagic grenadiers. This paper details the measurements and modeling that led to this conclusion and discusses the acoustic results on the basis that the scatterers are grenadiers.

METHODS

Measurements

Sound scattering from the ocean volume was measured with an explosive sound source and a directional receiver during an acoustic survey conducted by the Naval Research Laboratory (NRL) from August 14 to 29, 1992, aboard the U.S.N.S. *Wilkes* (T-AGS-33). Measurements were made at nine stations located on the continental slope, slope base, and abyssal plain between the Strait of Juan de Fuca and Cape Mendocino (Fig. 1). Stations 2 and 3 off the Washington coast were missed due to heavy seas.

Explosives provide a high source level over a wide frequency range. We employed a 0.23 kg TNT charge detonated at 0.5 m depth. The shallow depth allows the gas bubble created by the explosion to vent and avoids the multiple sound pulses caused by bubble oscillations characteristic of charges detonated at greater depth.

Scattered signals were received by a downward-looking array consisting of a 32-element line hydrophone on the axis of a 45° reflective cone of 1.8 m aperture. Simultaneous listening on all elements, in combination with the reflective cone, forms a main beam equivalent to that of a 1.8 m diameter plane circular array. Ideal beam widths can be maintained between approximately 10° and 20° between 20 kHz and 2.5 kHz by using signals from 8, 16, or all 32 elements of the array. Beam width grows to 58° at 800 Hz.

Received signals from each TNT shot were amplified, high- and low-pass filtered at 400 and 6000 Hz, respectively, digitized at a 20 kHz sampling rate, and stored. Digitally stored signals were subsequently filtered into 21 1/6-octave bands from 500 to 5000 Hz and amplitude versus time envelopes calculated for each band. There was little variation between shots in a sequence, so average envelopes were used to calculate volume scattering strength, S_v, the scattering strength of a unit volume of water, as a function of depth. The exception was for scattering from fish near the bottom, where a shot by shot examination was required to ensure bottom echoes were not included in subsequent calculations. Data were displayed as 2-dimensional images showing S_v in dB on a color scale as a function of frequency and depth. Scatterer depths were determined from the S_v images; integration over

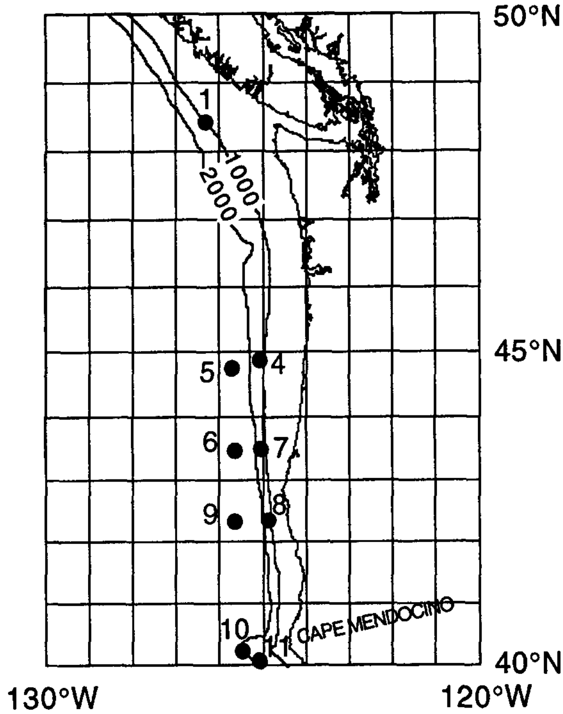

Fig. 1. Volume reverberation station locations.

these depths produced a series of layer scattering strength (S_L) versus frequency curves. S_L curves were compared to results from the swimbladder model.

Swimbladder model

Based on the nature of the S_L curves, scatterers were assumed to be swimbladder-bearing fish. Swimbladders resemble prolate spheroids or cylinders with major-to-minor axis (length-to-diameter) ratios up to 10. However, it has been shown that, near resonance, spherical, spheroidal, and cylindrical air bubble models produce nearly identical results (Weston, 1967; Feuillade and Werby, 1994). Thus, we have chosen to use the model of Love (1978), which models a fish as an air-filled viscous spherical shell. This model has recently been used successfully to examine scattering from commercial-size fish in the Norwegian Sea (Love, 1993).

Love's model (1978) gives the acoustic cross-section in the backscattered direction, σ_{bs}, for a single swimbladder of radius, r, as

$$\sigma_{bs} = \frac{r^2}{\left(\frac{f_0^2}{f^2 H^2} + \left(\frac{f_0^2}{f^2} - 1\right)^2\right)}, \quad (1)$$

where σ_{bs} is in m^2, r is in m, f is the insonifying frequency in Hz, f_0 is the swimbladder's monopole resonance frequency in Hz, and H is a damping factor. The resonance frequency is

$$f_0^2 = \frac{3\gamma_a P}{4\pi^2 r^2 \rho}, \tag{2}$$

where γ_α is the ratio of specific heats of air ($\gamma_\alpha = 1.4$), P is the ambient pressure in Pa, and ρ is the density of fish flesh in kg/m^3. The damping factor is

$$\frac{1}{H} = \frac{2\pi r f^2}{f_0 c} + \frac{\xi}{\pi r^2 f_0 \rho}, \tag{3}$$

where c is the speed of sound in water in m/s, and ξ is the viscosity of fish flesh in Pa s. Love's model includes a term in equation (2) that accounts for the effects of swimbladder wall tension on f_0 and a thermal damping term in equation (3). However, Love (1978) shows that these terms are negligible for the present case, so they have been omitted for clarity. The physical properties of fish used here were taken from Love (1978): $\rho = 1050$ kg/m^3 and $\xi = 50$ Pa s.

The only model inputs are swimbladder size and depth. In the present case depth is easily obtained from the acoustic results, so that only swimbladder size must be determined. One of the primary functions of a swimbladder is to act as a hydrostatic organ, making a fish neutrally buoyant, which requires ratios of swimbladder volume to fish volume of about 0.04 to 0.05 (Jones and Marshall, 1953). Measurements have shown that these values can vary significantly among individuals of a species (Sand and Hawkins, 1973; Jones and Scholes, 1985; Foote, 1985; Ona, 1990). A simple distribution of swimbladder volume to fish volume ratios was developed as a rough approximation of these measurements, as follows: 10% of the fish have ratios of 0.02, 20% have 0.03, 30% have 0.04, 30% have 0.05, and 10% have 0.06.

Fish size distributions are usually given as distributions of total length L. However, length-weight relations are available for many fish, and they can be used to determine swimbladder size directly. The length–weight relations are regression equations, but fish weight (W) can vary significantly at a given length (e.g. for grenadiers see Stein and Pearcy, 1982). An approximate normal distribution of W on L was developed, where 20% of the fish have the mean W given by the regression equation, 17% are 10% heavier (lighter), 12% are 20% heavier (lighter), 7% are 30% heavier (lighter), and 4% are 40% heavier (lighter).

In applying this model to the unknown fish, the swimbladder was assumed to be a prolate spheroid with a major-to-minor axis ratio of 5. The resonance frequency of such a spheroid is about 10% higher than for a sphere (Weston, 1967); this correction factor was taken into account by increasing f_0 given in equation (2) by a factor of 1.1. Recently, Feuillade and Werby (1994) have shown that the broadside target strength of such spheroids is about 0.5 dB less than that of a sphere. Because this difference is well within the expected error of our measurements, it was not incorporated into our model calculations. Bowne (1982) shows a cross-section of a grenadier swimbladder that has a major-to-minor axis ratio of about 2.5. Hence, Love's model with Weston's correction should accurately model near-resonance scattering from grenadiers.

The backscattering cross section of a unit horizontal area of a layer of dispersed, acoustically noninteracting scatterers, σ_{bs_L} is calculated as

$$\sigma_{bs_L} = \sum_{i=1}^{\Phi} \sigma_{bs_i} \tag{4}$$

where σ_{bs_i} is the backscattering cross section of the i^{th} scatterer and Φ is the number of individuals within a 1 m^2 vertical column that extends over the depth of the layer. The layer strength is

$$S_L = 10 \log \sigma_{bs_L} \tag{5}$$

This value is compared to the acoustic data.

Model calculations were made over a broader frequency range (100 Hz–5 kHz) than the acoustic measurements to allow representation of the shape of a particular resonance response. Three parameters, r, Φ, and depth, z can be varied to provide a "fit" of the model to measured resonance spectra. The shape of the scattering curve is determined by r and z. For most modeling, swimbladder radii, r, were determined by knowledge of length distributions and previously known length–weight relationships; both obtained from independent trawl surveys. The depth range, z, is determined by the acoustic measurement and is considered fixed. The density, Φ, of fish adjusts the level of the scattering curve. A good "eye fit" of the model level to measured level can provide a result useful for quantitative census of the density of deep water fish populations.

A more precise determination of scatterer size and number than that obtained from the "eye fit" above, can be provided by the "inverse solution" for an assemblage of scatterers (Holliday, 1977b). Swimbladder and presumed body sizes of the scatterers are obtained using the nonnegative least squares solution of

$$\sigma \cdot \mathbf{n} = \mathbf{S}, \tag{6}$$

where $\mathbf{n}$ is a column vector of densities Φ for p scatterer sizes (Holliday, 1977b). $\mathbf{S}$ is a column vector of measured layer backscattering cross-sections σ_{bs_L} for q frequencies at which measurements were made. The matrix σ is of dimension $q \times p$ and contains individual backscattering cross-sections σ_{bs_i} calculated using (equation (1)) over the q measurement frequencies and p scatterer sizes. In this study $q = 12$ (1/6 octaves from 1400 to 5000 Hz) and $p = 21$ (4, 8, 12,...,84 cm).

VOLUME REVERBERATION RESULTS

Color images of volume reverberation for stations 9 (Fig. 2) and 7 (Fig. 3) are included as representative examples of data taken at all acoustic stations. Station 9 was in deep water, 3000 m. Station 7 was on the slope in approximately 1000–1200 m of water (day and night locations at station 7 were about 8 km apart). In each image, S_v is shown as a function of frequency and depth. For shallow stations, bottom echoes are black (Fig. 3). In all images, what appears to be intense scattering near the surface is actually the direct blast from the shot and close-in surface scatter.

Three groups of scatterers are apparent at both stations. The most obvious scattering layer is between 100 and 500 m with a resonance peak at about 1000 Hz. This layer, termed the midwater layer, is intense at both the slope and abyssal stations. At the abyssal stations, it is confined to a narrow depth range by day and partially migrates vertically at night. At the slope stations, this layer is generally thicker and shallower, and its vertical migration less extensive. A second layer occurs at about 50–200 m at night and is resonant at 3000–5000 Hz. This layer, termed the shallow layer, is presumed to be deeper during the day and, therefore, resonant above 5000 Hz. (Fig. 2a shows weak scattering above 4000 Hz at 250 m. This is possibly the low frequency end of the daytime shallow layer.) The third layer begins at about 1000 m and extends to the end of the data record, which was just below 1500 m at abyssal stations. This layer, which is resonant near 2000 Hz, is referred to as the deep layer. This layer is confined between 1000 m and the bottom at slope stations. The deep layer was not found at station 1, where the bottom depth was 900 m.

The midwater layer is presumed to be caused by Pacific whiting, *Merluccius productus*. Pacific whiting are the most abundant midwater fish on the continental shelf and slope of the west coast of the United States (Ware and McFarlane, 1989). A detailed analysis of scattering from this layer compared with National Marine Fisheries Service trawl data collected during a concurrent fisheries survey demonstrates that the size distribution of the whiting matches the observed resonance frequency of this layer. A complete analysis and interpretation of this layer are in progress (NRL, unpubl. data).

Kalish *et al.* (1986) conducted biological trawls and acoustic scattering measurements at a single station in 2800 m depth about 100 km off the Oregon coast. They found a nighttime high frequency scattering layer that extended from the upper 100 m to at least 400 m. During the day, this layer began around 200 m, peaked at 235 m, and extended to at least 400 m. They correlated this scattering with mesopelagic fish that were 1–10 cm long. The nighttime depth of this layer matches that of our shallow layer. In the present case, Pacific whiting occupy much of the daytime depth of this layer, but the weak layer at 250 m matches their daytime depth of peak scattering. Thus, the results of Kalish *et al.* (1986) provide strong evidence that our shallow layer is caused by mesopelagic fish.

The presence of the third scattering layer, the deep layer, was a surprising finding. Small mesopelagic fishes, such as those presumed to cause our shallow layer, are the typical cause of deep water scattering (e.g. Farquhar, 1970). The deep water layer, resonant at a rather low frequency, is likely caused by fish much larger than the mesopelagics.

Layer strength curves for the deep layer peak at 2000 or 2240 Hz (Fig. 4). All curves show a rapid decline below 2000 Hz and a slow decline above resonance, dropping 6–10 dB below the peak at 5000 Hz. Curves from eight different stations are similar in shape, although layer strengths do vary by as much as 12 dB. Stations on the abyssal plain (5, 6, 9, and 10) all have similar layer strengths. Stations located on the slope have both higher and lower strengths than those on the abyssal plain. Stations 4 and 8 have the lowest strengths and stations 7 and 11 have the highest. The southernmost stations (10 and 11) have a less defined resonance peak, with a slower decline at frequencies above resonance, than do the more northern sites.

There were no obvious day–night differences in scattering from the deep layer. At each station, day and night spectral shapes match each other, with little or no change in strengths (Fig. 4). This is because the fish exhibit little diurnal migratory behavior; at five stations where comparable data were collected day and night, the top of the deep layer moved less than 50 m. Equation (2) indicates that, because these fish are so deep, 1000–1500 m, this small day/night difference in fish depth introduces minimal changes in resonance frequencies.

Because the observation of a low frequency resonance at depths greater than 1000 m was unexpected, causes other than scattering from fish inhabiting these depths were explored. Other potential causes considered were artifacts attributed to shallower scatterers or noise generated by the measurement itself. Our calculation of scattering strength versus depth uses an iterative approach similar to that used by Bluy (1970). This approach removes contributions to the received signal that originate outside the ideal beam width of the receiver. This technique eliminates the possibility that the deep scattering is actually off-axis scatter from shallower depths. This was confirmed by comparing receiver beam patterns to

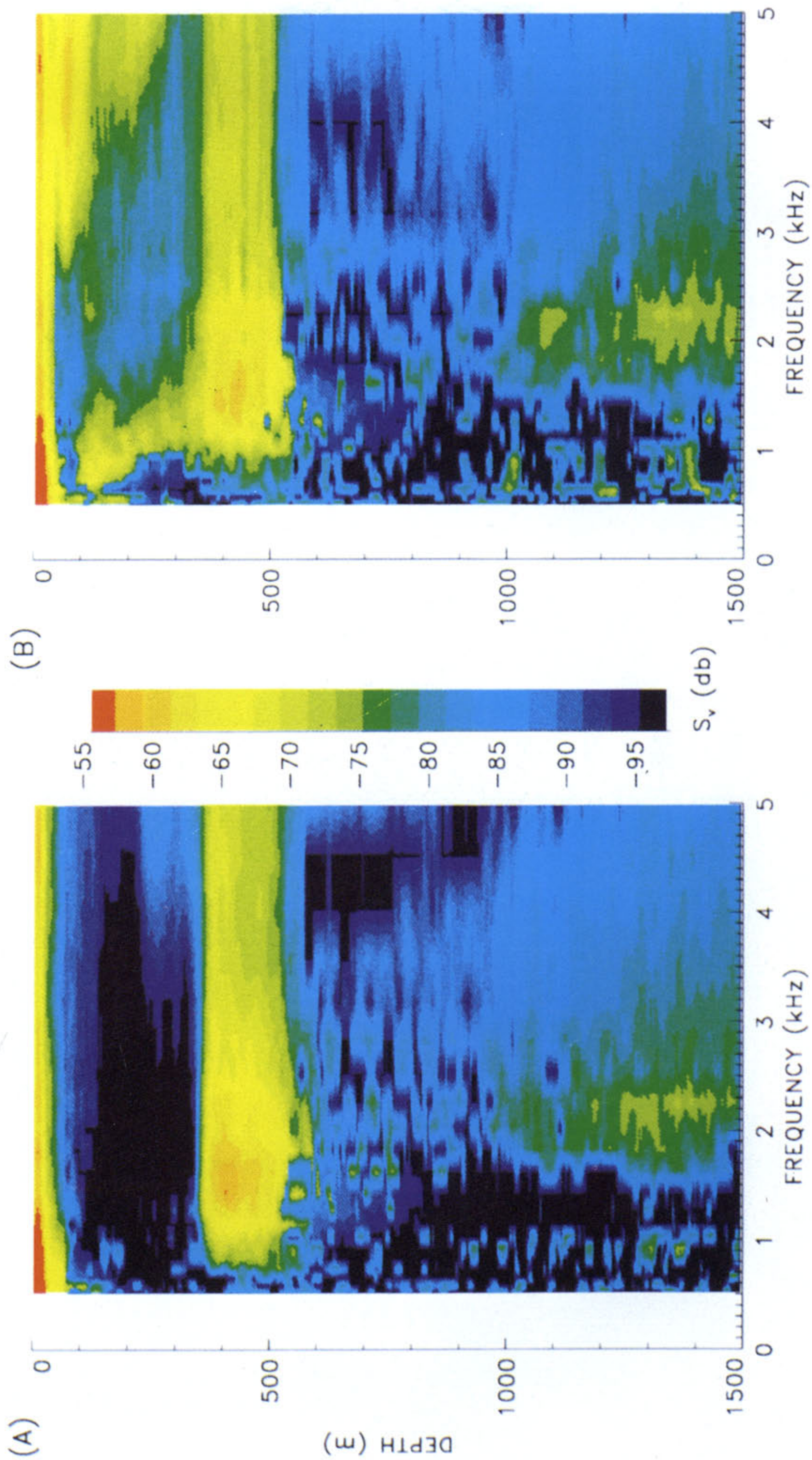

Fig. 2. Volume reverberation at station 9, an abyssal site: (A) day, (B) night.

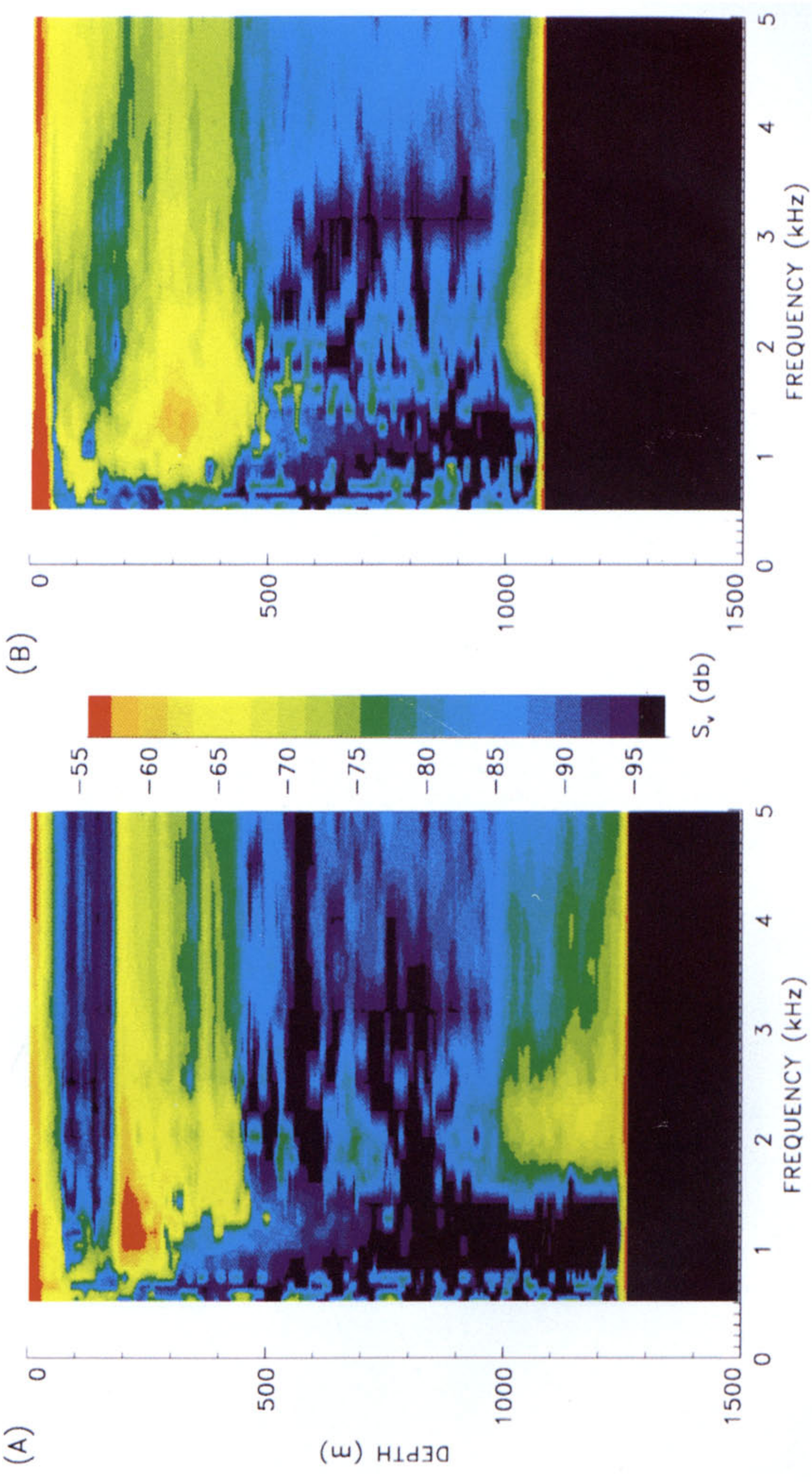

Fig. 3. Volume reverberation at station 7, a slope site: (A) day, (B) night.

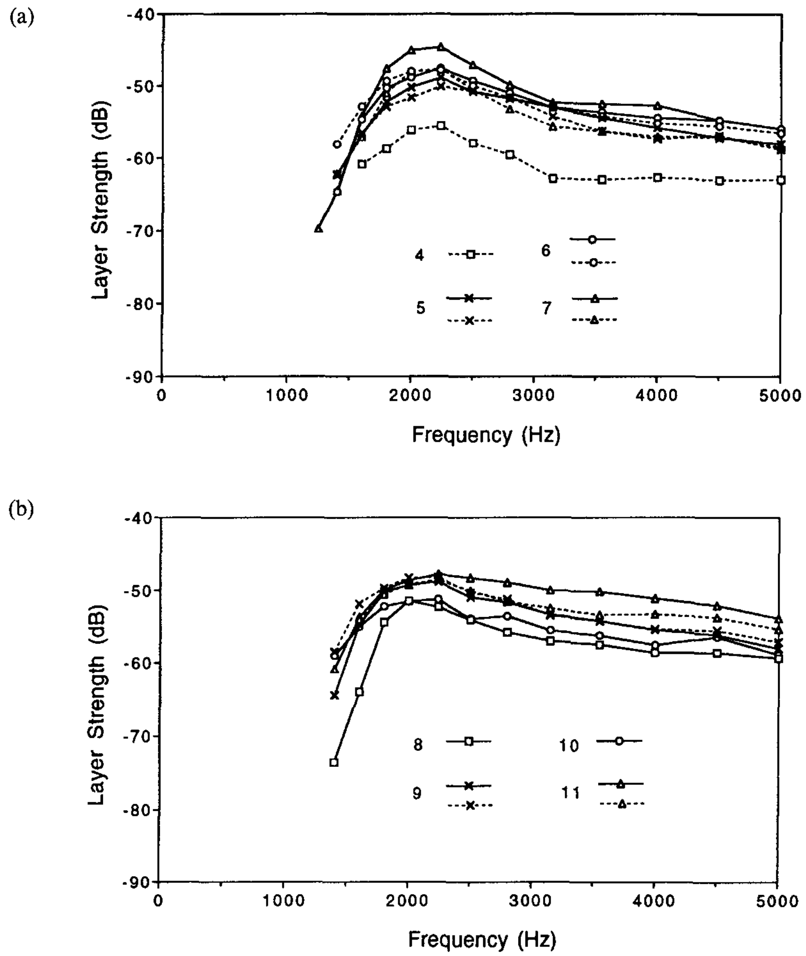

Fig. 4. Layer strength curves from below 900 m depth: (a) stations 4, 5, 6 and 7 (b) stations 8, 9, 10, 11. Solid lines indicate day, dashed lines indicate night.

calculations of the angle and time of flight necessary for the shallower layers to have produced this signal. Another possibility considered was that this signal might be a combination of source bounces between scattering layers and surface to the receiver. No combination was found that would consistently predict a signal increase at these depths, since the other scattering layers were observed to vary in depth but the top of the deep layer was always near 1000 m. Also, the peak scattering strength in the deep layer was always about 2000 Hz, and the shallower layers always peaked either higher or lower in frequency, indicating that there is no relationship between the deep layer and any of the shallower layers. The other possibility investigated was that water thrown into the air by detonation of the explosive source was creating enough noise while falling back to the surface to be detected by the receiver. This was considered unlikely since the sensitivity of the receiver in the upward direction is extremely low. Additionally, during previous experiments, efforts have been made to visually and aurally determine how much time passes between the shot and when most of the splash occurs; the results indicated that any increase in received signal would not correlate with the deep layer. Finally, data have been taken in numerous other locations where no low frequency scattering was observed at these depths. The elimination of other possibilities and the overall persistence of shape of the layer strength curves suggest a widespread population of similarly sized deep water fish as the cause of the deep layer.

SWIMBLADDER MODELING

Potential scatterers

The first step in identifying potential scatterers was to review information on abyssopelagic fishes in the region. Data on larger pelagic fauna deep off the coast of Oregon and northern California are limited to a few midwater trawls. The only large fish caught in trawls at depths to 2200 m over bottoms of 2700–2800 m off central Oregon were four adult grenadiers, *Coryphaenoides filifer*, caught approximately 540–850 m above the bottom (Pearcy, 1976). In addition, three adult *C. armatus* were captured in midwater off California, approximately 50–400 m above a bottom depth of 3800 m (Smith *et al.*, 1979).

Adult grenadiers, family Macrouridae, have been found well above bottom in very small numbers in other widely separated regions (Marshall, 1964; Haedrich, 1974; Smith *et al.*, 1979). Hence, they were the most likely candidate cause of the deep layer. However, grenadiers are generally considered to be bottom dwellers (Marshall, 1964). Thus, we next examined bottom trawl data to determine if any other species living primarily near the bottom might also live well above it and be potential candidates.

Several hundred trawls have been taken on bottom at depths of 400–5200 m on the shelf edge, slope, and abyssal plains up to 2200 km off the Oregon and Washington coasts (Pearcy and Ambler, 1974; Pearcy *et al.*, 1982; Stein and Pearcy, 1982). Three groups of potentially important fishes dominated the catch: four grenadiers, two rockfish, and a flatnose. The two rockfish, longspine thornyhead, *Sebastolobus altivelis*, and shortspine thornyhead, *S. alascanus*, lack swimbladders. Fish without swimbladders would not be significant scatterers of sound at 2000 Hz. In addition, we found no records to indicate that Pacific flatnose, *Antimora microlepis*, have ever been caught off bottom. Since grenadiers have well developed swimbladders (Marshall, 1965) and have been found well above bottom, we concluded that grenadiers were the only known potential cause of our deep layer.

Grenadiers

The four adult *C. filifer* captured in midwater trawls off Oregon were 54–58 cm total length (Pearcy, 1976). The three adult *C. armatus* captured in midwater off California were 60–77 cm total length (Smith *et al.*, 1979). These are the only available size data for midwater grenadiers off the West Coast. Therefore, assuming that the sizes of grenadiers in midwater and on the bottom would be comparable, size frequency distributions and length–weight relationships used in the swimbladder scattering model were taken from fish caught in bottom trawls as reported in Stein and Pearcy (1982). Length distributions are shown in Fig. 5 for four species of grenadiers: *C. armatus*, *C. filifer*, *C. leptolepis*, and *C. acrolepis*. On the middle slope (800–2300 m), *C. acrolepis* made up 50% of the catch, with some *C. filifer*. On the abyssal plain, *C. armatus* and *C. filifer* made up 80% of the catch, with a few *C. leptolepis*. Length–weight relationships are $W = 0.00096L^{3.38}$ for *C. armatus* and $W = 0.0024L^{3.04}$ for *C. filifer*, with W in gm and L in cm. Length–weight relationships were not available for *C. acrolepis* and *C. leptolepis*, but they are not expected to differ greatly from those for *C. armatus* and *C. filifer*.

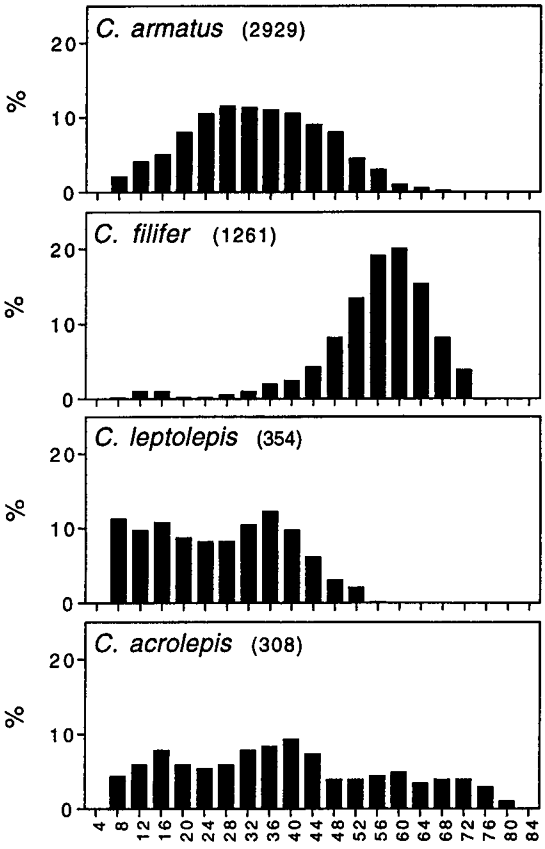

Fig. 5. Length distributions for four *Coryphaenoides* spp. determined from bottom trawls (after Stein and Pearcy, 1982). Numbers of individuals in parentheses.

On the Cascadia Abyssal Plain, *C. armatus*, *C. filifer* and *C. leptolepis* occurred at areal densities of 2.6×10^{-3}, 1.7×10^{-3}, and 0.3×10^{-3} ind./m^2, respectively (Pearcy *et al.*, 1982). Since *C. armatus* and *C. filifer* are the most numerous species over bottom depths of 3000 m or more, and since they are the only candidate species that have been found pelagically, they were chosen for swimbladder modeling for comparison to acoustic data from the abyssal stations.

Stein and Pearcy (1982) postulate that the liver is used as a supplemental buoyancy organ in large grenadiers because the liver is disproportionately large in large specimens. *C. armatus* liver weights increase from approximately 2% of body weight in 20 cm fish to 8% of body weight in 60 cm fish. In *C. filifer*, they increase from about 2% at 30 cm to 6% at 70 cm. To see if liver buoyancy had the potential to significantly decrease the need for swimbladder buoyancy, thereby decreasing swimbladder size, we examined the effects of a liver that was 5% of body weight. This percentage corresponds to 45 cm long *C. armatus* and 60 cm long *C. filifer*. Alexander (1993) gives a minimum liver density of 0.986 gm cm^{-3} and a body density (including flesh and bone but not the liver) of 1.075 gm cm^{-3} for marine teleosts. These values result in a potential 10% reduction in swimbladder volume, which increases f_0 by about 3% and decreases σ_{bs} by about 0.3 dB. These changes are small, so we ignored liver buoyancy and used the swimbladder volume to fish volume distribution given above.

Model results

Application of the swimbladder model to the sizes and densities of *C. armatus* and *C. filifer* obtained from bottom trawl data, and their depth ranges inferred from the acoustic measurements, gave the set of model curves shown in Fig. 6. The curve for the model total shows a surprisingly good fit to the measurements at the abyssal stations. This good fit is strong evidence that the scatterers are in fact deep water grenadiers.

If the areal density of *C. filifer* in Fig. 6 were doubled, its model curve would match the average data very well, implying that *C. armatus* were not important scatterers. However, when data for individual sequences are examined, it is apparent that *C. filifer* alone will not suffice. Thus, in an attempt to obtain a rigorous fit to the individual station measurements and more closely verify the sizes and densities of the scatterers, the inverse solution provided by Holliday (1977b) was applied to each measurement sequence. The inversion can be applied with only one length–weight relation. Therefore, it was assumed that there was a mixed assemblage containing equal numbers of *C. armatus* and *C. filifer*, and a combined relationship was determined by weighting the contributions of the two species at different size classes based on the distributions shown in Fig. 5: $W = 0.0020L^{3.12}$. Because weight–length differences among the different grenadier species are small (< 10%), and because the inclusion of swimbladder volume to fish volume and fish weight to length distributions tends to blur these small differences, errors caused by unequal numbers of *C. armatus* and *C. filifer* or the presence of *C. acrolepis* or *C. leptolepis* are small and were neglected.

The inverse solution produced extremely good fits to the measurement sequences. Example fits are shown in Fig. 7 for stations 9 and 7, the stations shown in Figs 2 and 3. Differences between data and inversion results are usually less than 1 dB for all sequences

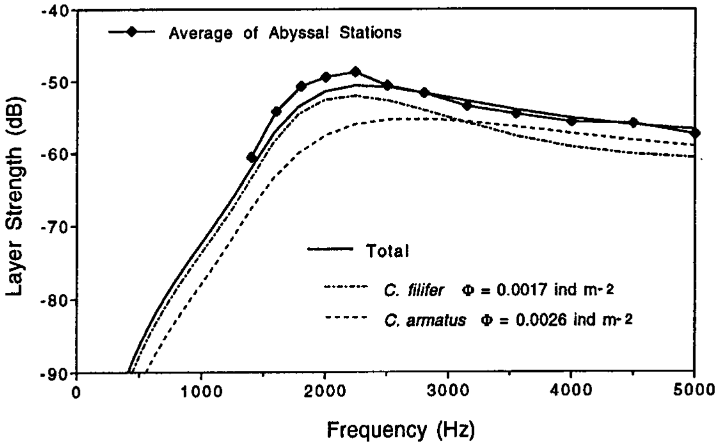

Fig. 6. Average deep-water layer strength for all abyssal stations (curve with diamonds) compared to model estimates (curves only) based on the two most abundant species of grenadiers found over the abyssal plain and slope base.

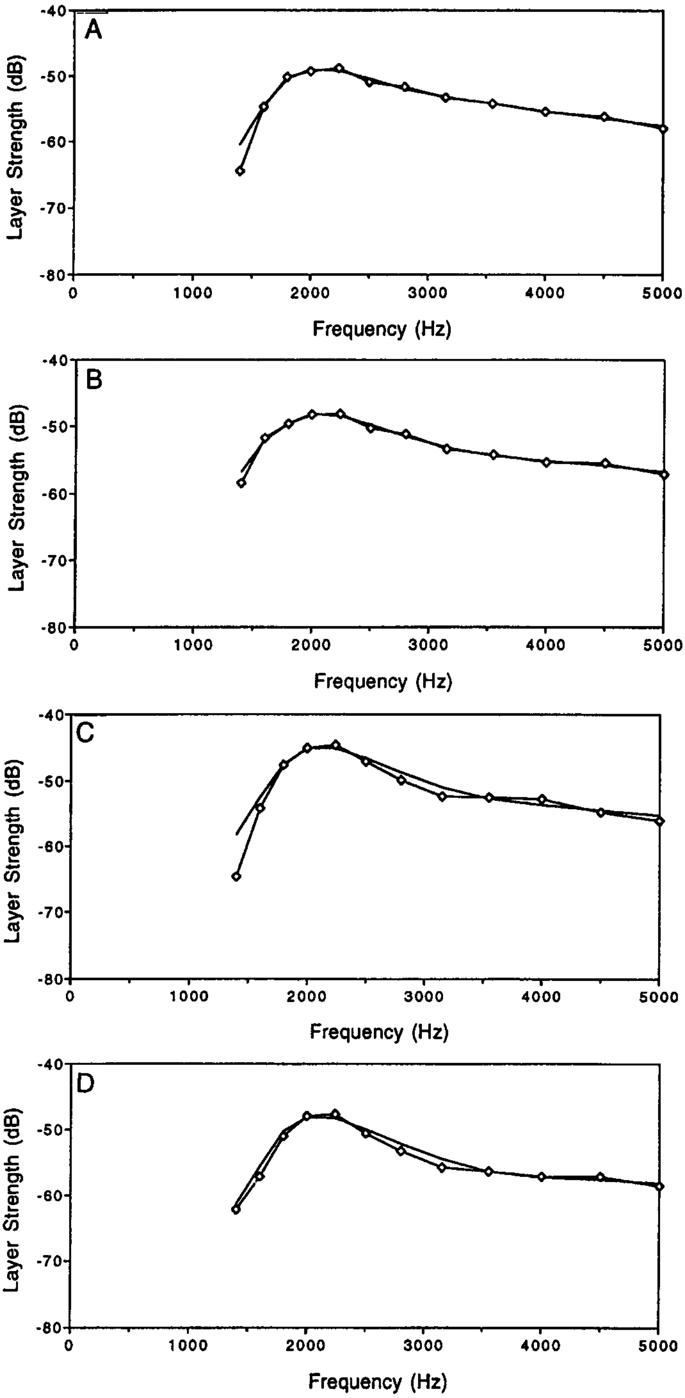

Fig. 7. Comparison of layer strength data (diamonds with curves) and the inverse solution (curves) for: (A) station 9 day; (B) station 9 night; (C) station 7 day; and (D) station 7 night.

and frequencies, except the lowest frequencies, where the data sometimes decrease with decreasing frequency faster than the theoretical 12 dB/octave of Rayleigh scattering assumed by the model.

For each sequence, the distribution of fish lengths derived from the inverse solution was essentially bimodal, with a distinct separation at 44–48 cm. However, since the solution attempts to match the acoustic data exactly, small variations in the data from one sequence to another can cause significant changes in individual length distributions. Thus, only average length distributions for the seven abyssal and six slope measurement sequences are presented (Fig. 8). Both averages exhibit a bimodal size distribution with peaks at 28–32 cm and 52–56 cm. Comparison of these distributions with those for the individual species (Fig. 5) indicates that the 52–56 cm peak is most likely caused by *C. filifer*. The 28–32 cm peak could be caused by *C. armatus* at abyssal stations and *C. acrolepis* at slope stations or, since pairs of abyssal and slope stations are only 40–60 km apart, either or both species could be at all stations. *C. leptolepis* could also be present.

The 52–56 cm fish (*C. filifer*) are the primary cause of the peak in the layer strength curves at 2000–2240 Hz. Small fish (other than *C. filifer*) less than 30 cm determine the level of the high frequency tail, and intermediate-sized, 30–40 cm, fish (any combination of species) determine the slope of the curve from the peak to the high frequency tail. The inversion shows that the southernmost stations, 10 and 11, whose curves slope gently away from the peak, have much higher proportions of 30–40 cm fish than do the more northern stations.

Estimates of grenadier density, Φ, for each site were also obtained from the inverse solutions for each measurement sequence (Table 1). For the abyssal stations, densities ranged from 2.7 to 5.0×10^{-3} ind./m^2, with a mean of 3.9×10^{-3} ind./m^2. This is comparable to a density of 4.6×10^{-3} ind./m^2 caught on the bottom by Pearcy *et al.* (1982) for the lower slope and abyssal plain. Densities were more variable at the slope stations, ranging from 1.1 to 8.4×10^{-3} ind./m^2, with a mean of 4.9×10^{-3} ind./m^2.

Densities plotted in relation to station depth (Fig. 9) show a distinct peak around 1500 m depth. This indicates that grenadier density as a function of station location is related to bottom depth rather than north/south position. Hence, the variability in densities among the slope stations may have been caused by the influence of the bottom on the grenadier's shoreward limit of occurrence. Lower abundances could be expected at the extreme edge of their preferred habitat, which would occur at the shallowest stations (4 and 8). Higher

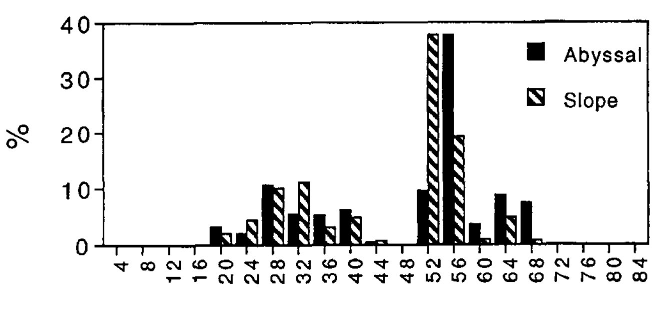

Fig. 8. Average fish length distributions for abyssal and slope sequences as determined from the inverse solution.

Table 1. Estimates of the density and depths of occurrence of deep water resonant sound scatterers at stations along the Washington–Oregon–California coast

	Day			Night		
St. No.	Water Depth (m)	Density ind./m^2	Depth Range (m)*	Water Depth (m)	Density ind./m^2	Depth Range (m)*
1	900	0	—	—	—	—
4	—	—	—	1110	0.0011	1000–1110
5	2800	0.0039	1100–1500	2900	0.0030	1100–1500
6	3100	0.0050	1050–1500	3100	0.0044	1100–1500
7	1245	0.0074	985–1245	1070	0.0039	985–1070
8	1025	0.0028	950–1025	—	—	—
9	2800	0.0037	1000–1500	2800	0.0042	1000–1500
10	2400	0.0027	1000–1500	—	—	—
11	1500	0.0084	1000–1500	1465	0.0057	995–1465

*Maximum depth of acoustic data is 1500 m.

abundances could be expected where their preferred depth range intersects the bottom, which could explain the high abundances at stations 7 and 11 (Table 1).

DISCUSSION

Deep-sea grenadiers are reported to be the most abundant large fish at depths over 1000 m off the central Oregon coast (Pearcy *et al.*, 1982). The swimbladder model results for deep-sea grenadiers match the acoustic measurements extremely well. This agreement was obtained using published values of both grenadier size and abundance from bottom trawls in the region. The inverse solution to the acoustic data gave bimodal distributions of fish

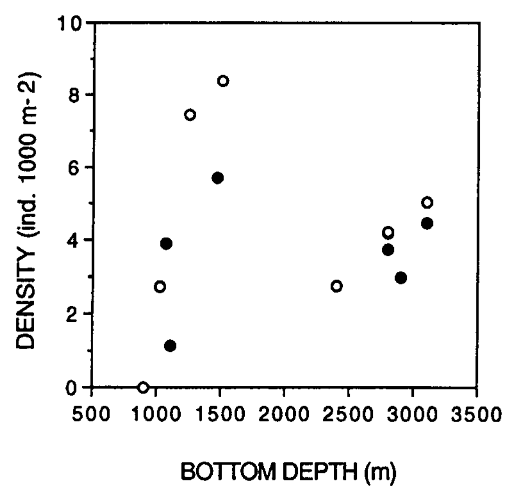

Fig. 9. Estimates of fish density at all stations in relation to bottom depth as obtained from the inverse solution. Symbols: open circles, day; black circles, night.

lengths that coincide with grenadier lengths obtained from these trawls. The inversion indicates that about two-thirds of the fish at both abyssal and slope stations are larger than 48 cm (Fig. 8). The peak at 52–56 cm indicates that most, if not all, of these larger fish are *C. filifer*, while some could be *C. armatus* or *C. acrolepis* (Fig. 5). The one-third of the fish smaller than 48 cm are probably *C. armatus* or *C. acrolepis*, or possibly, *C. leptolepis* (Fig. 5). Thus, the inverse solution indicates that *C. filifer* is the most abundant grenadier in the deep layer.

Pearcy *et al.* (1982) found a scarcity of small grenadiers in their bottom trawl catches and indicated this was because small grenadiers are predominantly pelagic, rather than benthic. Small fish, if present at the same densities and depths as large fish, are not readily detected by acoustic measurements, because high backscattering from the larger fish masks any scattering from the smaller fish. Thus, numbers of smaller grenadiers in the deep layer could be larger than our acoustic techniques imply.

We observed no diel changes in the upper depth limit (950–1100 m) of the deep layer. This observation is consistent with what is known about the biology of deep water grenadiers (Marshall, 1980). Observations from submersibles show grenadiers are adept at maintaining neutral buoyancy, and their long tapering tail is well adapted for extremely efficient slow speed swimming and maneuvering (Marshall, 1980). Their respiration rates are also extremely low (Marshall, 1980). They are considered to be a waiting-hovering predator (Marshall, 1980; Pearcy *et al.*, 1982). Thus, grenadiers are not well adapted for diel vertical migration.

Our observed upper depth of the grenadiers coincides with the approximate depth limit at which marine organisms can sense the difference between night and day (Clarke, 1970). The grenadiers may be cueing on this limit. During the day, the grenadiers could be feeding on pelagic prey that migrate downward from higher in the water column. Pelagic squid and fish frequently have been found in the stomachs of large grenadiers (> 30 cm) such as *C. armatus* and *C. leptolepis* (Pearcy and Ambler, 1974). During the night these prey presumably return to shallower depths, but the grenadiers do not follow.

Water temperature is a possible alternative to light as an environmental cue that maintains pelagic grenadiers below 1000 m depth. Temperature data collected with CTD probes to 1000 m at each station off Oregon and California do not show an obvious change as 1000 m is approached (Naval Oceanographic Office, unpubl. data). However, temperatures at all stations do show a steady decline from approximately 5°C at 500 m to approximately 3.5°–4°C at 1000 m. Off the Atlantic coast of Canada, several grenadier species have been found in greatest abundance at temperatures between 2° and 4.5°C (Parsons, 1976). Grenadiers off Oregon and California could have a similar preference.

The occurrence of very deep large scatterers has been observed on other acoustic surveys in other locations. Chapman *et al.* (1974) conducted a series of surveys of the Atlantic and Pacific Oceans and the Mediterranean Sea. They noted the occurrence of a deep, approximately 1000 m, layer, resonant between 1 and 2 kHz, indicative of large, 35–70 cm fish, in the Labrador Sea, south of Iceland, in the central North Atlantic between 25° and 40°N, in the North Pacific north of Hawaii between 40° and 55°N, and off the coast of California. Recent measurements in the Gulf of Alaska also found a layer below 900 m, resonant at 1.6–2 kHz (Thompson *et al.*, 1995). Smailes (1976) observed a scattering layer resonant at 2 kHz around 1000 m depth northeast of the Azores.

Adult grenadiers have been found in midwater in regions other than off the U.S. West Coast. North of Hawaii at 28°N, Smith *et al.* (1979) caught one 36 cm *C. armatus* about

700 m above a bottom depth of 5700 m. In the North Atlantic south and west of Iceland, Haedrich (1974) caught 49 *C. rupestris* 7–94 cm total length. All but one of these fish were caught 260–710 m above bottom depths of 1270–2810 m. The other individual was caught 1440 m above bottom. Marshall (1964) reported the midwater capture of *Cynomacrurus piriei* in the Atlantic section of the Southern Ocean and *Odontomacrurus murrayi* in the Arabian Sea. However, both of these species had regressed swimbladders and would, therefore, be poor scatterers at 2 kHz.

The regions where pelagic adults of *Coryphaenoides* spp. have been caught are also regions where deep 1–2 kHz scattering layers were found by Chapman *et al.* and NRL: off Oregon and California, well north of Hawaii, and south of Iceland. Depths of grenadier capture match the acoustically determined layer depths only in the Icelandic region. At the Pacific locations, the fish were caught well below the acoustic layers. This apparent discrepancy is quite likely caused by different experimental techniques and objectives. Acoustic research focused on the upper 1000 m or less and the deep layers were at the limit of the recorded data. Biological research focused on the height above the sea floor of these normally demersal fish. Heights of fish capture above bottom were similar in Pacific and Icelandic regions, but bottom depths in the Icelandic region were shallower. That is probably why acoustic and biological depths correlate near Iceland but not in the Pacific. The most likely explanation for these results is that grenadiers are responsible for the deep acoustic layers off Oregon and California, well north of Hawaii, and south of Iceland and that these layers extend from about 1000 m to near the bottom.

Grenadiers have not yet been reported from other areas where a deep layer has been seen: the Labrador Sea, the central North Atlantic, and northeast of the Azores. These fish may or may not be responsible for these layers; Smailes (1976) believes that the cause of the layer northeast of the Azores was the cutlass fish, *Aphanopus carbo*.

SUMMARY

A deep scattering layer resonant at 2000–2200 Hz was observed along the coasts of Oregon and California at depths of 950 to at least 1500 m, over bottom depths of 1025–3100 m on the slope and abyssal plain between 40° and 45°N. The strengths and depths of scattering were similar for day and night, indicating that the scatterers did not undertake a diel vertical migration.

Application of an acoustic model of swimbladder resonance to length distributions and abundances obtained from published trawl data for deep water grenadiers, *Coryphaenoides* spp. (Pearcy *et al.*, 1982), gave close agreement with measured scattering levels, suggesting these fish were the scatterers. An inverse solution applied to the measurements further suggested that the scattering was caused by a mixed assemblage of *C. filifer* and *C. armatus*, *C. acrolepis*, and/or *C. leptolepis*. The model estimates also indicate that the grenadiers occurred at average densities of 0.004 ind./m^2 with a range of 0.001–0.008 ind./m^2.

Other acoustic and biological data suggest that grenadiers living from 1000 m depth to near the bottom are the cause of deep scattering layers resonant between 1000 and 2000 Hz in the North Atlantic, and other parts of the North Pacific.

Acknowledgements—The collection of acoustic data was sponsored by the Office of Naval Research. Logistic support at sea was provided by the Naval Oceanographic Office's Senior Representative, E. Beeson, and staff. Assistance at sea was provided by N. V. Lombard and the Captain and crew of the U.S.N.S. *Wilkes*. We thank W. G. Pearcy for kindly providing information on the biology of deep sea grenadiers.

REFERENCES

Akal, T., Dullea, R. K., Guidi, G. and Stockhausen, J. H. (1993) Low-frequency volume reverberation measurements. *Journal of the Acoustical Society of America*, **93**, 2535–2548.

Alexander, R. McN. (1993) Buoyancy. In *The Physiology of Fishes*, ed. D. H. Evans, pp. 75–97, CRC Press, Boca Raton, FL.

Andreeva, I. B. (1964) Scattering of sound by air bladders of fish in deep sound-scattering layers. *Soviet Physics—Acoustics*, **10**, 17–20.

Batzler W. E., Reese, J. W. and Friedl, W. A. (1975) Acoustic volume scattering: its dependence on frequency and biological scatterers. NUC TP 442, Naval Command, Control and Ocean Surveillance Center RDT and E Division, San Diego, CA.

Bluy, O. Z. (1970) Transducer sidelobe corrections for deep scattering layer data. *Deep-Sea Research*, **33**, 397–399.

Bowne, P. S. (1982) Swimbladder deposits: occurrence and morphology in Macrouridae, Moridae and Ophidiiformes. *Copeia*, **1982**(1), 205–208.

Brown C. L. and Brooks, A. L. (1974) A summary report of progress in the Ocean Acre Program. NUSC TR 4643, Naval Undersea Warfare Center Detachment, New London, CT.

Chapman, R. P., Bluy, O. Z., Adlington, R. H. and Robison, A. E. (1974) Deep scattering layer spectra in the Atlantic and Pacific Oceans and adjacent seas. *Journal of the Acoustical Society of America*, **56**, 1722–1734.

Clarke, G. L. (1970) Light conditions in the sea in relation to the diurnal vertical migrations of animals. In *Proceedings of an International Symposium on Biological Sound Scattering in the Ocean*, ed. G. B. Farquhar, pp. 41–59, Maury Center for Ocean Science Report 005, Washington, DC.

Clay, C. S. (1991) Low-resolution acoustic scattering models: fluid-filled cylinders and fish with swim bladders. *Journal of the Acoustical Society of America*, **89**, 2168–2179.

Dark, T. A., Nelson, M. O., Traynor, J. J. and Nunnallee, E. P. (1980) The distribution, abundance, and biological characteristics of Pacific whiting, *Merluccius productus*, in the California–British Columbia region during July–September 1977. *Marine Fisheries Review*, **42**(3-4), 17–33.

Farquhar, G. B. (ed.) (1970) *Proceedings of an International Symposium on Biological Sound Scattering in the Ocean*. Dept. of the Navy, Maury Center for Ocean Science, Report no. MC-005.

Feuillade, C. and Werby, M. F. (1994) Resonances of deformed gas bubbles in liquids. *Journal of the Acoustical Society of America*, **96**, 3684–3692.

Foote, K. G. (1985) Rather-high-frequency sound scattering by swimbladdered fish. *Journal of the Acoustical Society of America*, **78**, 688–700.

Haedrich, R. L. (1974) Pelagic capture of the epibenthic rattail *Coryphaenoides rupestris*. *Deep-Sea Research*, **21**, 977–979.

Hall, M. (1981) Measurements of acoustic volume backscattering in the Indian and Southern Oceans. *Australian Journal of Marine and Freshwater Research*, **32**, 855–876.

Hall, M. and Quill, A. F. (1983) Biological sound scattering in an ocean eddy. *Australian Journal of Marine and Freshwater Research*, **34**, 563–572.

Holliday, D. V. (1972) Resonance structure in echoes from schooled pelagic fish. *Journal of the Acoustical Society of America*, **51**, 1322–1332.

Holliday, D. V. (1977a) The use of swimbladder resonance in the sizing of schooled pelagic fish. *Rapports et Proces—Verbaux des Reunions*, **170**, 130–135.

Holliday, D. V. (1977b) Extracting bio-physical information from the acoustic signatures of marine organisms. In *Oceanic Sound Scattering Prediction*, ed. N. R. Anderson and B. J. Zahuranec, pp. 619–624, Plenum Press, New York.

Jones, F. R. H. and Marshall, N. B. (1953) The structure and functions of the teleostean swimbladder. *Biological Review of the Cambridge Philosophical Society*, **28**, 16–83.

Jones, F. R. H. and Scholes, P. (1985) Gas secretion and resorption in the swimbladder of the cod *Gadus morhua*. *Journal of Comparative Physiology B*, **155**, 319–331.

Kalish, J. M., Greenlaw, C. F., Pearcy, W. G. and Holliday, D. V. (1986) The biological and acoustical structure of sound scattering layers off Oregon. *Deep-Sea Research*, **33**, 631–653.

Love, R. H. (1975) Predictions of volume scattering strength from biological trawl data. *Journal of the Acoustical Society of America*, **57**, 300–306.

Love, R. H. (1978) Resonant acoustic scattering by swimbladder-bearing fish. *Journal of the Acoustical Society of America*, **64**, 571–580.

Love, R. H. (1993) A comparison of volume scattering strength data with model calculations based on quasisynoptically collected fishery data. *Journal of the Acoustical Society of America*, **94**, 2255–2268.

McCartney, B. S. and Stubbs, A. R. (1970) Measurements of the target strength of fish in dorsal aspect, including swimbladder resonance. In *Proceedings of an International Symposium on Biological Sound Scattering in the Ocean*, ed. G. B. Farquhar, pp. 180–211, Maury Center for Ocean Science Report 005, Washington, DC.

Marshall, N. B. (1964) Bathypelagic Macrourid fishes. *Copeia*, **1964**(1), 86–93.

Marshall, N. B. (1965) Systematic and biological studies of the Macrourid fishes (Anacanthini—Teleostii). *Deep-Sea Research*, **12**, 299–322.

Marshall, N. B. (1980) *Deep-Sea Biology, Developments and Perspectives*, Garland STPM Press, New York. pp.

Nero, R. W. (1992) Estimates of low frequency volume scattering off the Oregon–Washington coast. NOARL TN 206, Naval Research Laboratory, Stennis Space Center, MS.

Ona, E. (1990) Physiological factors causing natural variations in acoustic target strength of fish. *Journal of the Marine Biological Association of the U.K.*, **70**, 107–127.

Parsons, L. S. (1976) Distribution and relative abundance of roundnose, roughhead and common grenadiers in the northwest Atlantic. *International Commission for the Northwest Atlantic Fisheries Selected Papers*, **1**, 73–88.

Pearcy, W. G. (1976) Pelagic capture of abyssobenthic macrourid fish. *Deep-Sea Research*, **23**, 1065–1066.

Pearcy, W. G. and Ambler, J. W. (1974) Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep-Sea Research*, **21**, 745–759.

Pearcy, W. G., Stein, D. L. and Carney, R. S. (1982) The deep-sea benthic fish fauna of the northeastern Pacific Ocean on Cascadia and Tufts Abyssal Plains and adjoining continental slopes. *Biological Oceanography*, **1**, 375–428.

Sand, O. and Hawkins, A. D. (1973) Acoustic properties of the cod swimbladder. *Journal of Experimental Biology*, **58**, 797–820.

Smailes, I. C. (1976) Observations of volume scattering strength in the northeast Atlantic. *Journal of the Acoustical Society of America*, **86**, 1056–1060.

Smith, K. L., White, G. A., Laver, M. B., McConnaughey, R. R. and Meador, J. P. (1979) Free vehicle capture of abyssopelagic animals. *Deep-Sea Research*, **26**, 57–64.

Stanton, T. K. (1989) Simple approximate formulas for backscattering of sound by spherical and elongated objects. *Journal of the Acoustical Society of America*, **86**, 1499–1510.

Stein, D. L. and Pearcy, W. G. (1982) Aspects of reproduction, early life history, and biology of macrourid fishes off Oregon, U.S.A. *Deep-Sea Research*, **29**, 1313–1329.

Thompson, C. H., Love, R. H. and Levenson, C. (1995) Volume reverberation on CST IV. NRL/FR/7174–95–9622, Naval Research Laboratory, Stennis Space Center, MS.

Ware, D. M. and McFarlane, G. A. (1989) Fisheries production domains in the northeastern Pacific Ocean. In *Effects of Ocean Variability on Recruitment and an Evaluation of Parameters used in Stock Assessment Models*, ed. R. J. Beamish and G. A. McFarlane, pp. 359–379, Canadian Special Publication of Fisheries and Aquatic Sciences, No. 108.

Weston, D. E. (1967) Sound propagation in the presence of bladder fish. In *Underwater Acoustics*, ed. V. M. Albers, Vol. 2, pp. 55–88, Plenum, New York,