Low-frequency acoustic measurements of Pacific hake, *Merluccius productus*, off the west coast of the United States

Redwood W. Nero
Charles H. Thompson
Richard H. Love
Naval Research Laboratory, Code 7174
Stennis Space Center, Mississippi 39529-5004
E-mail address for R.W. Nero:woody.nero@nrlssc.navy.mil

Abstract.–Low-frequency volume scattering measurements were conducted by the Naval Research Laboratory (NRL) on the upper slope, slope base, and abyssal plain along the U.S. west coast between the Strait of Juan de Fuca, Washington, and Cape Mendocino, California. Comparisons of swimbladder radii estimated from resonances with those estimated from fish lengths obtained from quasisynoptic National Marine Fisheries Service (NMFS) trawl catches of Pacific hake, *Merluccius productus*, strongly suggest that the major source of the low-frequency scattering were Pacific hake. Estimates of hake density from the NRL low-frequency measurements and the NMFS acoustic, midwater trawl survey on the slope gave comparable values of 195–439 kg/ha and 91–369 kg/ha respectively. However, NRL measurements, up to 50 km offshore of the outer limit of the NMFS survey, found densities of 270–300 kg/ha in layers peaking at 225 to 450 m depth. This finding suggests that high densities of hake may occur farther offshore of the traditional limit of NMFS surveys and at depths which may be difficult to survey with conventional fisheries sounders.

Manuscript accepted 2 October 1997.
Fishery Bulletin 96:329–343 (1998).

Pacific hake, *Merluccius productus*, are the most abundant large midwater fish on the continental shelf and slope of the west coast of the United States during summer (Ware and McFarlane, 1989). Hake winter between Point Conception, CA, and Baja California. In spring they migrate northward to feed in the productive waters along the continental shelf from northern California to Vancouver Island. They remain in this area from May through October. The migration between the winter spawning grounds and the summer feeding grounds is size structured, i.e. related to fish length and optimum swimming velocity (Francis, 1983; Smith et al., 1992), with the larger fish swimming faster and farther. Large fish migrate farthest north to near Vancouver Island, smaller fish reach only as far as southern Oregon and northern California (Stauffer, 1985).

A midwater trawl fishery targets hake occurring in dense feeding aggregations along the shelf break in midsummer (Stauffer, 1985). Since 1977, the National Marine Fisheries Service (NMFS) has conducted a triannual acoustic, midwater trawl survey to determine hake distribution and abundance (Dorn et al., 1994). During the 1992 survey, NMFS integrated volume scattering with a high-frequency (38-kHz) echo sounder and corroborated fish identity and size with midwater trawls. Volume scattering was converted to fish biomass with a volume scattering to biomass regression (Dorn et al., 1994).

Coincident with the 1992 fishery survey, the Naval Research Laboratory (NRL) conducted an acoustic survey of volume scattering using a broad-band low-frequency measurement system (Thompson and Love, 1996). Because the NRL survey was conducted quasisynoptically with the fisheries survey, comparisons were possible between the two surveys.

Although echo sounders at relatively high frequencies (>20 kHz) are a standard tool in fisheries surveys (MacLennan and Simmonds, 1992), a broad-band low-frequency sound at the natural resonance of the population of fish swimbladders at depth have been used as an alternative tool (Holliday, 1972; 1977a). A variety of acoustic models has been developed to help predict and understand various aspects of this resonance (Anderson, 1950; Andreeva, 1964; Love, 1978; Stanton, 1989; Clay, 1991, Feuillade and Werby, 1994). With these models, the acoustic resonance of a population of fish swimbladders at depth can provide quantitative information about the fish population. The spectrum of the resonance is dependent on swimbladder size, depth, and fish behavior (Sand and Hawkins, 1973; Love, 1993). The scattered sound at resonance is almost completely omnidirectional, independent of fish aspect (Feuillade and Werby, 1994). As a result, resonance measurements are useful for inferring the size and abundance of the swimbladders. An inverse solution of measured scattering levels can be used to generate a size-frequency distribution of swimbladders (Holliday, 1977b), from which fish size can then be inferred.

On the U.S. west coast, Pacific hake, measuring 45 cm in fork length and occupying depths of 50 to 500 m, are expected to be resonant near 500 to 1,500 Hz (Love, 1978). Midwater trawls show that no other large pelagic fish are as abundant as hake (Dorn et al., 1994). Other fishes expected to contribute to scattering are anchovy and mesopelagic fishes (Kalish et al., 1986). Both are much smaller than hake and at depths of 50 to 500 m should only contribute to scattering above 2 kHz.

This study reports on low-frequency volume scattering measurements from what are assumed to be Pacific hake at depths of 50 to 500 m over the continental slope off the Strait of Juan de Fuca and the Oregon–California coasts. Bioacoustic models are used to estimate the number and size of swimbladders at depth. These results are compared with estimates of swimbladder size and abundance obtained from quasisynoptic acoustic data and midwater trawl catches collected by the National Marine Fisheries Service.[1] A comparison of swimbladder size is problematic. Fish can either let their swimbladders compress according to Boyle's law during descent, or they can actively add gas to the swimbladder to maintain neutral buoyancy. In addition, the relation between fish size and swimbladder volume is also highly variable within a group of fish and is affected by feeding and other aspects of fish behavior (Ona, 1990). We consider these possibilities and suggest several hypotheses about the swimbladder behavior of Pacific hake.

Materials and methods

Measurements

The NRL low-frequency acoustic measurements were made from 14 to 29 August 1992 aboard the USNS *Wilkes* (T-AGS-33) in conjunction with a Naval Oceanographic Office (NAVOCEANO) survey. The NRL conducted measurements at 9 stations located on the continental slope and abyssal plain between the Strait of Juan de Fuca and Cape Mendocino (Table 1; Fig. 1). Stations 2 and 3 off the Washington coast were missed owing to heavy seas. Because we expected a north–south trend in the size composition of the hake, stations at similar latitude were grouped and named according to their proximity to geographic features: station 1—La Perouse; 4 and

[1] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. data.

Table 1
Volume reverberation stations conducted by the Naval Research Laboratory.

Station no.	Date	Time (local [h])	Day or night	Lat. N	Long. W	Bottom depth (m)
1	14 Aug	1836–1920	day	48°26'	126°20'	900
4	18 Aug	0120–0223	night	44°44'	125°04'	1,100
5	19 Aug	1325–1420	day	44°45'	125°42'	2,800
5	20 Aug	0145–0240	night	44°38'	125°43'	2,900
6	21 Aug	0000–0105	night	43°28'	125°40'	3,100
6	21 Aug	0925–1032	day	43°27'	125°38'	3,100
7	23 Aug	0025–0109	night	43°26'	125°04'	1,070
7	23 Aug	0858–0935	day	43°30'	125°06'	1,245
8	24 Aug	0905–0936	day	42°18'	124°54'	1,025
9	25 Aug	2212–2248	night	42°19'	125°40'	2,800
9	26 Aug	0856–0927	day	42°23'	125°39'	2,800
10	27 Aug	0925–1001	day	40°15'	125°35'	2,400
11	28 Aug	0117–0200	night	40°04'	125°09'	1,465
11	29 Aug	0931–1006	day	40°03'	125°08'	1,500

5—Heceta North; 6 and 7—Heceta South; 8 and 9—Sebastian; and 10 and 11—Mendocino.

Just prior to the NRL survey, NMFS conducted a high-frequency acoustic-midwater trawl survey of Pacific hake. The survey began just south of San Francisco and ended off Cape Scott, Vancouver Island (Dorn et al., 1994). Generally, trawls were located inshore of the NRL stations. The NRL and NMFS surveys were separated by 43 days in the south (station 11, trawl 8), but only 5 days in the north (station 1, trawl 45)(Fig. 1). The NMFS survey provided information on fish size and abundance that could be compared with the results of the low-frequency acoustic analysis. Comparisons were restricted to midwater trawls located close to the NRL stations within each of the above named latitudinal regions. A north–south trend in fish size was evident, although a gap occurred in the size distributions between 38 and 40 cm (Fig. 2). Trawls appeared to catch fish on either side of this gap; only a few trawls contained both size classes. This finding suggests that, at sea, different size classes remain spatially separate (Fig. 1).

The NRL sound scattering measurements used an explosive sound source and a directional acoustic receiver. A 0.23-kg TNT charge detonated at 0.5 m depth provided a high source level over a wide frequency range. The shallow detonation depth allowed the gas bubble created by the explosion to vent to the surface and prevented the multiple sound pulses caused by bubble oscillations characteristic of charges detonated at greater depth. Measurement sequences consisted of 4 to 6 shots over a 30-min period. Because the ship typically drifted at 1–2 knots, the distance over which data were collected was on the order of a mile.

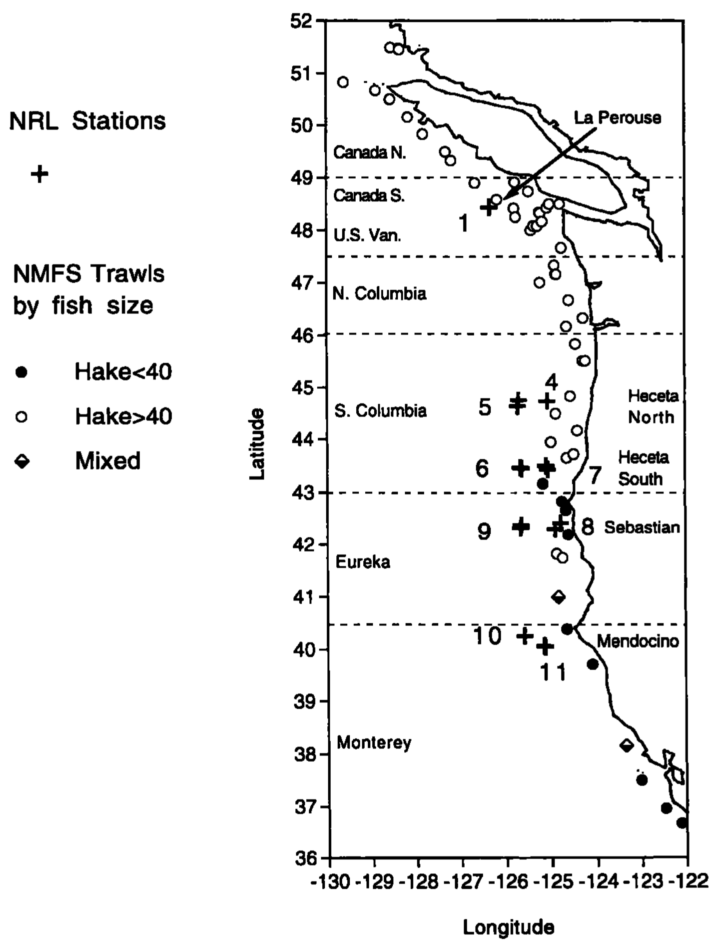

Figure 1

Map of the U.S. west coast showing Naval Research Laboratory (NRL) stations and locations where pertinent National Marine Fisheries Service (NMFS) midwater trawls were undertaken.

The acoustic receiver used for these measurements consists of a thirty-two element line hydrophone, 0.9 m long, mounted along the axis of a conical reflector that had a height of 0.9 m and an open base with a diameter of 1.8 m. The purpose of the reflector was to map an annular area of the opening to each hydrophone element for sound entering the reflector parallel to the axis and to decrease sensitivity to sound entering the reflector from other directions. The receiver was originally designed for use at frequencies between 2.5 and 20 kHz. By varying the number of active hydrophone elements, the receiver's 3-dB beam width can be maintained between 10° and 20° in that frequency range. The eight elements nearest the vertex of the cone form a 45-cm aperture and are used for frequencies from 10 to 20 kHz. By doubling the active length with eight additional elements, a 90-cm aperture is formed that can be used for frequencies between 5 and 10 kHz, and all 32 elements form a 180-cm aperture that can be used below 5 kHz. Between 2.5 and 5 kHz, measured beam patterns of the receiver show a main lobe with shape and 3-dB beam width similar to the main lobe of theoretical beam patterns (Urick, 1983) for a plane circular array 1.8 m in diameter, whereas the side lobes are lower than those for a plane circular array. Below 2.5 kHz, the main beam widens beyond 20°, reaching 38° at 1,600 Hz, 58° at 800 Hz, and 74° at 500 Hz.

Received signals from each TNT shot were amplified, high- and low-pass filtered at 400 and 6,000 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 5,000 Hz and amplitude versus time envelopes calculated for each band. There was little variation between shots in a sequence. Envelopes of all shots in a sequence were averaged to obtain a single set that was representative of scattering during that sequence, and this averaged data was used to calculate volume scattering strength, S_v, the scattering strength of a unit volume of water, as a function of depth. 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 these depths produced a series of layer scattering strength (S_L) versus frequency curves. On the basis of the distinct nature of the S_L curves, scatterers were assumed to be swimbladder-bearing fish. Hence, S_L curves were used to determine swimbladder size with a swimbladder scattering model. Fish swimbladders are not spherical, nonetheless their size may be conveniently expressed in terms of equivalent spherical radii (ESR) (i.e. the radii of spheres of equivalent volume). Thus ESR can be derived independently from acoustic data and trawl data and compared to evaluate each method for assessing population statistics.

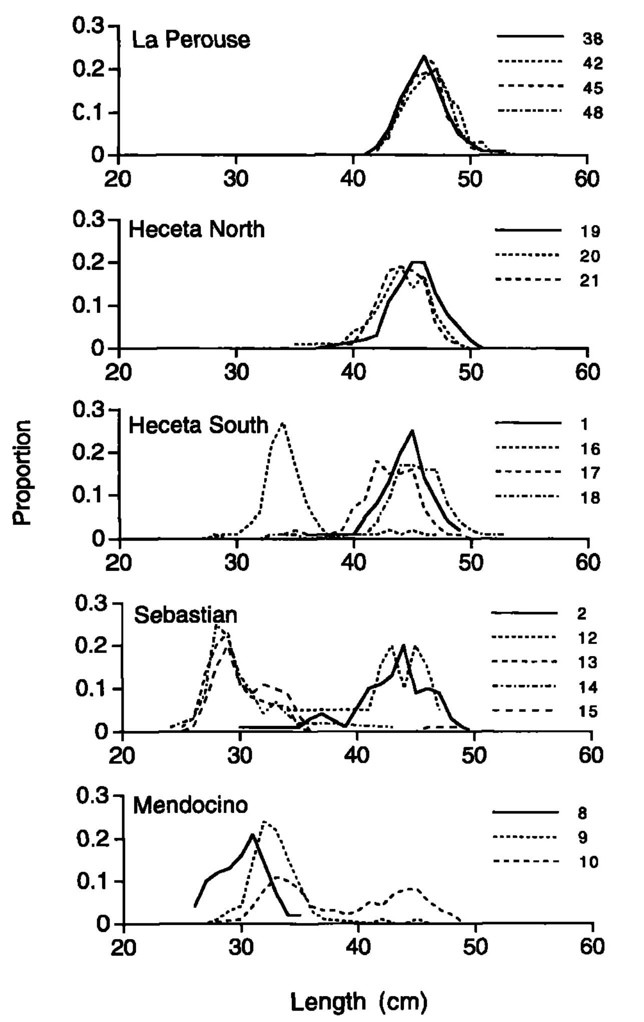

Figure 2

Length of hake taken in the 1992 NMFS acoustic-midwater trawl survey. Lengths are shown for trawls grouped by geographic region. Numbers indicate NMFS trawl number.

Inverse solution

The ESR of the scatterers were obtained from the S_L curves of the acoustic data with the nonnegative least squares solution of

$$\mathbf{S} = \sigma \mathbf{n}, \qquad (1)$$

(Holliday, 1977b) for $\mathbf{n}$, a column vector containing the number of scatterers in each of p size classes of swimbladder radii. $\mathbf{S}$ is a column vector of measured layer backscattering cross sections σ_{bs_L} ($S_L = 10 \log \sigma_{bs_L}$) for the 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} that are calculated over each of the $q = 21$ measurement frequencies (1/6 octaves from 500 to 5,000 Hz) and $p = 18$ semilogarithmically spaced radii (r=0.25, 0.3, 0.35, 0.4, 0.45, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0, 1.2 1.4, 1.6, 1.8, 2.0, 2.25, and 2.5 cm) with a model of swimbladder resonance (Eq. 3 below). In solving Equation 1, the number of measurement frequencies varied from station to station depending on data quality, with from 4 to 6 of the lower 1/6 octaves excluded. This variation was usually due to lower-frequency data that were low level and affected by noise. The inverse solution was also restricted to exclude radii smaller than the radius expected to be resonant at 5,000 Hz at the depth of each layer. These radii were calculated with the subsequent Equation 4 for the resonance frequency, f_0. The quality of the inverse solution of Equation 1 for $\mathbf{n}$ was examined by comparing the original data, $\mathbf{S}$, to an estimate of the layer strength obtained from the forward calculation $\hat{\mathbf{S}} = \sigma \mathbf{n}$.

Solution of Equation 1 above assumes that the σ_{bs_L} are the backscattering cross sections of a unit horizontal area of a layer of dispersed acoustically noninteracting scatterers, such that

$$\sigma_{bs_L} = \sum_{i=1}^{\Phi} \sigma_{bs_i}, \qquad (2)$$

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. At some stations, usually at night, several layers were evident. In these cases, Equation 1 was solved for each individual layer, and the subsequent distributions of ESR were summed.

Swimbladder model

The matrix σ of individual backscattering cross sections σ_{bs_i} was calculated with Love's model (1978) which models a fish swimbladder as an air-filled viscous spherical shell. The acoustic cross section in the back-scattered direction, σ_{bs}, for a single swimbladder of radius r is given by

$$\sigma_{bs} = \frac{r^2}{\left(\frac{f_0^2}{f^2 H^2} + \left(\frac{f_0^2}{f^2} - 1\right)^2\right)}, \qquad (3)$$

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

The resonance frequency is

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

where γ_α = the ratio of specific heats of air (γ_α=1.4);
P = the ambient pressure in Pa; and
ρ = the density of fish flesh in kg/m^3.

The damping factor is

$$\frac{1}{H} = \frac{2\pi r f^2}{f_0 c} + \frac{\xi}{\pi r^2 f_0 \rho}, \qquad (5)$$

where c = the speed of sound in water in m/sec; and
ξ = the viscosity of fish flesh in Pa sec.

Love's model includes a term in Equation 4 that accounts for the effects of swimbladder wall tension on f_0 and a thermal damping term in Equation 5. However, Love (1978) shows that these terms are negligible for the present case, therefore they were omitted for clarity. The physical properties of fish used here were taken from Love (1978): ρ = 1050 kg/m^3 and ξ = 50 Pa sec.

Swimbladders are not spherical but resemble prolate spheroids or cylinders with major-to-minor axis (length-to-diameter) ratios up to 10. However, it has been shown that spheroidal and cylindrical air bubbles have only a slightly higher resonance frequency than spherical bubbles (Weston, 1967; Feuillade and Werby, 1994; Ye, 1997). Love's model with Weston's correction to the resonance frequency has recently been used successfully to examine scattering from commercial-size fish in several ocean regions (Love, 1993; Thompson and Love, 1996) and what are presumed to be deep-water grenadiers off Oregon (Nero et al., 1997).

To model hake for this study, we assumed the swimbladder to be a prolate spheroid with a major-to-minor axis ratio of 8. This assumption is reasonable based on our at-sea measurements on Pacific hake (see below) and reported measurements on 13 pollack, *Pollachius pollachius,* from the North Atlantic (Foote, 1985), both of which gave major-to-minor axis ratios near 8. The resonance frequency of such a spheroid is about 20% higher than for a sphere of equal volume (Weston, 1967); this correction factor was taken into account by increasing f_0 given in Equation 4 by a factor of 1.2. 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.

Fish length and bladder size

We made direct comparisons of ESR derived from the NRL acoustic data with estimates of ESR from the lengths of fish obtained in NMFS trawls. However, the process of deriving swimbladder size from fish length is problematic. Because one of the primary functions of a swimbladder is to act as a hydrostatic organ, making a fish neutrally buoyant, one can assume ratios of swimbladder volume to fish volume near 0.05 (Jones and Marshall, 1953). However, many fish are frequently less than neutrally buoyant. In addition, food and gonadal products can crowd the abdominal cavity and reduce swimbladder volumes. Repeated measurements indicate values near 0.03 are common for gadoids (Foote, 1985; Ona, 1990) but that they are highly variable (Sand and Hawkins, 1973; Jones and Scholes, 1985; Foote, 1985; and Ona, 1990). Our field measurements on five hake caught by angling at the surface at night gave values ranging from 0.03 to 0.09 (rough approximations from fish length and swimbladder dimensions). Because these fish had ascended several meters to take artificial bait at the surface, we chose to use the more accurate determination of 0.03 for pollack and saithe, *Pollachius virens*, calculated from data in Foote (1985). For converting fish length to weight we used $W = 0.0057L^{3.026}$, determined from lengths and weights of hake captured in the 1992 NMFS trawls, males and females combined.

Calculated swimbladder size distributions were modified to account for two sources of variability expected in the natural hake population. First, for variability of bladder radii due to the above mentioned effects of food and gonadal products, we approximated the distribution of swimbladder volume to fish volume as follows: 30% of the fish had the mean value of 0.03 whereas 10% of the fish had swimbladders 50% smaller, 20% had swimbladders 25% smaller, 30% had swimbladders 25% larger, and 10% had swimbladders 50% larger than the mean. These values were based on rough approximations of information contained in Ona (1990). Second, for variability in the fish weight (W) to length (L) relationship, we approximated a normal distribution of W on L, where 20% of the fish had the mean W given by the regression equation $W = 0.0057L^{3.026}$, and 17% were 10% heavier (lighter), 12% were 20% heavier (lighter), 7% were 30% heavier (lighter), and 4% were 40% heavier (lighter) than the mean.

Abundance and biomass estimates

Abundance data for hake were determined by summing **n**, the column vector of fish number to obtain Φ. Biomass was determined by summing the product of **n**, the column vector of fish number, and the expected weight of each fish (r to L and L to W, relationships above). Biomass values were averaged for the NRL stations, grouped according to NMFS fisheries assessment regions: Canada South (Sta. 1); Southern Columbia (Sta. 4, 5, 6, and 7); and Eureka (Sta. 8, 9, 10, and 11) and compared with reported surface biomass of hake obtained from the NMFS high frequency acoustic survey (Fig. 10 in Dorn et al., 1994).

Results

Volume scattering data

Stations 1 (Fig. 3), 7 (Fig. 4), and 11 (Fig. 5) were selected to show representative volume scattering because they are on the slope in 900 to 1500 m of water and encompass the latitudinal range of stations covered by the NRL survey (Fig. 1). Stations 7 and 11 had day and night data; station 1 had only day data. In each image, S_v is shown as a function of frequency and depth. For shallow stations, bottom echoes are black. 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. Most stations show three layers of scatterers.

All stations had a strong scattering layer between 100 and 500 m both day and night. During the day the layer was strongest at 200 to 300 m with a resonance peak at about 1,000 Hz. This layer becomes progressively deeper to the south, being centered at 200 m at station 1, 220 m at station 7, and 320 m at station 11. This layer was presumed to be composed of Pacific hake on the basis of a prior consideration of the most likely abundant scatterers.

A second layer occurred at about 50 to 200 m at night and scattered sound at 3 to 5 kHz, frequencies well above the strongest (peak) scattering from the hake (Figs. 4B and 5B). The depth and frequency of occurrence of this layer matches the findings of Kalish et al. (1986) who provide a detailed study of the composition and scattering strengths of mesopelagic fish off Oregon. Therefore, we conclude this nighttime layer to be mesopelagic fishes that, during the day, should be deeper (near 200 to 300 m), resonant above 5,000 Hz, and not detectable by our measurements. This is supported by weak daytime scattering above 4,000 Hz at 250 m (Fig. 5B), which may be the low-frequency end of this daytime mesopelagic layer.

A third layer, beginning at about 1,000 m and extending to the end of the data record was evident in all data extending beyond 1,000 m. On the basis of this layer's resonance near 2,000 Hz and its location in depth, Nero et al. (1997) concluded that this scattering layer was caused by pelagic grenadiers. In subsequent analysis we considered only the low-frequency scattering from the hake—those scattering layers that are above 600 m and have a resonance below 2 kHz.

The acoustic resonance of the hake swimbladders is evident in the layer strength data for both day and night (points, Figs. 6 and 7). During the day, the majority of the scattering occurred in a fairly narrow depth range (Figs. 3–5); therefore only one set of layer strength data was calculated at each station (Fig. 6). During the night, the fish were more dispersed, and therefore the hake layer was separated into sublayers, and layer strengths were calculated for each (Fig. 7). Day layer strengths in the north at station 1 peaked at a slightly lower frequency (1,050

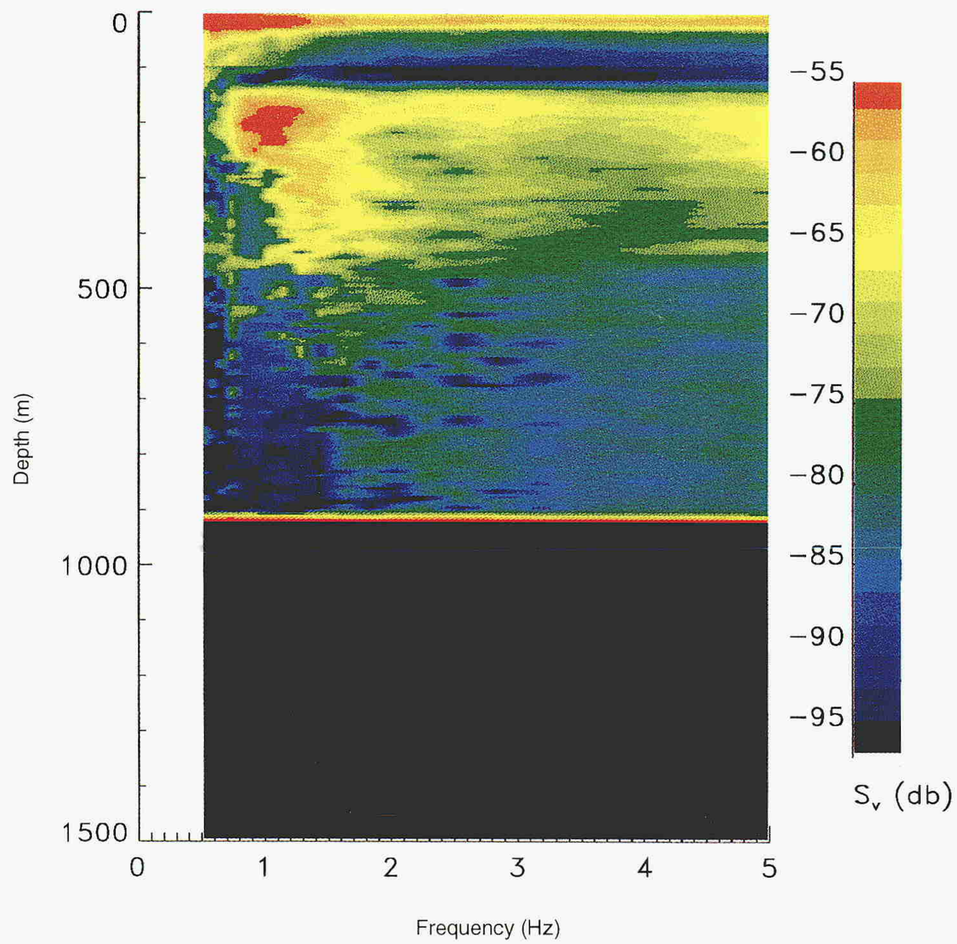

Figure 3
Volume reverberation at NRL station 1, during the day.

Hz) than at station 11 in the south (1,400 Hz). At night the resonance peaks of the individually integrated layers differed, with the peaks of the shallow sublayers occurring at about 1,000 Hz and the resonance peaks of the deep sublayers occurring at about 1,500 Hz.

Bladder size and number

The inverse analysis resulted in the determination of a distribution of ESR for each station grouped by geographic area (Fig. 8). The inversion gave an almost exact fit to the scattering data (curves and points in Figs. 6 and 7) indicating that the estimates of the distributions of ESR were quite good. Overall, the largest radii are near 2.2 cm, peaks occur between 1.2 and 1.8 cm, there is a dip at 0.8 cm, and smaller peaks occur between 0.5 and 0.7 cm. With the weight-length regression for hake given earlier, a swimbladder volume to fish volume ratio of 0.03, and if variabilities in either are ignored, $L = 28r$. Thus, the inversion tells us that, if the larger scatterers are hake, they are between 22 and 62 cm long with the greatest number between 34 and 50 cm (ignoring that variabilities increase the size range slightly). Figure 2 indicates that NMFS caught hake between about 25 and 55 cm length, with the greatest number between 28 and 46 cm length. Hence, we believe the estimated size range agrees well with trawl data, and we feel confident in our assumption that the scatterers with ESR of 0.8 to 2.2 cm are, indeed, Pacific hake.

Scatterers with ESR below 0.8 cm were present at all stations with the greatest numbers occurring between 0.5 and 0.7 cm (Fig. 8). According to their ESR, these fish are probably a mixture of mesopelagic fish and northern anchovy. This is consistent with findings of Kalish et al. (1986) who caught several spe-

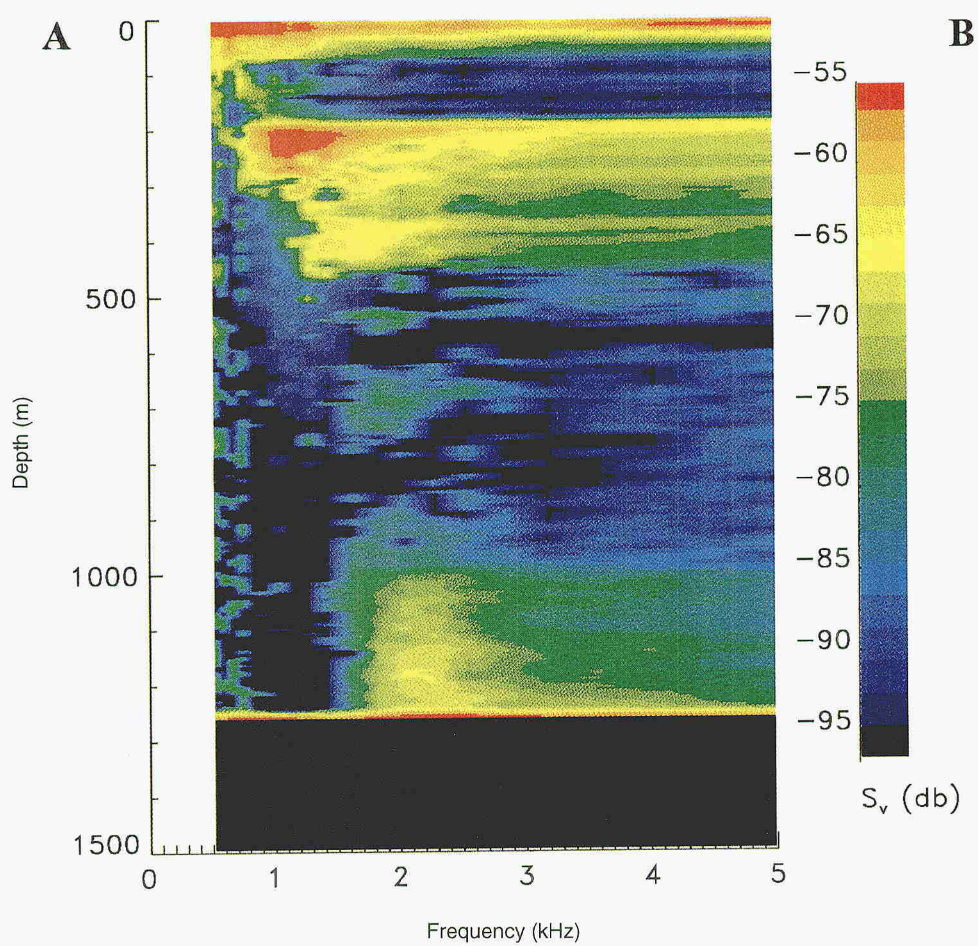

Figure 4

Volume reverberation at NRL station 7; (**A**) during the day, and (**B**) during the night.

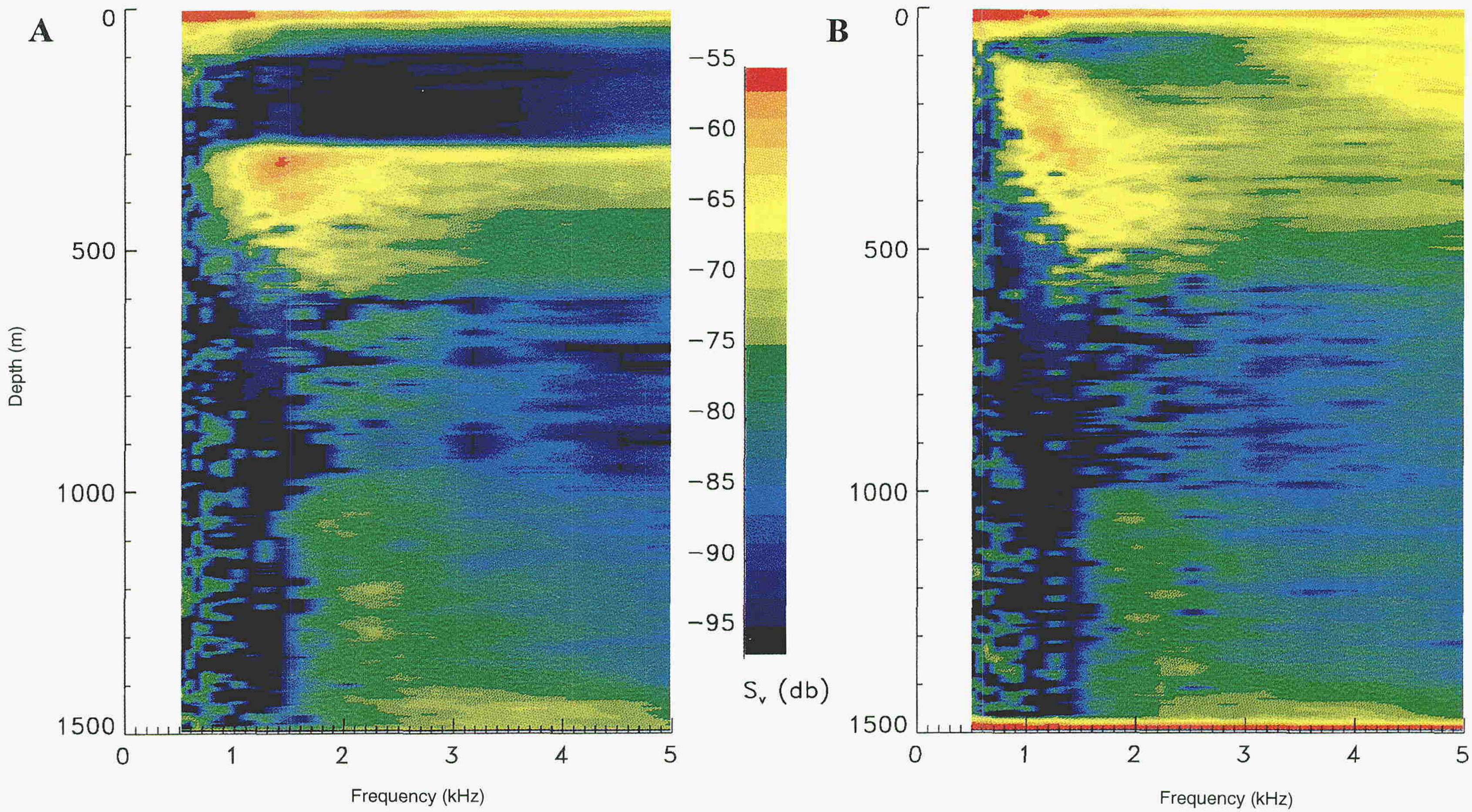

Figure 5

Volume reverberation at NRL station 11; (**A**) during the day, and (**B**) during the night.

cies of mesopelagic fish (*Symbolophorus californiensis*, *Tarletonbeania crenularis*, and *Diaphus theta*) and northern anchovy (*Engraulis mordax*) off the coast of Oregon at depths corresponding to our acoustic layer depths and had ESR between 0.1 and 0.7 cm. Thus, we expect that the fish with ESR between 0.25 and 0.7 cm in the present study are most likely these species.

For a more complete comparison of the trawl and low-frequency acoustic data, the lengths of hake caught in trawls were converted to ESR by using the previously mentioned weight-length regression and the swimbladder-volume-to-fish-volume ratio. The conversion included the variability in both relationships so that these ESR would be equivalent to the measured ESR. Figure 9 shows the resulting trawl estimates of ESR. The estimated distributions agree well with the measured ESR in the north at La Perouse, Heceta North, and Heceta South but not at the southern stations of Sebastian and Mendocino. The trawl data show a clear north–south trend in fish size (Figs. 2 and 9), whereas the acoustic data (Fig. 8) indicate that ESR, and presumably hake body size, do not change with latitude. The NRL low-frequency acoustic measurements did not show the same north–south trend in fish size that was apparent in the trawl data.

A summary of the number of swimbladders for small, 0.25–0.7 cm, and large fish, 0.8–2.5 cm, determined from the low-frequency acoustic data is given in Table 2, which includes information on the peak depth at which scattering occurred and the depth range of each layer. The density of small fish was much greater at night than during the day because these fish probably migrated to below 200 m during the day where they were resonant well above 5 kHz. For the large fish (presumably hake), at all stations where day–night measurements were made, densities were determined to be higher during day than at night. These higher daytime densities likely occurred because some hake migrated above 50 m depth at night and were missed because of the signal saturation caused by the explosion. (Measurements with an upward-looking system indicated that hake migrated to within several meters of the surface at some stations at night[2]).

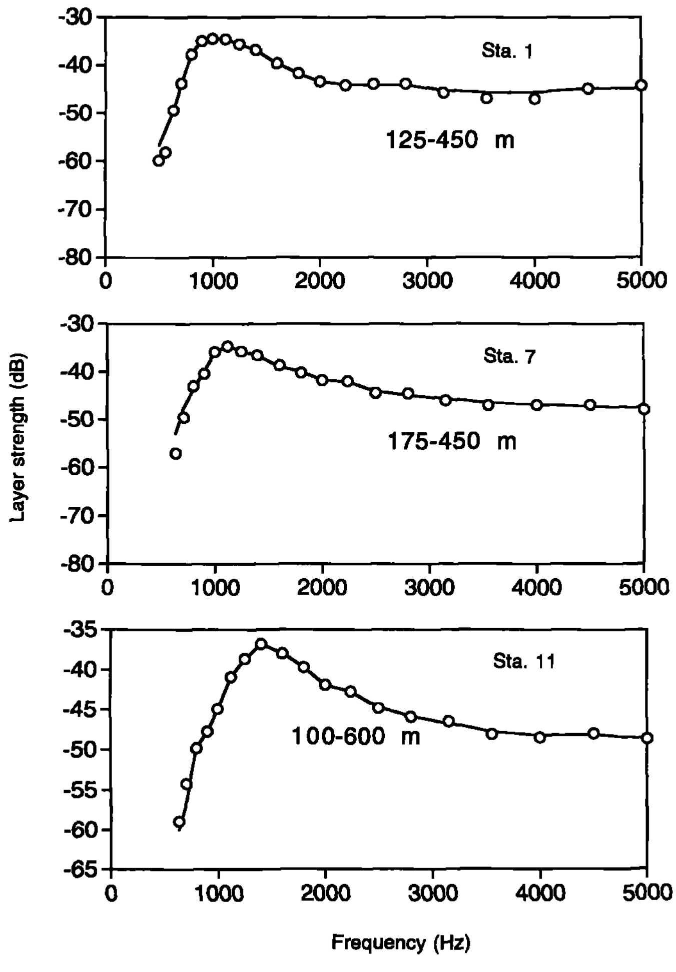

Figure 6

Layer strength data (open circles) for the daytime. Curves show inverse analysis fit to the data.

The quasi-synoptic NRL and NMFS measurements provided an opportunity to compare two independent measures of the surface density of hake for several large regional areas of the U.S. West Coast. Only daytime density estimates were compared because data suggested that hake near the surface at night were missed by NRL acoustic measurements. Daytime surface density estimates for both surveys are given in Table 3. The estimates differ most for Canada South (NRL station 1) where NRL saw an abundance of fish over bottom depths near 1,000 m whereas the NMFS acoustic-midwater trawl survey saw approximately 1/4 that number. NRL station 1 was within the region covered by the NMFS survey tracklines (Dorn et al., 1994) and was sampled by NRL 5 days

[2] 1992. Naval Oceanographic Office (NAVOCEANO), Acoustics Div., Stennis Space Center, MS, 39522-5001. Unpubl. data.

after the NMFS survey. At all other NRL inshore stations, densities were similar to the NMFS survey estimates. At all offshore NRL stations, densities remained high. Comparisons between the offshore NRL station data and the NMFS data were not possible because the NMFS survey did not extend beyond bottom depths of approximately 1,200 m. The offshore NRL measurements, approximately 50 km beyond the NMFS survey, gave densities as high as 300 kg/ha in layers at 300 to 400 m depth.

An examination of swimbladder behavior in hake was conducted on the NRL data by determining the relation between the acoustically measured swimbladder radii and depth for all stations (Fig. 10). In this analysis, it was assumed that hake at one station do not exhibit a size-dependent stratification in the water column. At night, hake were spread throughout the water column, allowing estimates of average ESR for several distinct layers at some stations. During the day, the hake were in a more compact single layer, resulting in only one estimate.

In Figure 10 curve, "A" depicts the shape of the relation between swimbladder radii and depth that is expected if the gas volume changed according to Boyle's Law and the bladder radius decreased with increasing depth. If hake maintain a near constant volume of gas in their bladders by adding or removing gas, then they would have a constant swimbladder radius, as depicted by line "B" in Fig. 10. There are no clear trends in the data. However, several weak relationships are worth noting. First, data taken from less than 100-m depth at stations 5 and 7 show unusually small radii suggesting some size-dependent stratification. Excluding these two values gives a weak but significant correlation for the remaining data (correlation coefficient=–0.373). In addition, two sets of data, from stations 9 and 11, and possibly from station 5, exhibit a decrease in bladder radius with depth. Stations 6 and 7 show an increase in radius with depth whereas station 4 shows maximum radius at middepth.

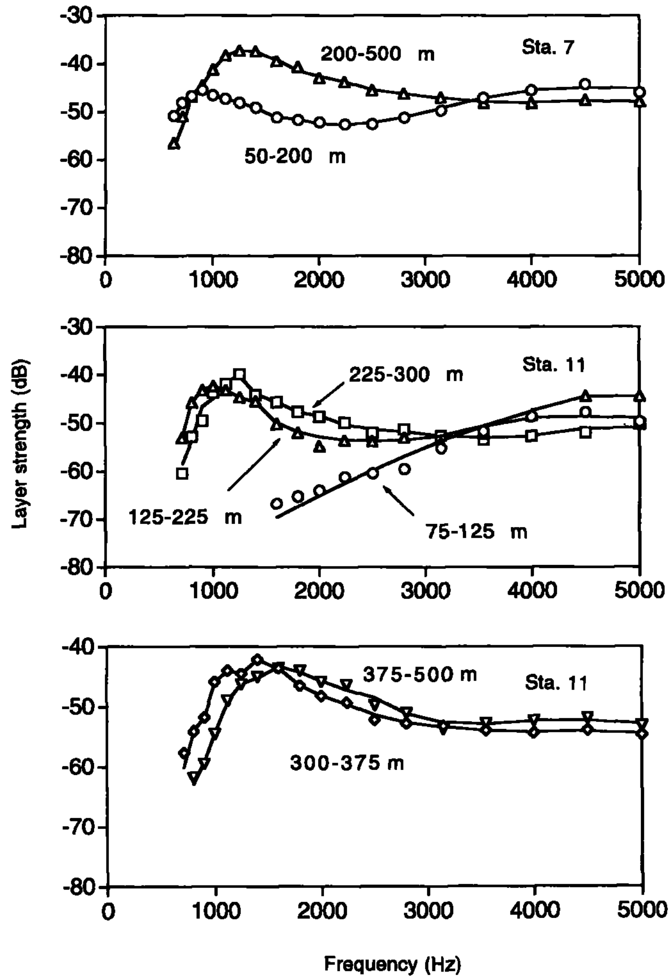

Figure 7

Layer strength data (symbols) for the nighttime. Curves show inverse analysis fitted to the data (note: no data were collected during night at station 1 and station 11 is separated into two panels for clarity).

Discussion

Pacific hake are believed to be the main cause of midwater scattering at frequencies of 1–2 kHz along the continental shelf and slope of the west coast of the United States (Figs. 6–7). No other large bodied midwater fishes are as abundant as hake (Ware and McFarlane, 1989). In addition, hake made up 97% of the catch in midwater trawls taken during the NMFS triennial acoustic-midwater trawl survey in the summer of 1992.[3] Other small fishes, mesopelagic fish, and northern anchovy may be abundant but will resonate well above 2 kHz. They are believed to be the source of scattering above 3 kHz in the upper 200 m at night (Fig. 7).

[3] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. data.

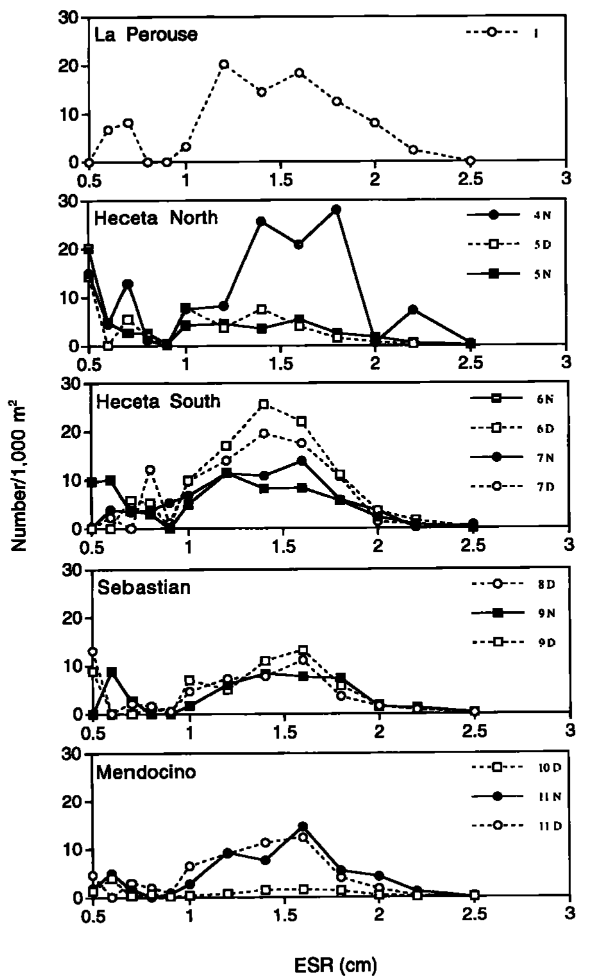

Figure 8
The equivalent spherical radius (ESR) of swimbladders for the NRL stations.

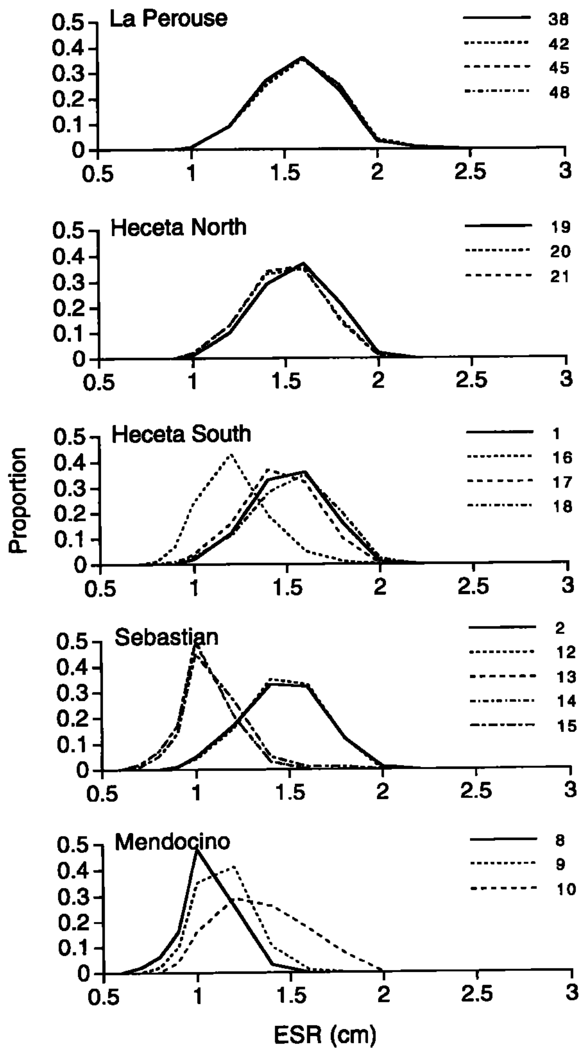

Figure 9
The equivalent spherical radius (ESR) calculated from the length of hake obtained from NMFS midwater trawls. Numbers indicate trawl number.

Discrepancies exist between the NMFS trawl estimates of hake size and our acoustic estimates at stations in the south of the study area. Only the larger size class of hake was detected acoustically whereas both large and small size classes of hake were caught in the trawls. Several explanations are suggested.

One possibility is that large hake mask the scattering from small hake. However, if ratios of small to large hake are anywhere close to those seen in the Sebastian and Mendocino trawls (Fig. 2), our inverse solution of the acoustic data would easily have detected both size classes.

Another possibility is that a physiological phenomenon caused the observed absence of a north–south trend in swimbladder size even though the southern fish were smaller. Such a phenomenon would have to cause the swimbladder-volume-to-body-volume ratio to increase in smaller hake. Differences in stomach fullness could cause such a trend. Food evacuation times are different for different food types: large hake eat fish that are evacuated slowly, small hake eat crustaceans that are evacuated quickly (Durbin et al., 1980, *in* Livingston, 1983) In addition, hake swimbladders could regress slightly in the larger fish. Although these hypotheses are possible, they would need to result in a complete cancellation of the north–south trend in fish size. This result is unlikely.

Table 2

Volume reverberation estimates of the density and depths of occurrence of probable fish swimbladders at stations along the Washington–California coast. Numbers in parentheses following densities in the 0.25 to 0.7 cm radius category are the smallest radii included in the estimates. ind. = individuals.

	Day			Night		
	Depth (m)			Depth (m)		
Station no.	Peak	Range	Density (ind./1,000 m²)	Peak	Range	Density (ind./1,000 m²)
0.25–0.7 cm radius						
1	200	125–450	162 (0.35)	—	—	—
4	—	—	—	70	50–550	4,855 (0.25)
5	380	250–525	21 (0.45)	70	50–550	7,974 (0.25)
6	225	125–475	30 (0.4)	<50	100–525	393 (0.3)
7	n/a	175–450	6 (0.4)	75	50–500	1,440 (0.25)
8	325	150–550	17 (0.4)	—	—	—
9	400	200–600	10 (0.45)	75	50–550	1,695 (0.25)
10	325	150–550	6 (0.45)	—	—	—
11	300	100–600	14 (0.4)	175	125–500	648 (0.3)
0.8–2.5 cm radius						
1	200	125–450	79	—	—	—
4	—	—	—	245	100–550	99
5	380	250–525	28	375	50–550	25
6	225	125–475	96	200	100–525	45
7	220	175–450	87	300	50–500	62
8	350	150–550	39	—	—	—
9	400	200–600	46	425	100–550	34
10	450	375–550	7	—	—	—
11	325	100–600	48	275	125–500	46

More likely possibilities are biogeographic effects of species composition and fish size. One possibility is that the NRL measurements were not on hake but another fish such as jack mackerel or chub mackerel, which may not have exhibited a north–south trend in fish size. However, the predominant fish in the area sampled were hake. Trawls close to the NRL stations contained only 1% jack and chub mackerel.[4] Another possibility is that large hake migrated southward with the NRL survey. This is also unlikely. The NRL survey took place in the last two weeks of August. At about the same time (17 Aug) NMFS was still collecting large hake in trawls near 51°30'N (Queen Charlotte Sound). Furthermore, the commercial fishery caught large hake off Washington as late as September and October (Dorn et al., 1994).

Table 3

Surface density estimates (kg/ha) of Pacific hake as determined by NMFS acoustic-midwater trawl survey and NRL measurements (day only). Data are grouped by NMFS geographic regions. Numbers in parentheses indicate the number of stations included in the averages for the NRL stations.

	Bottom depth (m)		
Region	NMFS 1,000–1,200	NRL inshore 900–1,500 m	NRL offshore 2,400–3,100
Canada South	91	439 (1)	—
Southern Columbia	369	348 (1)	270 (2)
Eureka	238	195 (2)	300 (2)

The most reasonable hypothesis to explain the discrepancy between trawl and acoustic estimates in hake size in the south of the study area is that the same cohort of hake was encountered at all NRL sta-

[4] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. data.

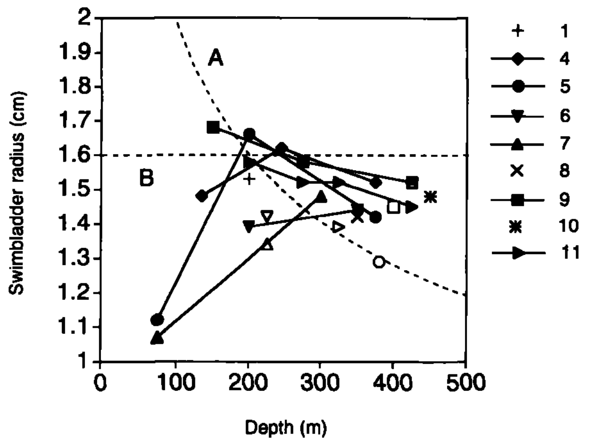

Figure 10

Mean equivalent spherical radius (ESR) in sublayers at night (dark symbols) and daytime (open symbols with same shape) for NRL stations. Stations 1, 8 , and 10 are daytime only. Dashed lines are (**A**) the calculated ESR for a swimbladder exhibiting constant mass of gas (decreases over depth), and (**B**) constant volume of gas (level with depth).

tions. There is some evidence that different cohorts stay together and remain separate from other size classes along the same section of coast. In the NMFS trawl data, most trawls show two predominant size groups, large hake (modal size >40 cm) and small hake (modal size <40 cm). These two groups rarely occurred in the same trawls. Where the two size groups overlapped (between 38°N and 43.5°N), two trawls caught large numbers of both size groups, two trawls caught large fish, and six trawls caught small fish. Some of the trawls with small fish were made near NRL stations 7 and 8. We hypothesize that at the time of the NRL survey (35 to 39 days after the NMFS survey), these small hake may have moved slightly inshore or south of the NRL stations and were replaced by larger fish.

Our interpretation of resonance and calculation of swimbladder size and fish size required assumptions of the relation of swimbladder radius, r, to fish length, L. We also assumed that this relation was constant with depth. As gadoids migrate they do adjust the gas volume of the swimbladder (Sand and Hawkins, 1973). Unfortunately our examination of swimbladder behavior in hake is inconclusive. The results of examining radius as a function of depth suggest that hake do compensate somewhat for pressure changes by adding and removing gas; however, they do not appear to compensate completely. We caution that this conclusion is conjectural and could be an artifact of size-dependent stratification of hake in the water column. Overall, bias introduced in our estimates by not accounting for the possible addition and removal of gas to the swimbladders of fish descending and ascending could have resulted in, assuming the worst case, an underestimate of length and biomass by 10% and 35%, respectively. This bias would not have affected our estimates of fish numbers because they were dependent on the number of radii independent of associated fish size.

Comparison of the NMFS survey estimates of surface density with the NRL estimates of surface density produced several important findings. First, although there were spatial and temporal differences in the surveys and although different acoustic techniques were used, the similarities between the surveys were encouraging and suggest that good accuracy is obtained with both techniques. Second, an NRL measurement at one station (one-mile drift) may be influenced by local minima or maxima in hake density. This hypothesis is suggested by the high values at station 1 where only a few days previously, in NMFS samples, much lower values were obtained. By chance at station 1, NRL may have made a measurement over an isolated concentration of fish. Third, relatively high densities of fish were seen at offshore stations in NRL sampling. Some NMFS acoustic transects suggest a high abundance of fish near the offshore limit of several transects taken near 43°N (Dorn et al., 1994). This high abundance would indicate that, at times, high densities of hake occur offshore, probably as a result of a particular set of as-yet-unknown oceanographic conditions.

This study has two important implications for fisheries surveys. First, hake may occur in high numbers, up to 300 kg/ha, approximately 50 km offshore of the outer edge of traditional fisheries acoustic surveys. Second, at these offshore sites the peak in the main scattering layer of hake may at times occur at depths of 400 to 450 m. At these depths hake could be difficult to assess by conventional 38-kHz fisheries sonars; therefore underestimates of the abundance of hake over deep water are possible.

Acknowledgments

We are indebted to J. J. Traynor, Alaska Fisheries Science Center, NMFS, for helping coordinate this incidental experiment and for providing a large amount of unpublished data. We thank N. V. Lombard, the Captain and crew of the USNS *Wilkes*, and E. Beeson, senior NAVOCEANO representative, for providing logistic support and assistance at sea. We also thank several anonymous reviewers who provided critical reviews of the manuscript. This research was supported by the Office of Naval Research.

Literature cited

Anderson, V. C.
1950. Sound scattering from a fluid sphere. J. Acoust. Soc. Am. 22:426–431.

Andreeva, I. B.
1964. Scattering of sound by air bladders of fish in deep sound-scattering ocean layers. Sov. Phys. Acoust. 10:17–20.

Clay, C. S.
1991. Low-resolution acoustic scattering models: fluid-filled cylinders and fish with swim bladders. J. Acoust. Soc. Am. 89:2168–2179.

Dorn, M. W., E. P. Nunnallee, C. D. Wilson, and M. E. Wilkins.
1994. Status of the coastal Pacific whiting resource in 1993. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-47, 101 p.

Feuillade, C., and M. F. Werby.
1994. Resonances of deformed gas bubbles in liquids. J. Acoust. Soc. Am. 96:3684–3692.

Foote, K. G.
1985. Rather high frequency sound scattering by swim-bladdered fish. J. Acoust. Soc. Am. 78:688–700.

Francis, R. C.
1983. Population and trophic dynamics of Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 40:1925–1943.

Holliday, D. V.
1972. Resonance structure in echoes from schooled pelagic fish. J. Acoust. Soc. Am. 51:1322–1332.
1977a. The use of swimbladder resonance in the sizing of schooled pelagic fish. Rapp P.-V. R. Cons. Int. Explor. Mer 170:130–135.
1977b. Extracting bio-physical information from the acoustic signatures of marine organisms. *In* N. R. Andersen and B. J. Zahuranec (eds.), Oceanic sound scattering prediction, p. 619–624. Plenum Publishing Corp., New York, NY.

Jones, F. R. H., and N. B. Marshall.
1953. The structure and functions of the teleostean swimbladder. Biol. Rev. 28:16–83.

Jones, F. R. H., and P. Schole
1985. Gas secretion and resorption in the swimbladder of the cod *Gadus morhua*. J. Comp. Physiol. B 155:319–331.

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

Livingston, P. A.
1983. Food habits of Pacific whiting, *Merluccius productus*, off the west coast of North America, 1967 and 1980. Fish. Bull. 81:629–636.

Love, R. H.
1978. Resonant acoustic scattering by swimbladder-bearing fish. J. Acoust. Soc. Am. 64:571–580.
1993. A comparison of volume scattering strength data with model calculations based on quasisynoptically collected fishery data. J. Acoust. Soc. Am. 94:2255–2268.

MacLennan, D. N., and E. J. Simmonds.
1992. Fisheries acoustics. Chapman and Hall, London, 325 p.

Nero, R. W., C. H. Thompson, and R. H. Love.
1997. Abyssopelagic grenadiers: the probable cause of low frequency sound scattering at great depths off the Oregon and California coasts. Deep-Sea Res. 44:627–645.

Ona, E.
1990. Physiological factors causing natural variations in acoustic target strength of fish. J. Mar. Biol. Assoc. U.K. 70:107–127.

Sand, O., and A. D. Hawkins.
1973. Acoustic properties of the cod swimbladder. J. Exp. Biol. 58:797–820.

Smith, B. D., G. A. McFarlane, and M. W. Saunders.
1992. Inferring the summer distribution of migratory Pacific hake (*Merluccius productus*) from latitudinal variation in mean lengths-at-age and length frequency distributions. Can. J. Fish. Aquat. Sci. 49:708–721.

Stanton, T. K.
1989. Simple approximate formulas for backscattering of sound by spherical and elongated objects. J. Acoust. Soc. Am. 86:1499–1510.

Stauffer, G.
1985. Biology and life history of the coastal stock of Pacific whiting, *Merluccius productus*. Mar. Fish. Rev. 47:2–7.

Thompson, C. H., and R. H. Love.
1996. Determination of fish size distributions and areal densities using broadband low-frequency measurements. ICES J. Mar. Sci. 53:197–201.

Urick, R. J.
1983. Principles of underwater sound, 3rd ed. McGraw-Hill Book Co., New York, NY, 423 p.

Ware, D. M., and G. A. McFarlane.
1989. Fisheries production domains in the northeast pacific ocean. *In* R. J. Beamish, and G. A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 359–379. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Weston, D.
1967. Sound propagation in the presence of bladder fish. *In* V. M. Albers (ed.), Underwater acoustics, vol 2, p. 55–88. Plenum Press, New York, NY.

Ye, Z.
1977. Low-frequency acoustic scattering by gas-filled prolate spheroids in liquids. J. Acoust. Soc. Am. 101:1045–1052.