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Title: The Biological and Acoustical Structure of Sound Scattering Layers in the Ocean off Oregon

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Dr. William G. Pearcy

Biological and acoustical methods were used to determine the composition of sound scattering layers in the ocean off Oregon. An arcer was used as a broad-band low-frequency (1-30 kHz) acoustic source. Acoustical data were also collected at four discrete frequencies, primarily to determine the depths of migratory and non-migratory scattering layers before carrying out sampling with the arcer and net. Collections of fishes were made with a 100 m^2 rope trawl with five opening and closing codends.

The predominant fish caught in deep (188 to 250 m) daytime layers were Protomyctophum crockeri and P. thompsoni , whereas Protomyctophum spp. and Diaphus theta were the most common species in deep (125 to 255 m) nighttime layers. The major scatterers in shallow (0 to 80 m) nighttime layers were D. theta , Stenobrachius leucopsarus (less than 35 mm), Tarletonbeania crenularis , Symbolophorus californiensis and Engraulis mordax .

The acoustically estimated distributions of bubble radii are similar for deep day and deep night scattering layers. Arcer estimates of distributions of bubble radii show a wider range of bubble sizes in shallow nighttime layers than in deep day and deep night layers.

Gas-filled swimbladder sizes for fishes in the net collections were estimated by three techniques; 1) measurement of the long and short axes of swimbladders in dissected specimens, 2) a neutral buoyancy model and 3) a model which considered species-specific parameters of morphology, physiology and behavior. Application of the third model to the net catch data resulted in predicted distributions of swimbladder radii that most closely matched the distributions of bubble radii as estimated acoustically. Comparisons of acoustic data and net catch data indicate that myctophids with gas-filled swimbladders may maintain swimbladder volume at a level below that required for neutral buoyancy. Furthermore, there is some

evidence for the existence of size-related strategies of swimbladder gas regulation. Some of the larger myctophids seem to maintain a constant swimbladder volume during vertical migrations, but at volumes that result in negative buoyancy. Medium size myctophids may not regulate their swimbladders, keeping them at a constant volume during vertical migration.

The Biological and Acoustical Structure of Sound Scattering Layers in the Ocean off Oregon

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THE BIOLOGICAL AND ACOUSTICAL STRUCTURE OF SOUND SCATTERING LAYERS IN THE OCEAN OFF OREGON

INTRODUCTION

Marshall (1951) suggested that fishes with gas-filled swimbladders were the principal organisms producing low frequency (1-30 kHz) sound scattering layers. Subsequent research has supported this hypothesis (Hersey and Backus, 1962; Hersey et al., 1962; Marshall and Chapman, 1964; Barham, 1966, Backus et al., 1968).

The composition of sound scattering layers in many geographical regions has been documented utilizing both acoustical and biological sampling methods. These studies have generally involved estimating the depths of sonic scattering layers by means of single frequency echosounders, and sampling using opening and closing nets (Foxton, 1963; Bradbury et al., 1971; Ebeling et al., 1971; Pickwell et al., 1971; Kleckner and Gibbs, 1972; Badcock

and Merrett, 1976; Pearcy et al., 1977; Friedl et al., 1977; Sameoto et al., 1980 and others).

Most acoustical studies of sound scattering layers have used single-frequency echosounders. However, there are considerable advantages to the use of multiple frequencies because of the properties of frequency-dependent sound scattering, that is, variations in backscattered intensity that are based on the relationship between the frequency of sound impinging upon a scatterer and the size of the scatterer (Anderson, 1950; Johnson, 1977; Greenlaw, 1977; Clay and Medwin, 1977).

Frequency-dependence is also a critical attribute of resonant sound scattering. Backscattering intensity from a resonating body generally is much greater than that from a nonresonant body of equal size. Scattering strengths from a nonresonant euphausiid and from fishes with gas-filled swimbladders are compared in Figure 1. Resonant sound scattering in the ocean is most commonly attributed to fishes with gas-filled swimbladders (Marshall, 1971) and physonect siphonophores (Barham, 1963). The resonant frequency of a gas-filled swimbladder or gas-filled float depends on its size, shape and compressibility (Weston, 1967). Andreeva (1964), Weston (1967), Batzler and Pickwell (1971), McCartney and Stubbs (1971), Lebedeva (1972), Love (1973, 1974, 1978), Hall (1981) and others

have made significant contributions to the theoretical and experimental understanding of swimbladder resonance.

Using an explosive broad-band sound source, Hersey, Johnson and Davis (1952) found frequency-dependent sound scattering in the North Atlantic Ocean. They attributed frequency-dependent peaks in scattered sound intensity at frequencies above 5 kHz to organisms smaller than 30 cm. Hersey and Backus (1954) and Hersey et al., (1962) attributed changes in the frequency of peak sound scattering to changes in the resonant frequency of gas-filled swimbladders during vertical migration. Biological sampling was not a part of these early acoustic studies and no efforts were made to estimate the sizes of the resonating bodies responsible for the backscattering. Recent coordinated biological-acoustical studies have employed a wider range of frequencies, and higher frequency echosounders (>50 kHz) to eliminate resonant scattering in sound scattering layer studies (Baird and Wilson, 1977; Pieper, 1977; Greenlaw, 1979; Pieper, 1979; Pieper and Bargo, 1980; Sameoto, 1982). In most cases, the resulting scattered intensities have been used to estimate animal biomass.

Few studies have employed multiple-frequency sound scattering techniques in conjunction with biological sampling. Holliday (1972) utilized an arcer to study

resonant sound scattering from fishes with gas-filled swimbladders. He found that the low-frequency structure of the echoes from single-species schools could be correlated with resonant scattering from swimbladders. Partial collection of the targets (northern anchovy schools) made it possible to predict scattering spectra based on models of sound scattering from swimbladder fishes. The agreement between predicted and actual spectra showed the potential of multiple-frequency acoustical studies as a biological tool. Later studies by Batzler et al. (1973), Batzler et al. (1975) and Love (1975, 1977) have attempted to predict volume scattering intensities based on trawl collections and models of sound scattering.

Holliday (1977), Johnson (1977) and Greenlaw and Johnson (1983) present solutions to the inverse problem involving the prediction of sound scattering layer composition based on multiple-frequency acoustic data. Both Johnson (1977) and Holliday (1978, 1980) found some agreement between estimates of the abundance of fishes with swimbladders based on multiple-frequency backscattering data and estimates of abundance from fish catch data. Holliday (1976, 1980) dealt with schools consisting predominantly of northern anchovy, which simplified the problem of attributing acoustically estimated swimbladders to a particular size of fish. Johnson (1977) compared

volume scattering measurements from a sound scattering layer with net collections made 3 to 5 years earlier in the same area. Although raw acoustical data from studies by both Johnson (1977) and Holliday (1978, 1980) can yield data on the estimated abundance of bubble radii using similar algorithms, the final biological interpretation is potentially far more complex in Johnson's study of a sound scattering layer.

Biological studies of sound scattering layers indicate that at least five species of myctophids with gas-filled swimbladders commonly occur in the upper mesopelagic zone off Oregon (Pearcy and Laurs, 1966; Pearcy and Mesecar, 1971; Pearcy et al., 1977). Kleckner and Gibbs (1972) noted the importance of understanding species composition in acoustic studies of scattering layers because of species-specific differences in swimbladder size and shape. Studies by Kanwisher and Ebeling (1957), Marshall (1960), Capen (1967), Zahuranec and Pugh (1971), Butler and Pearcy (1972), Kleckner and Gibbs (1972), Brooks (1976, 1977), Johnson (1979) and Neighbors and Nafpaktitis (1982) have all considered the relationship between fish species and swimbladder size for midwater fishes. These studies acknowledge the importance of swimbladder size in acoustical studies and, concomitantly, indicate the significance of an understanding of buoyancy regulation for

the analysis of acoustical observations. Therefore, a thorough understanding of scattering layers based on acoustical studies requires knowledge of species composition and buoyancy regulation in the midwater environment.

In this paper I present data from multiple-frequency acoustical measurements and concurrent trawl samples and describe the acoustical and biological structure of migratory and non-migratory sound scattering layers off Oregon.

METHODS

Data were collected from the F/V Pat San Marie from September 10 through September 19, 1981 in an area between 44° 25' and 44° 41'N and between 125° 49' and 126° 05'W, approximately 100 km west of Newport, Oregon. Bottom depth was approximately 2800 meters.

Acoustical Sampling Techniques

Two acoustical sampling techniques were used on this cruise.

1) Arcer: Multi-frequency measurements.

The arcer produces an electric underwater spark between two electrodes approximately one meter apart which serves as a broad band (1-30 kHz) acoustic source. The system employed was similar to that used by Holliday (1978, 1980).The arcer consists of three components: a bank of storage capacitors (60 kjoules capacity), which is charged to approximately 7500 volts through a step-up transformer; an air-gap switch or control section, which fires the arcer; and an electrode assembly. The

electrodes were lowered to a specific depth together with an omnidirectional hydrophone located at the same depth approximately 15 meters from the acoustic source. Based on power output and attenuation of the arcer signal and geometry and sample durations, insonified volumes were calculated to be ellipsoidal shells of approximately 19,000 m^3 effective volume. Firing of the arcer was controlled from on board the ship. Echoes were displayed in real time aboard ship and only those echoes which displayed high reverberation levels were recorded. This resulted in a positive bias to our acoustic abundance estimates. Echoes were recorded as voltage versus time on a digital computer. For acoustic data collections all ship power was turned off and acoustic equipment was powered by two 110 volt diesel generators on deck in order to reduce ambient noise.

2) V-Fin: Discrete-frequency measurements.

Two transducers mounted in an Endeco V-Fin and suspended from a boom at a depth of 3 to 5 m were used to obtain data on signal strength versus depth at four discrete frequencies (15, 20, 25 and 30 kHz). These measurements were essential for determining the depth of the scattering layer before carrying out sampling with the arcer and net. Discrete frequency data were collected

before and after each arcer cast and during net tows.

The acoustic data were collected and analyzed by C. Greenlaw of Tracor, Inc., Philomath, Oregon and D.V. Holliday of Tracor, Inc., San Diego, California.

Biological Sampling Techniques

Biological collections were made with a rope trawl, mouth area of about 100 m^2, equipped with a Multiple Plankton Sampler (MPS) with five opening and closing codend nets (see Pearcy et al., 1977 for a description of the MPS). The trawl was lined with 19 mm stretch mesh and MPS nets were 6 mm mesh with 0.505 mm Nitex codend nets. The depth of the trawl was monitored either by an Institute of Oceanographic Sciences (IOS) acoustical net monitoring system (Baker et al., 1973) or a Furuno netsonde. Net tows were made in full daylight or during the night in order to avoid the dawn and dusk periods of most active vertical migration. Daytime tows were positioned near the migratory sound scattering layer which was centered at a depth of 235 m. Shallow (0 to 80 m) and deep (125 to 255 m) nighttime tows sampled migratory and non-migratory scattering layers, respectively. Volumes filtered were estimated by multiplying the distance travelled by the ship (based on LORAN-C fixes) times the

mouth area of the trawl. A total of 33 collections were made from 8 tows (Table 1).

Selected fresh specimens of fishes were dissected at sea and the long and short axes of swimbladders were measured using a dissecting microscope with an ocular micrometer. Collections were also frozen or preserved in 10% buffered Formalin and sea water. Micronekton were sorted into major groups (fishes, squid, shrimp and euphausiids). Fishes were transferred to 20% and then 50% isopropyl alcohol and identified, counted and measured (standard length). Selected frozen and preserved specimens were dissected in the laboratory and the size of the swimbladder was measured by means of an ocular micrometer in a dissecting microscope.

Data Analysis

Algorithms for estimating the biological composition of scattering layers based on acoustic data are discussed in Holliday (1977), Johnson (1977) and Greenlaw and Johnson (1983). Estimates of the size and abundance of gas bubbles, presumably swimbladders of fishes, were obtained from the arcer data by inversion of the following set of equations (Greenlaw and Johnson,1983).

$$I_T(t,f) = I_o(t) \int_0^\infty R(f,a) N_c(a) da$$

where I_T is the scattered intensity at a time t after transmission and frequency f, $R(f,a)$ is a coefficient for a scatterer of size a and $N_c(a)$ represents the number of scatterers of size a in the insonified volume. In cases where the number of scatterers is not large enough to assume a continuous distribution of sizes or where the size distribution is discontinuous we can apply the summation

$$I_T(t,f) = I_o(t) \sum_{i=1}^{s} N_d(a_i) R(f,a_i)$$

where s represents the number of size classes. Applying this equation to each of the frequencies sampled we obtain a set of equations

$$\begin{aligned}
I(f_1) &= N(a_1)R(f_1,a_1) + N(a_2)R(f_1,a_2) + \ldots + N(a_3)R(f_1,a_3) \\
I(f_2) &= N(a_1)R(f_2,a_1) + N(a_2)R(f_2,a_2) + \ldots + N(a_3)R(f_2,a_3) \\
&\vdots \\
I(f_F) &= N(a_1)R(f_F,a_1) + N(a_2)R(f_F,a_2) + \ldots + N(a_3)R(f_F,a_3)
\end{aligned}$$

The abundance of different sizes of gas-filled swimbladder radii can be estimated from the solution of this set of equations. Greenlaw and Johnson (1983) describe several solution methods. A constrained least-squares algorithm (NNLS: Lawson and Hanson, 1976) was applied to the arcer data. The coefficients $R(f,a_i)$, in this case for fishes with gas-filled swimbladders, were estimated using the model of Weston (1967).

Initial estimates for the volumes of gas-filled

swimbladders, (V_{gas}) of fishes captured with the 100 m^2 midwater trawl were obtained from a neutral buoyancy model:

$$V_{gas} = \left(\frac{P_{fish} - P_{sea}}{P_{sea}} \right) V_{fish}$$

where P_{fish} and P_{sea} are the specific gravities of fish and sea water (1.027 gms/cm^3) respectively. Specific gravities of fishes were obtained from the literature (Butler and Pearcy, 1972; Johnson, 1979; Neighbors and Nafpaktitis, 1982), and fish volumes (V_{fish}) were estimated from the weight and specific gravity of fishes. Fish weights for fishes of known length were estimated using length-weight regressions based on preserved specimens captured in the 100 m^2 trawl.

RESULTS

Biology

Data on the biomass ($g/1000m^3$) for each major group of micronekton, for fishes with and without gas-filled swimbladders and for species of fishes with gas-filled swimbladders caught in the rope trawl during daytime and nighttime periods and at different depths are shown in Table 2. Based on net collections in sound scattering layers the average biomass of all micronekton caught in the deep (125 to 255 m) nighttime tows was almost ten times that caught in deep (188 to 250 m) daytime tows, and the biomass of micronekton captured in shallow (0 to 80 m) nighttime tows was almost fifty percent greater than that in deep nighttime tows.

These biomass differences are largely attributable to euphausiids (primarily Euphausia pacifica) and myctophid fishes. Euphausia pacifica was the major biomass component caught in both the deep daytime and shallow nighttime scattering layers, whereas myctophids were most important in the deep nighttime scattering layer. Biomass

estimates of euphausiids (approximately 2 cm in total length) and small fishes are underestimates of true biomass because of escapement through the net mesh of the trawl. However, relative differences in biomass between net collections indicate real variation. In the deep daytime scattering layer, fishes with and without gas-filled swimbladders contributed equally to the total biomass. Fishes without gas-filled swimbladders (primarily Stenobrachius leucopsarus greater than 35 mm) made up the bulk of the biomass in deep night collections, whereas myctophids with gas-filled swimbladders dominated the shallow nighttime collections (Table 2).

Based on our examinations of fresh specimens at sea and frozen specimens in the laboratory, six species of myctophids generally had thin-walled or gas-filled swimbladders, and were, therefore, assumed to be the predominant low-frequency sound scatterers. These were Stenobrachius leucopsarus (less than 35 mm), Protomyctophum crockeri , P. thompsoni , Symbolophorus californiensis , Tarletonbeania crenularis and Diaphus theta . The northern anchovy (Engraulis mordax), which has a gas-filled swimbladder, was present in two shallow nighttime net collections. Catch data for the most abundant fishes with gas-filled swimbladders are shown in Table 3. Other fishes with gas-filled swimbladders

occurred in insignificant numbers and are not considered in the analysis.

Physonect siphonophores may make a significant contribution to resonant sound scattering at low frequencies (Barham, 1963; Pickwell et al., 1964), but it was difficult to determine the abundance of these animals. I found very few floats from physonect siphonophores in the samples. Floats collected were smaller than 6 mm by 2 mm and only the codend mesh of the MPS was small enough to collect them.

Butler and Pearcy (1972) reported both thin-walled, gas-filled swimbladders and small, reduced swimbladders in large D. theta and T. crenularis . Neighbors and Nafpaktitis (1982) did not find gas in any of the large D. theta they examined. All of the 33 fresh D. theta (36-73 mm SL) and 7 of 9 fresh Tarletonbeania crenularis (34-81 mm) examined for this study had thin-walled or gas-filled swimbladders. For subsequent calculations all D. theta and T. crenularis were assumed to possess gas-filled swimbladders.

Acoustics

Volume scattering strength profiles at four discrete frequencies (15, 20, 25 and 30 kHz) provide some evidence

for depth and frequency-dependent sound scattering (Figures 2, 3 and 4). Differences in volume scattering strength between day and night profiles are evident at all depths. The daytime vertical profile (Figure 2) is characterized by a distinct peak scattering layer at 235 m and reduced scattering at shallower depths. Volume scattering strength at depths of less than 75 m cannot be accurately determined with the towed acoustic array because of surface reverberation. Volume scattering during the night (Figure 3) is more uniform with depth, however, peak volume scattering occurs at 235 m as in the daytime profile.

In the scattering layer at 235 m, the frequency response at 15, 20, 25 and 30 kHz is the same during the day and night (Figures 2 and 3). In both cases maximum volume scattering occurs at frequencies of 20, 25 and 30 kHz with scattering at 15 kHz being approximately 4 dB lower. Overall peak volume scattering strength is approximately -57 dB and -62 dB during the day and night, respectively. The 5 dB change in scattering volume at 235 m between daytime and nighttime profiles corresponds to a difference in biomass of approximately three times, if it is assumed that the volume scattering strength equals 10Log(abundance) + constants. This would indicate that 70% of the daytime biomass at 235 m has migrated upward

during the night, but not necessarily to the surface.

Biomass estimates for all micronekton from net collections made within the scattering layer indicate that nighttime biomass (Table 2) is almost 9 times higher than daytime biomass. Based on biomass estimates from net collections, it would be predicted that nighttime volume scattering at 235 m would be approximately 10 dB higher than daytime scattering at this depth, rather than the observed 5 dB decrease in volume scattering between day and night. This discrepancy in acoustic and net collection biomass estimates may be a result of more effective avoidance of the trawl during the daytime, changes in the orientation and scattering characteristics of the species present, or changes in species composition during the day and night.

Knowledge of frequency-dependent variations in backscattering at a particular depth permit estimation of the size of resonant bubbles. Peak volume scattering at the lowest (15 kHz) or highest (30 kHz) discrete frequency makes it possible to estimate the minimum or maximum resonant bubble size, respectively, assuming that peak scattering is caused by bubbles. Peak scattering at the intermediate discrete frequencies (20 and 25 kHz) provides an estimate of the actual resonant bubble size. Using the resonant frequency relationship it is estimated that the

predominant resonant bubbles at 235 m are smaller than 0.8 mm in radius during both the day and night. Discrete frequency data collected during an evening ascent of the scattering layer (Figure 4) indicates that resonant bubbles at 235 m are between 0.5 mm and 1.0 mm.

Arcer scattering strength spectra and estimated abundance of bubble radii required to produce these spectra are shown in Figures 5 to 12. The curves are based on the calculation of the scattering spectra from the acoustical abundance estimates of bubble radii. The total estimated numbers of gas bubbles were 1.49, 21.3 and 503.4 (standard deviation=679.4) per 1000 m for deep daytime, deep nighttime and shallow nighttime arcer data, respectively.

Scattering spectra at nighttime depths of less than 50 m indicated the presence of a wide range of bubble sizes with a peak swimbladder abundance at a radius between approximately 0.25 and 0.41 mm at 34 and 40 m respectively (Figures 10 and 12). The range of bubble sizes was narrower at depths of 200 to 250 m in both the daytime and the nighttime with the peak abundance at 0.6 mm radius (Figures 6 and 8). Greater numbers of small bubbles were present in surface waters at night than in deeper water during either daytime or nighttime.

Hall (1982) suggests that air bubbles below a size of

0.3 mm cannot be accurately measured with acoustical resonance because resonance is wholly damped by visco-elastic effects. Also, with the 1 to 30 kHz arcer, the smallest bubble sizes detected by resonance peaks are approximately 0.07 mm and 0.3 mm at 50 and 250 meters respectively. Therefore, the presence or absence of gas-filled swimbladders smaller than 0.07 mm (at 50 m) and 0.3 mm (at 250 m) cannot be determined unequivocally.

Constant Mass Versus Constant Volume Swimbladder Regulation

Analysis of broad-band acoustical records made during an evening ascent period of a sound scattering layer were used further to investigate whether midwater fishes were regulating the gases in their swimbladders or if the mass of swimbladder gases was kept constant. The collection of acoustic data during the evening ascent required that the arcer electrodes be placed within the migrating scattering layer as it moved upwards. The complex interaction of numerous migratory and non-migratory layers at a single location made it difficult to resolve a single discrete layer during the course of a vertical migration (see Figures 2, 3 and 4). The presence of a wide range of acoustically estimated swimbladder radii measured at five

depths during the vertical migration made it difficult to distinguish whether or not a single assemblage of fishes was being monitored or different fishes from other depths were moving within the range of the arcer. However, the occurrence of many size classes of swimbladder radii without significant changes in abundance throughout the vertical migration period was most consistent with constant volume migrations (Figure 13).

A log-log plot of the peak resonant frequency against the scattering layer depth plus 10 meters during the migration period is shown in Figure 14. Points plotted are the lowest frequency of peak scattering that can be attributed to resonance at a specified depth. By selecting the lowest frequency of peak scattering at each depth I assumed that a single assemblage of fishes was being followed in the course of a vertical migration, thereby making possible the detection of any systematic changes in swimbladder inflation with depth. The nature of the points in Figure 14 can be best illustrated by looking at the data sets used to determine these points. The point at 50 m corresponds to a frequency of 2.35 kHz. This point was obtained from the scattering spectrum taken at 40 m (Figure 11). The point at 245 m (Figure 14) relates to the low frequency peak scattering occurring at a frequency of 4.3 kHz at 235 m (Figure 5). In both these

cases the frequency is the lowest peak frequency at that particular depth. However, at 44 m the lowest frequency of peak scattering (1.0 kHz in Figure 9) is not used because this low-frequency peak is attributed to anchovies which were captured in the shallow nighttime net collections. I attribute the second lowest frequency of peak scattering (1.9 kHz) to migratory fishes (myctophids) with gas-filled swimbladders, and it is this point which is used in Figure 14. Following scattering peaks at the higher frequencies becomes more difficult because of increased nonresonant scattering and noise.

The least squares estimate of the straight line ($f=(.28)(d+10)^{.52}$, $r=.98$) is not significantly different from the line of the form $f=k(d+10)^{.5}$, which suggests that sound scattering at the lowest frequencies was due to migratory animals which maintained gas inclusions at a constant volume. This conclusion is based on the relationship for resonant frequency of a gas-filled swimbladder, where resonant frequency is proportional to pressure$^{.5}$ at a constant swimbladder volume. This analysis, which considers scattering at the lowest peak frequency, does not provide data on regulation of intermediate and small size swimbladders.

Biological-Acoustical Comparisons

Histograms of the average abundance of swimbladder sizes of trawl-caught fishes based on the neutral buoyancy model are shown for deep (188 to 250 m) daytime, deep (125 to 255 m) nighttime and shallow (0 to 80 m) nighttime net collections (Figures 15, 16 and 17). These results indicate that the numbers of swimbladders are greatest in surface waters at night and lowest in deep waters during the day (Table 3). These trends are similar to those for acoustical data. However, the acoustically measured abundances are much greater than those determined by the trawl collections. This is probably because only arcer data which showed high reverberation levels were recorded.

Using the neutral buoyancy model, the estimated range of swimbladder sizes in the net collections is 0.2 to 6.5 mm. The minimum swimbladder size is similar at all depths and times of day. The maximum swimbladder radius (6.5 mm), as estimated from the neutral buoyancy model, occurred in the shallow nighttime collections when northern anchovies, 100 to 160 mm SL were captured. The peak abundance of swimbladders in the net collections, based on the neutral buoyancy model, occurs at radii of 1.5, 0.6 and 2.0 mm for shallow night, deep day and deep night collections, respectively.

The range of swimbladder sizes estimated from the net collections and the neutral buoyancy model is similar to that estimated from the arcer distributions for the deep nighttime and deep daytime data. The discrepancy in the maximum swimbladder radius between the shallow nighttime net catches and the shallow nighttime arcer data sets may be the result of net avoidance by larger swimbladder fishes in surface waters during the night.

Because it is unlikely that all midwater fishes in the net collections were neutrally buoyant at all times, alternative models were considered for estimating the sizes of gas-filled swimbladders. Bubble radii distributions obtained from the neutral buoyancy model were adjusted by multiplying the radii by coefficients (α) ranging from 0.1 to 1.35. These distributions were correlated with the acoustically estimated bubble radii to determine the values of α that resulted in the best match of acoustical and biological data at similar depths and times of day. At a depth of 200 to 250 m, swimbladders filled to 3.9% (standard deviation, s=.02) and 22.5% (s=1.4) of the volume required for neutral buoyancy gave the best fit for daytime and nighttime periods respectively. Correlations between shallow nighttime arcer data and swimbladder distributions derived from shallow nighttime trawl collections indicate that

swimbladders were filled to 8.4% (s=0.6) and 13.4% (s=1.5) of the volume required for neutral buoyancy at 34 and 40 m respectively. These results suggest that swimbladders were usually inflated to only a fraction of the volume required for neutral buoyancy.

The neutral buoyancy model, both with and without coefficients, assumed that all species regulated swimbladder volume in a similar manner. However, species-specific differences in body and swimbladder morphology, lipid and water contents, and migratory behavior suggest that similar rules regarding swimbladder inflation do not apply to all migratory midwater fishes with gas-filled swimbladders. Therefore, the abundance of swimbladder sizes from shallow night, deep night and deep daytime net collections were estimated taking into consideration factors pertinent to buoyancy and vertical distribution (Table 4).

Because Protomyctophum spp. are non-migratory I assume that they maintain their swimbladders at a volume near to that required for neutral buoyancy and require a minimal degree of regulation to maintain neutral buoyancy. The remaining four species with gas-filled swimbladders all undertake diel vertical migrations into the upper 50 m at night (Pearcy et al., 1977). However, buoyancy control mechanisms may be somewhat different among these fishes.

Neighbors and Nafpaktitis (1982) found T. crenularis to be similar to Protomyctophum spp. in that these fishes were low in lipid and water content and were, therefore, negatively buoyant exclusive of the swimbladder. However, Protomyctophum spp. is non-migratory, whereas T. crenularis undergoes a vertical migration. The relatively narrow body, narrow caudal peduncle and large pectoral fins of T. crenularis are indicative of a fast swimming, active fish (Bone, 1973). These factors lead me to conclude that T. crenularis depends on hydrodynamic lift to maintain neutral buoyancy.

The remaining three myctophids with gas-filled swimbladders, S. leucopsarus (less than 35 mm), S. californiensis and D. theta have high lipid and low water contents (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1983). Stenobrachius leucopsarus larger than 35 mm achieve neutral buoyancy through the deposition of wax esters (Nevenzel et al., 1969; Butler and Pearcy, 1972). However, in small S. leucopsarus the swimbladder serves, most likely, to help achieve hydrostatic equilibrium. The swimbladder probably serves a similar hydrostatic function in both S. californiensis and D. theta . Stenobrachius leucopsarus and Triphoturus mexicanus were both observed hanging motionless at day depths in the water column (Barham, 1971). These fish

have lipid contents, water contents and body morphologies similar to those of D. theta and S. californiensis . Therefore, I conclude that they are almost neutrally buoyant and maintain their swimbladders at a constant volume during vertical migration.

Modeled distributions of shallow night, deep night and deep daytime net data appear in Figures 18, 19 and 20. The swimbladders of all species, with the exception of T. crenularis in the deep collections, are modeled as being inflated to 0.9 times the radius of the bubble required to maintain neutral buoyancy (72% of the neutral buoyancy volume). I have chosen to estimate the swimbladder volume as being somewhat below the neutral buoyancy volume in order to allow for potentially rapid upward movements during feeding or predator evasion without a loss of control due to positive buoyancy. Fishes with swimbladders inflated to 72% of the neutral buoyancy volume at depths of 235 m would be neutrally buoyant at 164 m, and similarly, those with swimbladders at 72% of the neutral buoyancy volume at 40 m would be neutrally buoyant at 24 m. The swimbladders of T. crenularis are inflated to 0.35 times the radius of the bubble required to maintain neutral buoyancy (4% of the neutral buoyancy volume), in which case a fish at 235 m would be neutrally buoyant at the surface if it made a constant mass

migration.

Histograms of swimbladder abundance based on the models of net collection data in the deep daytime and deep nighttime tows (Figures 18 and 19) have ranges which are similar to those of the acoustic estimates (Figures 6 and 8). However, abundance peaks for deep daytime data are found at 0.58 mm for acoustic data and between 0.97 and 1.6 mm for the modeled net catch data. The abundance peak for the deep nighttime acoustic data is the same as for the deep daytime data. Peak abundance occurs at a swimbladder radius of 1.6 mm for the deep nighttime modeled net catch data. The abundance peaks in both the deep day and deep night modeled net data are attributable to Protomyctophum spp. which are assumed to be near neutral buoyancy (α=.9). The largest acoustically estimated swimbladders in the deep daytime (Figure 6) and deep nighttime (Figure 8) measurements are attributed to S. californiensis and account for the largest modeled swimbladder sizes in Figures 18 and 19. Stenobrachius leucopsarus , which have gas-filled swimbladders at small sizes only, account for swimbladders smaller than 0.5 mm in the deep day and deep night models. Both D. theta and T. crenularis have relatively large size ranges in deep day and deep night tows (see Table 3) and, concomitantly, they have a wide range of estimated swimbladder sizes in

the models.

The modeled distribution of swimbladders based on shallow nighttime data (Figure 20) shows a range of swimbladder radii similar to that in the deep day and deep night data. However, the greater abundance of fishes with swimbladders and the lack of a distinct abundance peak distinguish the shallow nighttime net data from other net collections. Swimbladders of radius smaller than 0.5 mm are attributed to S. leucopsarus in the model, and D. theta and T. crenularis show a wide range of swimbladder sizes. The northern anchovy and S. californiensis , based on the model, have the largest swimbladders of the fishes collected in the shallow nighttime nets. The northern anchovy were collected in one of ten shallow nighttime nets, where they comprised 10% of the catch of fishes with gas-filled swimbladders and are represented by swimbladder radii of 3.8 to 5.3 mm in Figure 20. The maximum acoustically estimated swimbladder sizes agree with the swimbladder sizes estimated for northern anchovy by Holliday (1972, 1976, 1980).

DISCUSSION

Sound scattering layer organisms are an important component of oceanic ecosystems. However, studies of these organisms are limited by our inability to sample sound scattering layers effectively. Problems encountered in biological sampling, notably net avoidance and escapement, can be overcome by using acoustical sampling methodology (Pearcy, 1975). Because net avoidance and escapement are eliminated when using acoustics it is potentially possible to obtain more accurate biomass estimates of oceanic organisms. It is also possible to sample far greater water volumes and to consider questions of horizontal and vertical distribution. Moreover, acoustic sampling reduces the high costs incurred in net sampling. However, acoustic techniques are not adequately developed at the present time to perform many of the tasks that are carried out by sampling with nets. Characterization of the organisms responsible for backscattering is often particularly difficult, especially when mixtures of resonant and non-resonant scatterers occur. However, joint biological-acoustical studies may

make it possible to understand more fully the nature of sound scatterers, so that subsequent acoustic work can be interpreted accurately.

Potential Biases in Biological-Acoustical Interpretation

Correlations between acoustical and biological data provide results which must be used with some reservation. Errors in comparisons of acoustical and biological data can result from discrepancies between the depths sampled with the arcer and with the trawl. If biological collections are made at a depth somewhat different from the arcer data collections the size of the fishes in the net collections may be different from the size of the fishes in the insonified water volume. Willis and Pearcy (1980) found vertical segregation by size of *S. leucopsarus* and *D. theta* in shallow nighttime collections with the smaller fishes in shallower water. These distributional characteristics were evident in my shallow nighttime collections. Because arcer measurements were not always made at exactly the same depths as net collections, correlations between the two samples must carefully consider the depths sampled. This is especially critical for shallow nighttime measurements where

relatively fine-scale segregation of different size myctophids of the same species was found.

Acoustical estimates of swimbladder radii from two shallow nighttime arcer casts indicate the presence of detectable differences in the swimbladder distributions at slightly different depths (Figures 10 and 12). In both cases, peak abundances are probably due to the presence of small D. theta and S. leucopsarus . However, the radius abundance peak was smaller at 34 m than at 40 m. This is probably due to differences in the sizes of fishes found at these two depths, with smaller animals migrating to a shallower nighttime depth than larger animals. This supports conclusions of Willis and Pearcy (1980) regarding vertical size segregation in certain species of myctophids.

Differences in the adjusted swimbladder volumes which best fit the arcer data at different depths may result from the measurement of different acoustic targets in the deep daytime and shallow nighttime measurements. Clarke (1973) and Pearcy et al. (1979) found that not all individuals of a population of myctophids migrate to shallow nighttime depths each diel period. Also, discrete frequency profiles (Figures 2, 3 and 4) indicate that interaction and mixing of sound scattering layers occurs and, therefore, layers at daytime depths do not vertically

migrate as discrete units. Net collections from this study are not adequate to address this hypothesis based on acoustical data. However, it is clear from earlier studies of sound scattering layers off Oregon (Pearcy et al., 1977; Willis and Pearcy, 1980) that there are both interspecific and intraspecific differences in the extent of vertical migrations. Migrations of individuals must overlap to some degree, resulting in consolidation and mixing of scattering layer constituents. Therefore, I cannot conclude that all migratory fishes with a particular swimbladder size will migrate each day.

The detection of many large bubbles, presumably attributed to migratory fishes, at depth during the day does not imply that these same bubbles will be detected at shallower depths at night. For example, the large increase in the number of small bubbles in the surface night collections and arcer measurements can be attributed to small D. theta and S. leucopsarus . The relative abundance of these small fishes was much less in the deep daytime collections where both large and small migratory myctophids with gas-filled swimbladders were almost equally abundant. The increased number of small bubbles in surface nighttime measurements can explain why the adjusted swimbladder size which best fits the arcer data does not change according to Boyle's Law between deep

daytime measurements and shallow nighttime measurements.

Because of physical limitations of the acoustic gear it is difficult to make conclusions regarding the smaller swimbladders. The smallest resolvable bubble at a given frequency increases with increasing depth. Because the arcer provided adequate acoustic energy to a frequency of 30 kHz this study was able to resolve bubbles far smaller than those resolved in previous studies using explosive charges that produced adequate energy at frequencies up to only about 20 kHz. However, despite the wider bandwidth of the arcer, it was still a limitation in the study of the smaller size bubbles. The gradual decrease in the minimum estimated bubble radius at shallower depths (Figure 13) may be an artifact of the acoustical techniques used. As a result, the small bubbles that were detected at a depth of 40 m may have been present at a greater depth, but were too small to be resolved acoustically.

Some bias in the results may result because the trawl sampled water volumes in excess of 1 million m^3 (Table 1), whereas the arcer insonified a much smaller volume, approximately 19,000 m^3. Furthermore, the volumes of water sampled by the arcer were not sampled by the trawl and horizontal variability in the distribution of fishes may bias the samples. If fishes are distributed in single

species aggregations over space scales of tens to hundreds of meters it becomes difficult to relate the net collections to the arcer data. However, I assume that the net catches represent an unbiased sample of those fishes measured acoustically.

Constant Mass versus Constant Volume Swimbladder Regulation

Relatively simple models for estimating the distribution of swimbladder sizes from the net collections (Figures 18, 19 and 20) must consider whether fishes migrate with swimbladders at a constant volume, constant mass or some intermediate strategy. Earlier studies of midwater fishes and sound scattering layers tried to determine if vertical migrations were carried out with swimbladders maintained at constant mass or constant volume (Hersey et al., 1962; Vent and Pickwell, 1977), however, their results were not conclusive. Evidence presented in this study suggests that, off Oregon, fishes with large swimbladders at daytime depths migrate with swimbladders held at constant volume. Because an understanding of constant mass and constant volume migrations is critical to interpretation of the data these theories are discussed below.

Kanwisher and Ebeling (1957), Marshall (1960) and Alexander (1971, 1972) cited physiological evidence that implied that gas-filled swimbladders were maintained at a constant mass in vertically migrating fishes. These conclusions were based on both oxygen and energy requirements for gas secretion and resorption during vertical migration. Alexander (1971) concluded that it would be energetically less costly for a fish that undertakes vertical migrations greater than 200 m to maintain its position in the water column by hydrodynamic lift, rather than by inflating and deflating its swimbladder. Thus, migratory myctophids in the trawl collections would conserve energy by migrating with their swimbladders at a constant mass, while non-migratory species, such as Protomyctophum spp. would maintain constant volume over a more restricted vertical range.

Hersey and Backus (1954), Hersey et al. (1962) and Vent and Pickwell (1977) presented acoustical data that implied that the mass of gas-filled swimbladders in some sound scattering layers was kept constant while in other layers it varied with depth during vertical migrations. These conclusions were based on indirect evidence from broad band acoustic observations where the frequency of peak scattering intensity of the migratory layer, assumed to be the frequency of resonance, was proportional to

pressure (P). They used the relationship where the resonant frequency is proportional to $P^{.5}$ at constant swimbladder radius. If the swimbladder volume varies according to Boyle's Law, and is maintained at constant mass, the resonant frequency varies as $P^{.83}$. However, these acoustical measurements, made during the course of a vertical migration period, failed to consider changes in species composition or size-frequency in the monitored scattering layers. Net samples, which could be useful in observing such changes, were not taken.

Additional evidence for constant mass migrations comes from the condition of trawl collected specimens. Myctophids with gas-filled swimbladders collected in deep daytime, deep nighttime and shallow nighttime trawls on the September 1981 cruise and on later cruises were never observed with everted stomachs or swimbladders because of expansion of swimbladder gases, although the swimbladders of these fishes, when observed with a dissecting microscope, were intact. Other species of midwater fishes (Gonostomatidae and Sternoptychidae) have been observed with everted stomachs and swimbladders, and distended bodies (Kanwisher and Ebeling, 1957; Kleckner and Gibbs, 1972). Some moribund specimens of D. theta and S. leucopsarus were the only myctophids observed floating in sea water after our midwater trawl collections.

Indirect evidence in support of vertical migrations with swimbladders maintained at a constant volume comes from numerous sources. Comparative morphological studies of the rete mirabile, gas gland and oval of swimbladders in epipelagic and mesopelagic fishes indicated that these structures were relatively larger in mesopelagic fishes (Marshall, 1960) and, therefore, had greater gas secreting capacities. However, Marshall (1972) found that the predominantly non-migratory fishes of the lower mesopelagic possessed even larger gas secreting structures than migratory fishes of the upper mesopelagic. Barham (1966, 1971) and Backus et al. (1968), using submersibles, observed myctophids hanging motionless at daytime depths. However, Barham (1971) observed species which probably had fat-invested and reduced swimbladders (T. mexicanus and S. leucopsarus), whereas the single species observed by Backus et al. (1968) (Ceratoscopelus maderensis) has a gas-filled swimbladder. Hersey et al. (1962) presented acoustical data that implied that the volume of gas-filled swimbladders was sometimes kept constant during vertical migrations. The peak resonant frequency of the migratory scattering layer was proportional to $P^{.5}$. Although these data are not conclusive, they provide some indirect support for the theory that vertical migrations are sometimes carried out with swimbladders maintained at

constant volume.

Results from my study, discussed earlier, indicate that vertical migrations were carried out, by at least the larger fishes, with swimbladders maintained at a constant volume. The evidence is based primarily on acoustics. However, it is possible to relate the acoustical data in Figure 13 to the modeled net data and make some conclusions regarding the species that may migrate with swimbladders at a constant volume. For example, the acoustically estimated abundance of 0.5 mm radius bubbles remains constant during the course of the vertical migration. Bubbles in this size range correspond to D. theta and S. leucopsarus in the modeled distributions of net data (Figures 18, 19 and 20).

Neutral Buoyancy

Studies of buoyancy in midwater fishes with swimbladders have generally assumed that they were neutrally buoyant at some point in their vertical range (Marshall, 1960; Alexander, 1972; Vent and Pickwell, 1977). However, results of this study suggest that some myctophids may not achieve neutral buoyancy with gas-filled swimbladders.

The assumption that Protomyctophum spp. are neutrally

buoyant may not be valid although this was assumed earlier in producing the modeled distributions of swimbladder radii (Figures 18, 19 and 20). There is no direct evidence that these fishes are neutrally buoyant because of a gas-filled swimbladder and my conclusions were based on data which suggests that Protomyctophum spp. are non-migratory fishes with a specific gravity greater than that of sea water. If I had concluded that the swimbladders of Protomyctophum spp. were inflated to approximately 15% of the volume required for neutral buoyancy (α=.55) the peaks of both the acoustic data and the modeled net data would have coincided.

Observations I have made suggest that Protomyctophum maintains its swimbladder at a size below that required to maintain neutral buoyancy. This species is usually collected from depths of greater than 200 m but become moribund when brought to the surface. However, after being brought rapidly to the surface these fish do not float in sea water and they do not have everted stomachs or swimbladders. This would occur if the swimbladder ruptured during ascent, if gases were removed from the swimbladder by physiological mechanisms or if the swimbladders were not inflated to the neutral buoyancy volume at depth. Observations with a dissecting microscope on fresh specimens at sea showed that

swimbladders were not ruptured, although this does not discount the possibility of losses via gas diffusion or small leaks. Morphological and physiological studies (Marshall, 1960, 1972; Alexander, 1971, 1972; Butler and Pearcy, 1972) indicated that myctophids do not possess the capability to release swimbladder gases rapidly during a forced ascent, although they can probably resorb gases rapidly enough to migrate vertically without becoming positively buoyant (Marshall, 1960). Kleckner and Gibbs (1972) concluded that the organized and vascularized resorptive area of the oval in the Myctophidae has a far greater resorptive capacity than the resorptive area of the Gonostomatidae and Sternoptychidae which consists of a vascularized region in the swimbladder wall. They speculated that because of this, the swimbladders of gonostomatids and sternoptychids are frequently distended from the expansion of swimbladder gases, whereas the swimbladders of myctophids are rarely distended. Although myctophids may possess greater resorptive capabilities than gonostomatids and sternoptychids this is probably an inadequate explanation for the lack of ruptured or "overinflated" swimbladders, because in many cases the death of a fish during the process of trawling would significantly reduce or end further resorption (but not diffusion) of swimbladder gases. The third possibility,

that the swimbladders were not inflated to the neutral buoyancy volume at depth, seems the more probable.

Marshall (1960, 1972), in studies of midwater fishes, has shown that there are both migratory and non-migratory species with and without gas-filled swimbladders. Furthermore, many species of oceanic fishes are negatively buoyant, notably scombrids and sharks, many of which depend on hydrodynamic lift from extended pectoral fins and other surfaces to maintain equilibrium. Certain species in the genus Thunnus possess swimbladders, but are negatively buoyant (Magnuson, 1973, 1978). Bone (1973) concluded that this was the case for several species of myctophids, including T. crenularis . He also showed that the pectoral fins of Protomyctophum spp., T. crenularis and S. californiensis were relatively long when compared with other myctophids (Table 4). It would not be impossible to conclude that, like T. crenularis , Protomyctophum spp., were negatively buoyant and maintained position in the water column by swimming, despite the presence of a gas-filled swimbladder. This conclusion could also apply to the migratory species of myctophids in the collections.

Biological-Acoustical Interpretation

Comparison of biological and acoustic data sets indicate differences in the estimated distributions of bubble radii using the two methods. Initial interpretation of scattering spectra indicated that an abundance peak at a bubble radius of 0.6 mm in both deep daytime and deep nighttime arcer casts (Figures 6 and 8) was attributable to non-migratory, neutrally buoyant *P. thompsoni* and *P. crockeri* . Furthermore, because *Protomyctophum* spp. are the most abundant swimbladder fishes in deep night and deep day tows it is plausible that they are responsible for the gross similarities in deep day and deep night acoustic data. However, my calculations are that a swimbladder of 1.0 to 1.8 mm radius would be required to maintain *P. thompsoni* and *P. crockeri* of 15 to 50 mm SL at neutral buoyancy, which would place these fish above the range of peak abundance. Secondary peaks in the abundance of gas bubbles in deep daytime and deep nighttime arcer data did occur at radii of 1.0 to 1.8 mm. These peaks are similar in both day and night periods and they correspond to the swimbladder sizes required for neutral buoyancy in *Protomyctophum* spp. If *Protomyctophum* spp. are, in fact, neutrally buoyant at

depth they would probably not be responsible for the gross similarities in resonant scattering observed in deep daytime and deep nighttime acoustical records.

Correlations between the abundance distributions of bubble radii as derived both acoustically and from the neutral buoyancy model suggested that swimbladders were filled to volumes below that required to maintain neutral buoyancy both at daytime and nighttime depths. These correlations are most applicable to the more abundant medium sized swimbladders or fishes. These results are not implausible since it has been theorized that some midwater fishes perform vertical migrations with swimbladder gases maintained at a constant mass. If this were the case, swimbladders would provide greater lift at shallow, nighttime depths, after a vertical migration, due to expansion of swimbladder gases. However, correlations with shallow nighttime arcer data indicated that swimbladders were still inflated to only a fraction of the neutral buoyancy volume. These results indicate that swimbladders were filled to 3.9% (α=.35) of the volume required for neutral buoyancy at depths of 200 to 250 m during the daytime. A constant mass migration by these fishes to 40 m would result in expansion of their swimbladders to 18.3% (α=.6)of the volume required for neutral buoyancy. If these fishes were to migrate to

within 1 m of the surface their swimbladders would be inflated to 83.3% (α=.95) of the neutral buoyancy volume. Based on correlations between data from the shallow nighttime arcer and net data, I estimated that swimbladders were filled to 13.4% (α=.5) of the neutral buoyancy volume at 40 m. These same swimbladders would be inflated to 60.9% (α=.85) of the neutral buoyancy volume at a depth of 1 m if the migration was made while maintaining swimbladder gases at a constant mass, slightly less than the predicted swimbladder size of fishes migrating from 225 m to 1 m. These results suggest that myctophids with medium sized swimbladders were migrating with their swimbladders kept at a constant mass. Furthermore, correlations with deep nighttime arcer data showed that swimbladders were slightly larger (22.5% of the neutral buoyancy volume, α =.6) than in deep daytime correlations. This may result becauses fishes not vertically migrating on a particular evening may pump up their swimbladders so that they are closer to neutral buoyancy. Also, it may be due to fishes with swimbladders migrating from deeper depths to about 235 m.

Although the range of estimated swimbladder sizes in the histograms of acoustical (Figures 6, 8, 10 and 12) and biological (Figures 18, 19 and 20) data are similar, the mean values are significantly different. The shift in the

mean between the two data sets suggests that the models overestimate the swimbladder size. This is especially apparent in the deep daytime and deep nighttime data sets, where Protomyctophum spp. were the most common fish with gas-filled swimbladders.

CONCLUSIONS

Analysis of acoustic and biological data indicate that the swimbladders of some myctophid fishes off Oregon may be inflated to a volume less than is required to maintain neutral buoyancy. This applies particularly to those fishes which migrate vertically. Furthermore, these fishes may not achieve hydrostatic equilibrium at any point in their depth ranges. These results infer that some myctophids of the upper mesopelagic zone "over-regulate" swimbladder gases such that they are always slightly negatively buoyant.

The reason for an adaptation such as the over-regulation of swimbladder gases is not intuitively obvious, because the fish is not conserving energy by minimizing the energy expended to regulate the swimbladder. Although there are negatively buoyant fishes with swimbladders, i.e. tunas, the behavior, and concomitantly, buoyancy requirements of these fishes are very different from those of the myctophids.

Several strategies are suggested for vertical

migrations by myctophids. Based on acoustical evidence I concluded that some of the larger myctophids migrate with the swimbladder maintained at a constant volume. Correlations between acoustical and biological data sets indicated that medium sized fishes migrated with swimbladders maintained at a constant mass. Swimbladder regulation in the smaller myctophids was not considered because these fishes were not sampled in the deeper collections.

This study has shown the feasibility and effectiveness of combined biological-acoustical studies of sound scattering layers and the potential of relating multiple-frequency acoustical data to species composition. Furthermore, it presents a paradox of midwater buoyancy regulation which has received little or no consideration.

Table 1. Summary of acoustical and net data used in this study.

Arcer Cast	Date	Time (hrs)	Depth (meters)	Trawl Number	Date	Time (hrs) Nets 1-5	Depths Fished (meters) 1	2	3	4	5	Total Volume Filtered ($10^5 m^3$)[1]
-	--------	---------	----	2485	14 IX 81	1440-1800	0-120	115-122	120-225	225-232[2]	232-310	10.61
-	--------	---------	----	2486	14 IX 81	2237-0107	0-50	48-50[3]	50-78[3]	75-80[3]	75-80[3]	8.61
-	--------	---------	----	2487	15 IX 81	1552-1822	0-195	195-220[2]	208-225[2]	200-215[2]	215-220[2]	7.87
1	15 IX 81	2254-2325	34	2488	16 IX 81	0012-0242	0-30	30[3]	30-50[3]	50[3]	45-50[3]	9.49
2	16 IX 81	1029-1040	175	2489	16 IX 81	1131-1451	0-165	165-188	188-230[2]	230[2]	225-230[2]	13.86
3	16 IX 91	1600-1618	235	----	--------	---------	-----	-------	-------	-------	-------	-----
4	16 IX 91	1731-1905	160[5]	----	--------	---------	-----	-------	-------	-------	-------	-----
5	16 IX 81	1938-2010	97[5]	----	--------	---------	-----	-------	-------	-------	-------	-----
6	16 IX 81	2059-2120	235	----	--------	---------	-----	-------	-------	-------	-------	-----
7	16 IX 81	2219-	40	2490	16 IX 81	2253-0213	0-50[3]	50-240	220-235[4]	220-240[4]	215-230[4]	14.42
8	17 IX 81	1012-1117	277	----	--------	---------	-----	-------	-------	-------	-------	-----
9	17 IX 81	1302-1317	144	----	--------	---------	-----	-------	-------	-------	-------	-----
10	17 IX 81	1856-1930	123[5]	2491	17 IX 81	1448-1808	0-55	55	55-170	155-250[2]	240-255[2]	12.03
-	--------	---------	----	2492	17 IX 81	2113-0033	0-150	120-135	125-250[4]	250[4]	250-255[4]	13.46

[1] Volume filtered is for nets 2-5, except for trawl 2490 where volume is for nets 1-5.

[2] Nets used for deep daytime comparisons (n=10).

[3] Nets used for shallow nighttime comparisons (n=9).

[4] Nets used for deep nighttime comparisons (n=6).

[5] Arcer data collected during a vertical migration.

Table 2. Biomass Data. Mean biomass per net of major micronekton groups caught in the rope trawl (Wet weight in gms/1000m^3).

	Deep Day (n=10)	Deep Night (n=6)	Shallow Night (n=9)
Non-Fish			
Shrimp	.213 (.402)[1]	.975 (.504)	.315 (.322)
Squid	.060 (.038)	3.61 (2.45)	1.99 (1.92)
Euphausiids	1.32 (1.47)	.154 (.065)	19.87 (28.58)
Misc. Plankton	.994 (.938)	1.98 (1.88)	.175 (.197)
Total	2.587 (1.27)	6.719 (4.73)	22.350 (29.0)
Fish			
With gas-filled swimbladders			
Stenobrachius leucopsarus	.001 (.001)	.001 (.001)	.220 (.188)
Protomyctophum thompsoni and *P. crockeri*	.051 (.066)	.159 (.103)	.003 (.006)
Symbolophorus californiensis	.017 (.036)	.032 (.048)	2.95 (4.63)
Tarletonbeania crenularis	.001 (.015)	.073 (.052)	1.25 (1.57)
Diaphus theta	.005 (.008)	.604 (.236)	2.46 (2.59)
Engraulis mordax	0	0	2.87 (8.61)
Total	.075 (.063)	.869 (.311)	9.75 (13.7)
Without gas-filled swimbladders	.085 (.084)	15.9 (11.4)	1.87 (.808)
Total Fish	.160 (.127)	16.7 (11.7)	11.6 (14.0)
Total biomass	2.75 (1.30)	23.5 (16.3)	34.0 (36.0)

[1] Numbers in parentheses are one standard deviation

Table 3. Mean abundance (number/1000m^3) of fishes with gas-filled swimbladders grouped by length(mm).

	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	100-110	110-120	120-130	130-140	140-150	TOTAL
DEEP DAY (10 nets)															
Stenobrachius leucopsarus	.004	.011	.001												.003(.004)[1]
Protomyctophum crockeri and P. thompsoni	.018	.038	.042	.009											.107(.113)
Symbolophorus californiensis								.0013	.001	.0003					.003(.004)
Tarletonbeania crenularis				.0003	.003	.002	.001								.006(.009)
Diaphus theta	.006		.001	.002		.001									.010(.009)
														Total	.129
DEEP NIGHT (6 nets)															
Stenobrachius leucopsarus		.010	.001												.010(.008)
Protomyctophum crockeri and P. thompsoni	.010	.062	.148	.002											.242(.097)
Symbolophorus californiensis							.002	.002							.004(.009)
Tarletonbeania crenularis					.005	.014	.006		.002						.024(.017)
Diaphus theta	.019		.003	.033	.079	.063	.012								.209(.068)
														Total	.489
SHALLOW NIGHT (9 nets)															
Stenobrachius leucopsarus	.038	.951	.266												1.26 (1.30)
Protomyctophum crockeri and P. thompsoni		.001	.003	.001											.005(.010)
Symbolophorus californiensis							.044	.198	.094	.003					.339(.534)
Tarletonbeania crenularis		.023	.051	.048	.187	.197	.063								.569(.640)
Diaphus theta	1.110	.033	1.314	.486	.144	.054	.003								3.14 (2.92)
Engraulis mordax										.007	.079	.034	.011	.012	.143(.427)
														Total	5.456

[1] Numbers in parentheses are one standard deviation

Table 4. Buoyancy-related characteristics of myctophids with gas-filled swimbladders.

Species	Swimbladder Characteristics	Specific Gravity (g/cm^3)	Lipid Content	Water Content	Relative size of Pectoral Fin	Migratory Behavior	Nighttime Depth of Maximum Abundance (m)	Daytime Depth of Maximum Abundance (m)	α Value for Deep Daytime Model	Constant Mass or Constant Volume Migrator	References
Stenobrachius leucopsarus	Only specimens below 40mm with gas-filled swimbladder	1.025-1.031	high	low	short	migratory	0-100	300-500 (<30mm) 300-600 (>30mm)	.9	Constant Volume	1,2,3,4,5,6
Protomyctophum thompsoni	All sizes with gas-filled swimbladder	1.055	low	low	long	non-migratory	300-400	300-400	.9	Constant Volume	1,2,3,5,6
Protomyctophum crockeri	All sizes with gas-filled swimbladder	1.055	low	low	long	non-migratory	300-400	300-400	.9	Constant Volume	1,2,3,5,6
Symbolophorus californiensis	All sizes with gas-filled swimbladder	1.056	high	low	long	migratory	0-100	300-600	.9	Constant Volume	2,5,6
Tarletonbeania crenularis	All sizes with gas-filled swimbladder	1.084	low	low	long	migratory	0-100	300-400	.35	Constant Mass	1,2,3,5,6
Diaphus theta	All sizes with gas-filled swimbladder	1.037	high	low	short	migratory	0-100	300-400	.9	Constant Volume	1,2,3,4,5,6

1. Butler and Pearcy (1972)
2. Neighbors and Nafpaktitis (1982)
3. Johnson (1979)
4. Capen (1967)
5. Bone (1973)
6. Pearcy et al. (1977)

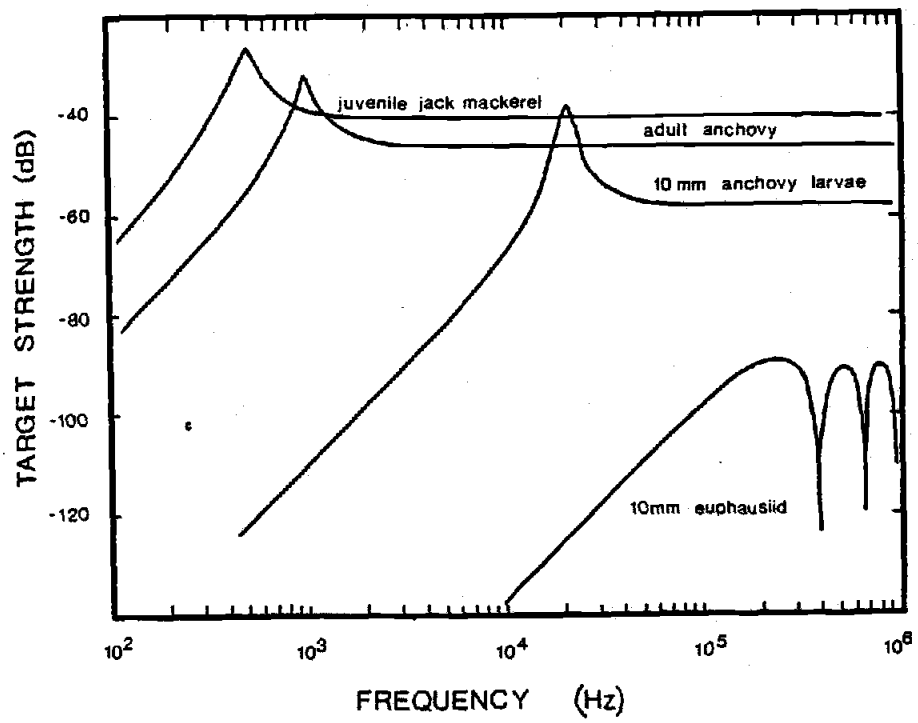

Figure 1. A comparison of the estimated target strengths of three fishes with gas-filled swimbladders and a euphausiid. The fishes are resonant sound scatterers whereas the euphausiid is a nonresonant scatterer. (From Holliday, 1980)

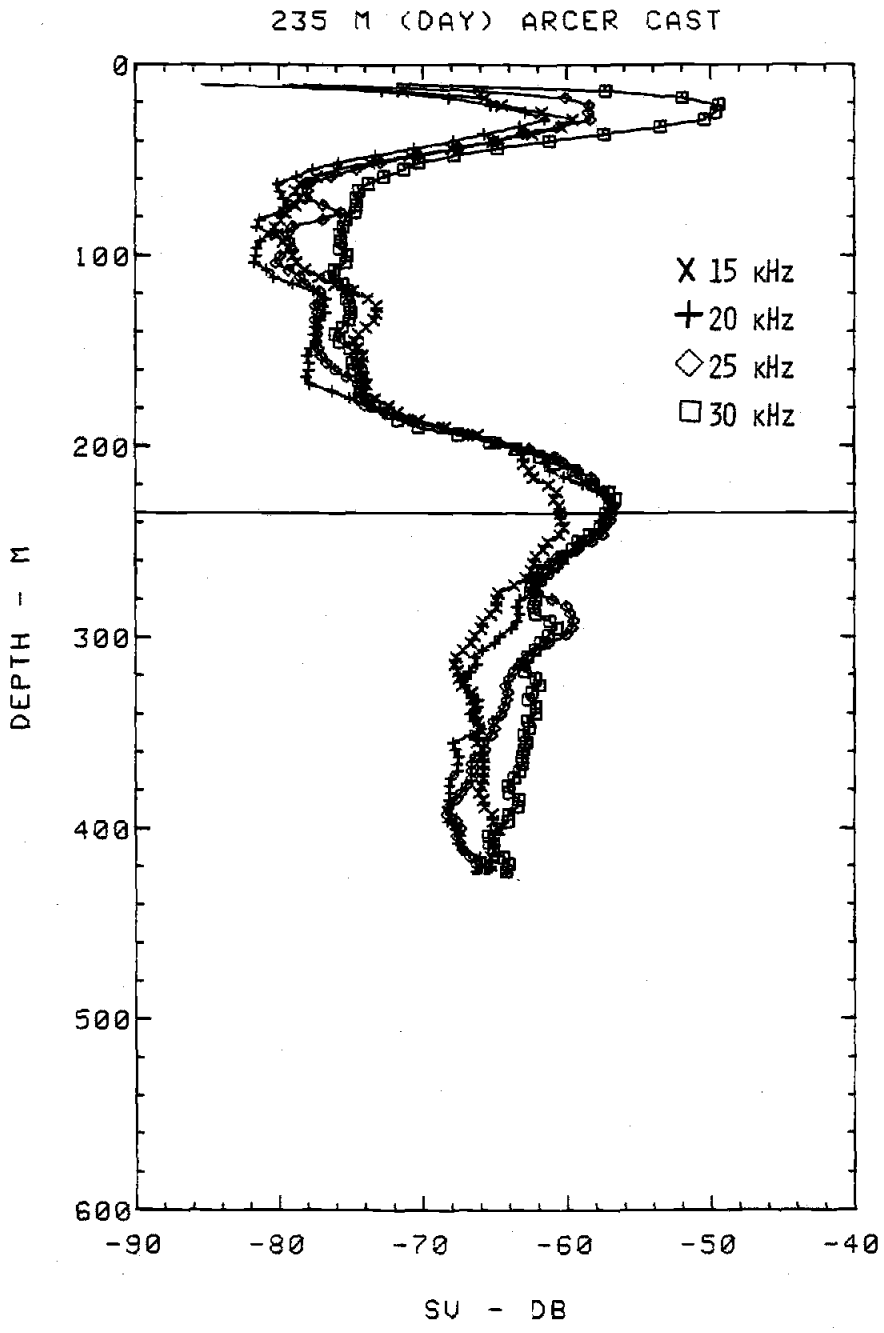

Figure 2. Plot of depth versus volume scattering strength during the daytime (1600 hrs.) at four frequencies. The horizontal line at 235 m indicates the depth of the arcer cast taken at a time close to that of these discrete frequency measurements.

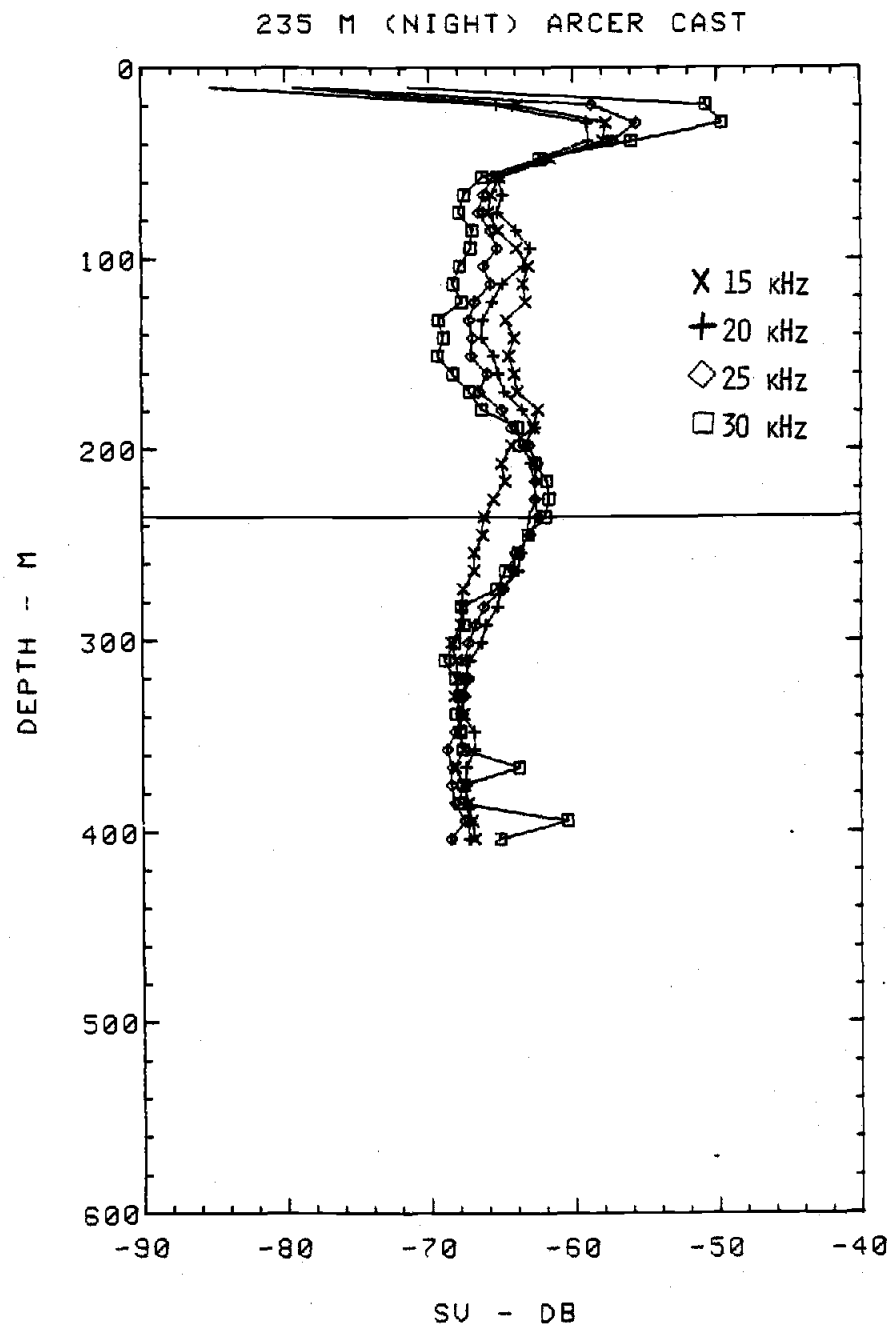

Figure 3. Plot of depth versus volume scattering strength during the nighttime (2130 hrs.) at four frequencies. The horizontal line at 235 m indicates the depth of the arcer cast taken at a time close to that of these discrete frequency measurements.

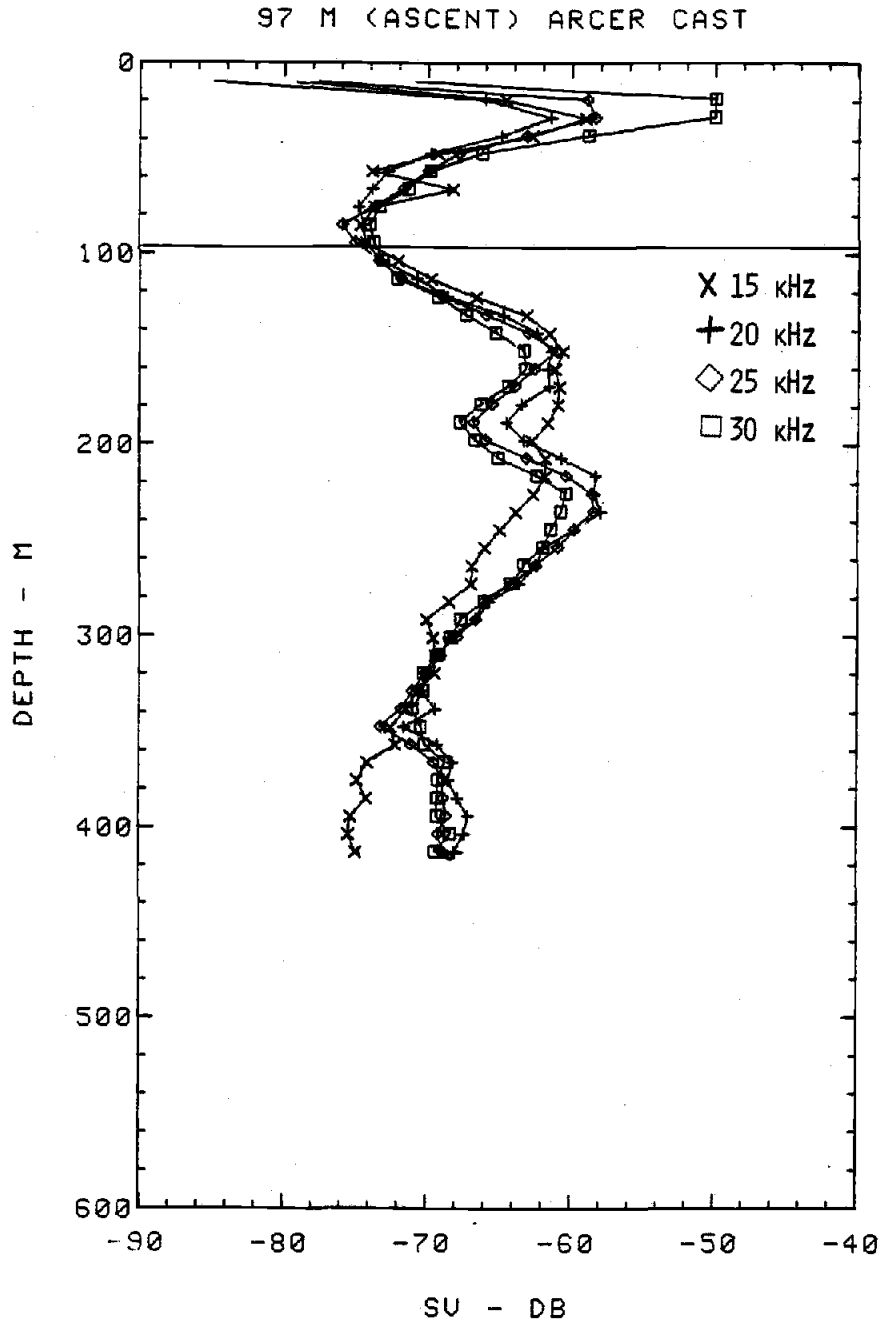

Figure 4. Plot of depth versus volume scattering strength during an early evening (2000 hrs.) ascent period at four frequencies. The horizontal line at 97 m indicates the depth of the arcer cast taken at a time close to that of these discrete frequency measurements.

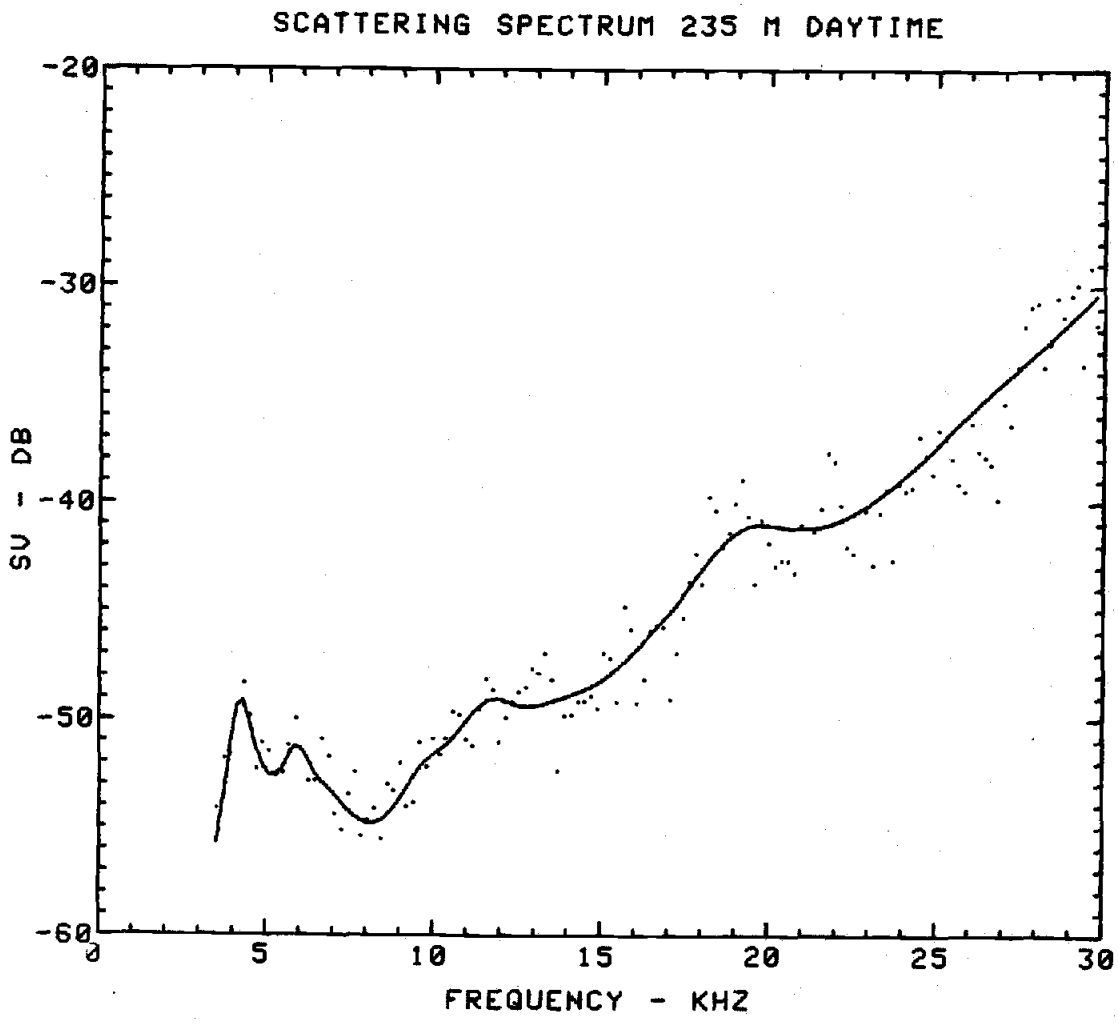

Figure 5. Scattering spectrum from deep daytime (1600-1618 hrs.) arcer cast. Points are mean volume scattering strengths determined from multiple firings of the arcer. Curves are based on the calculation of the scattering spectrum from the acoustical abundance estimates of bubble radii.

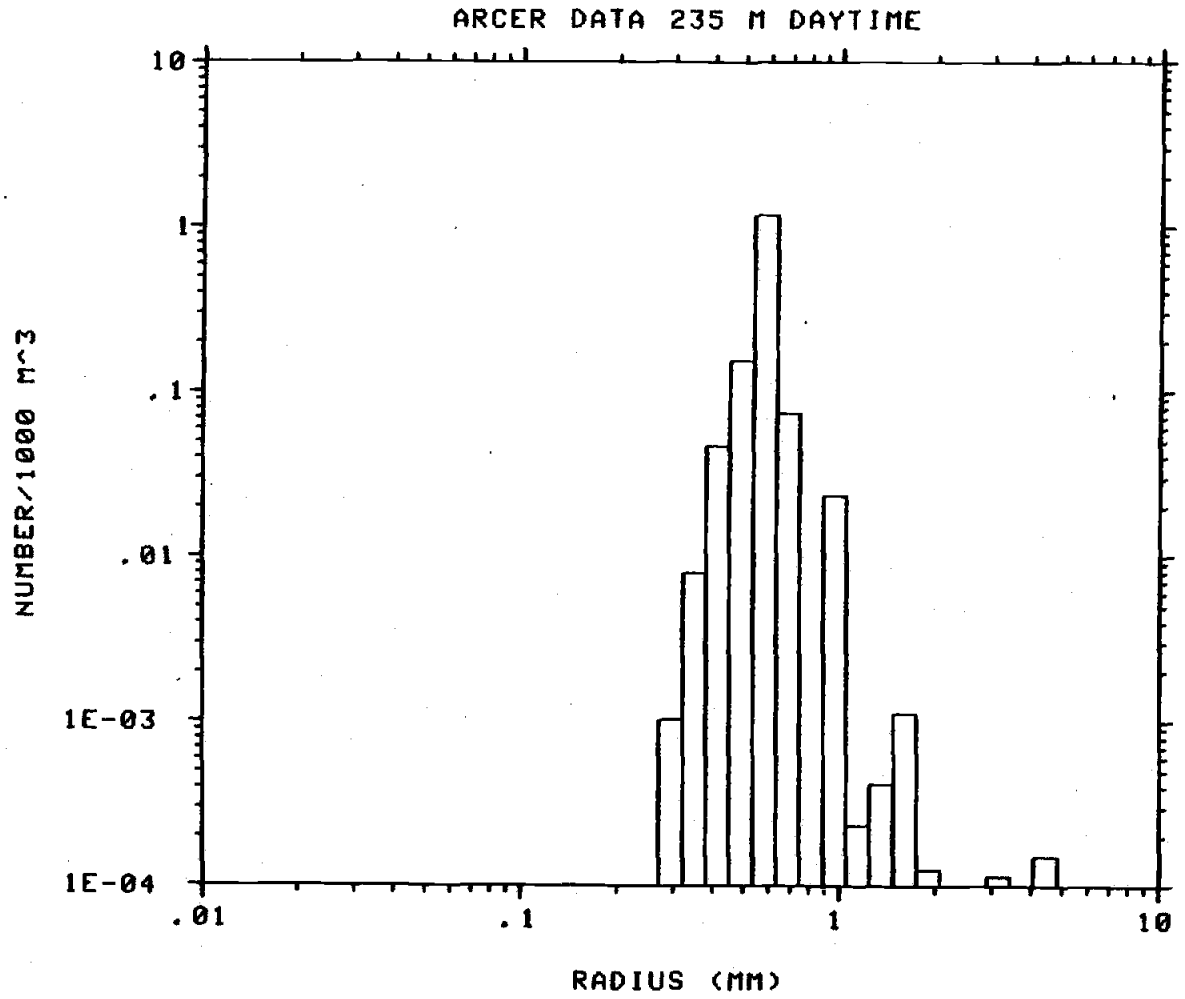

Figure 6. Acoustically measured abundance of bubble radii measured at 235 m during the daytime (1600-1618 hrs.). The total estimated number of gas bubbles is 1.49/1000 m^3.

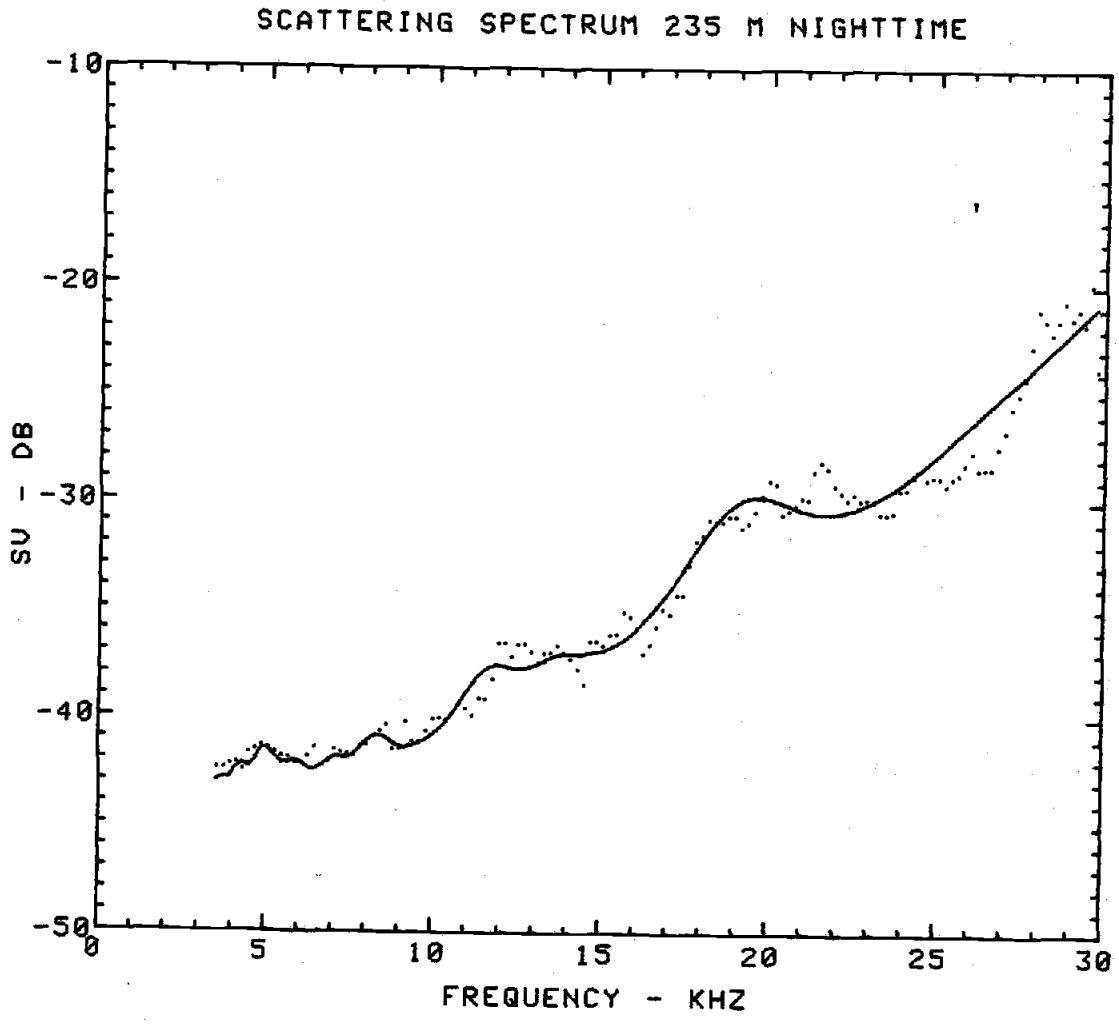

Figure 7. Scattering spectrum from deep nighttime (2059-2120 hrs.) arcer cast. Points are mean volume scattering strengths determined from multiple firings of the arcer. Curves are based on the calculation of the scattering spectrum from the acoustical abundance estimates of bubble radii.

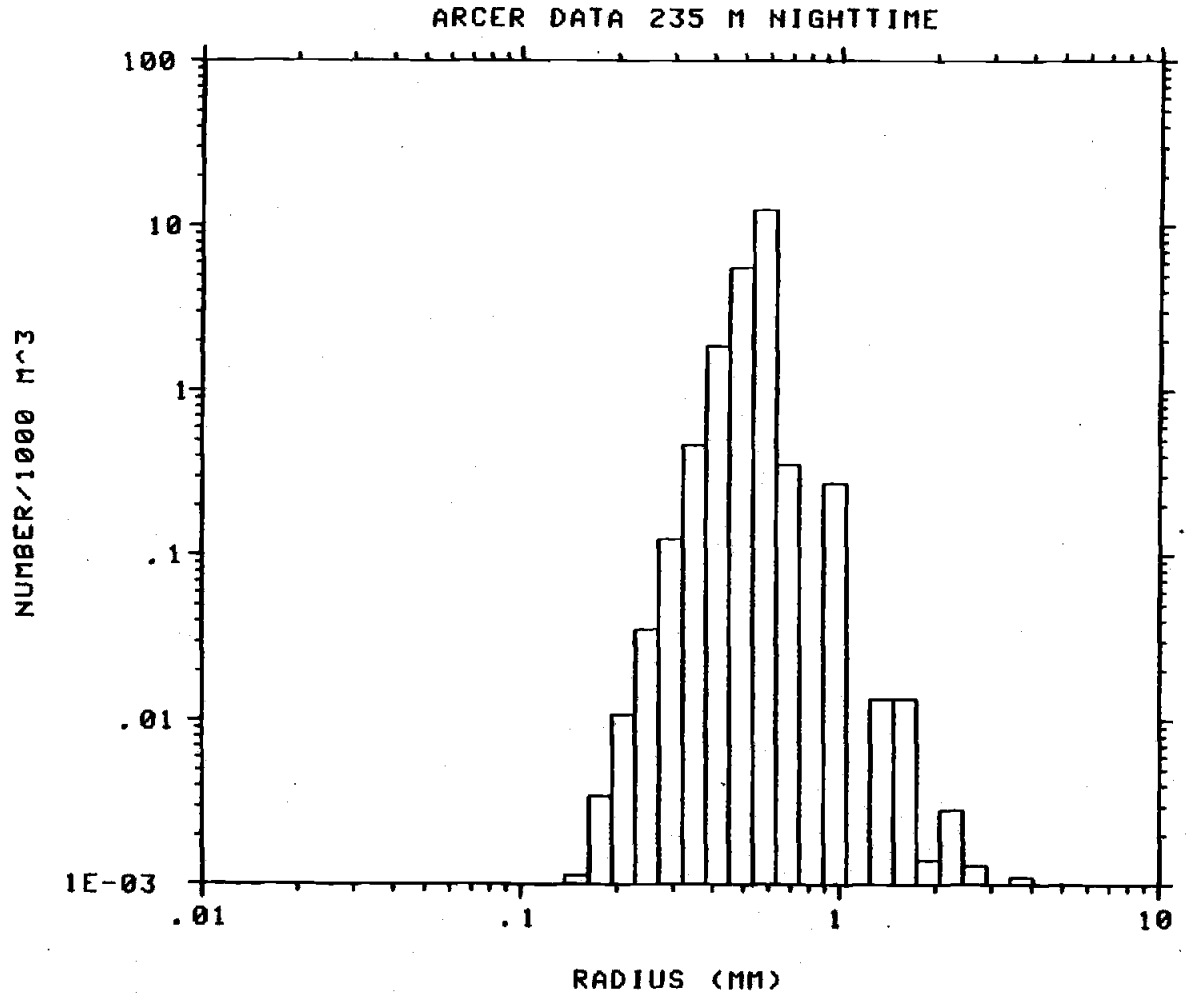

Figure 8. Acoustically estimated abundance of bubble radii measured at 235 m during the nighttime (2059-2120 hrs.). The total estimated number of gas bubbles is 21.3/1000 m^3.

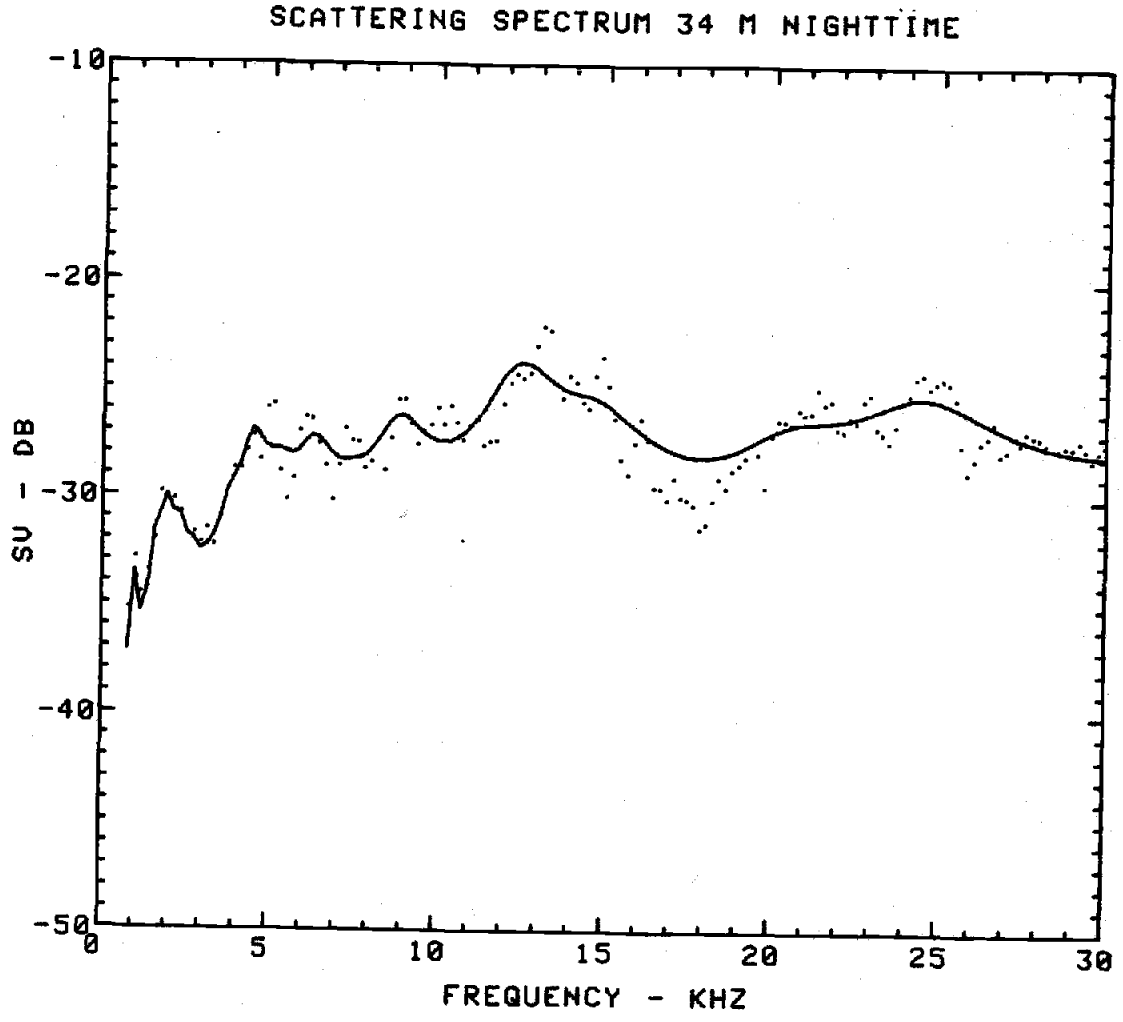

Figure 9. Scattering spectrum from shallow nighttime (2254-2325 hrs.) arcer cast. Points are mean volume scattering strengths determined from multiple firings of the arcer. Curves are based on the calculation of the scattering spectrum from the acoustical abundance estimates of bubble radii.

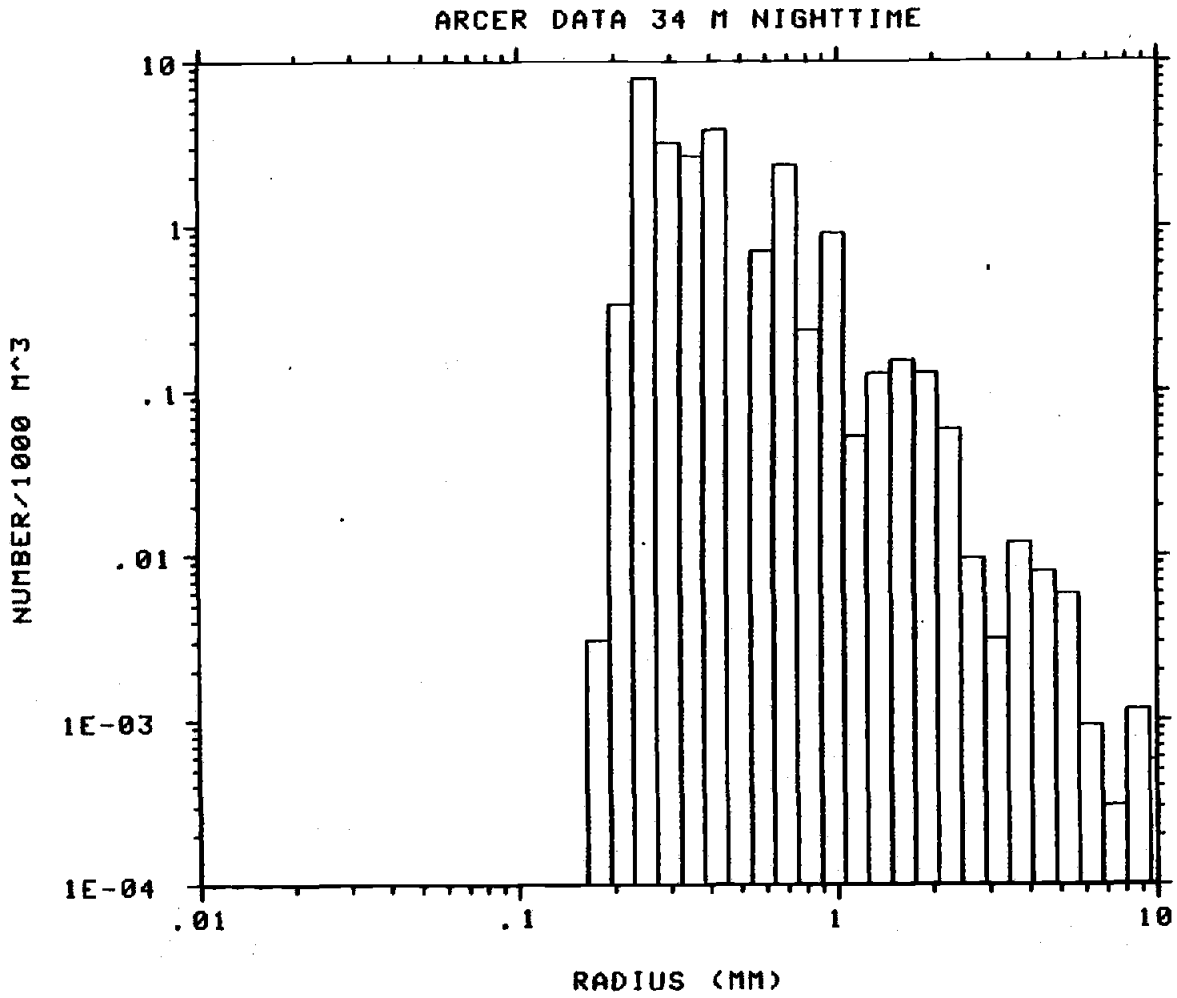

Figure 10. Acoustically estimated abundance of bubble radii measured at 34 m during the nighttime (2254-2325 hrs.). The total estimated number of gas bubbles is 23.0/1000 m^3.

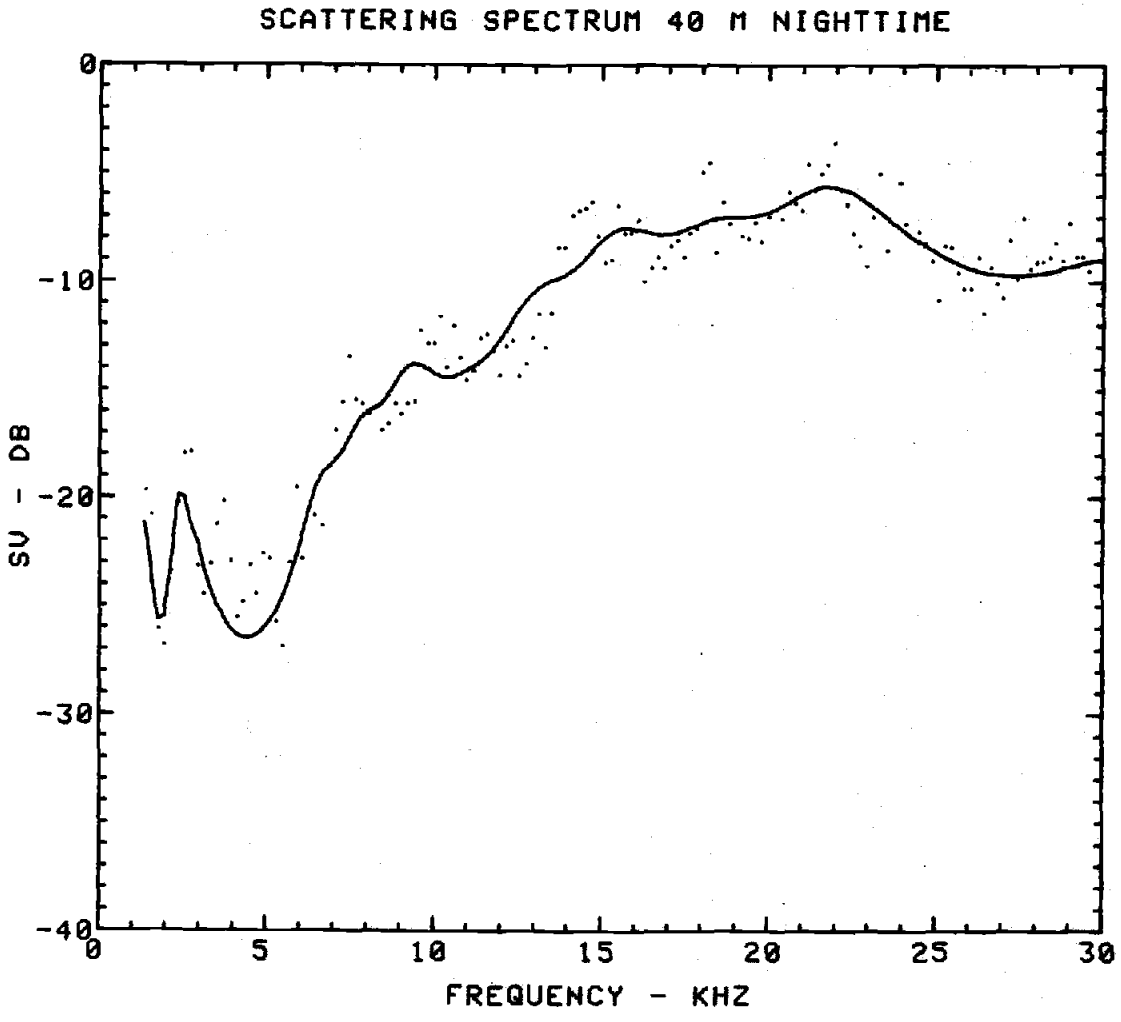

Figure 11. Scattering spectrum from shallow nighttime (2219 hrs.) arcer cast. Points are mean volume scattering strengths determined from multiple firings of the arcer. Curves are based on the calculation of the scattering spectrum from the acoustical abundance estimates of bubble radii.

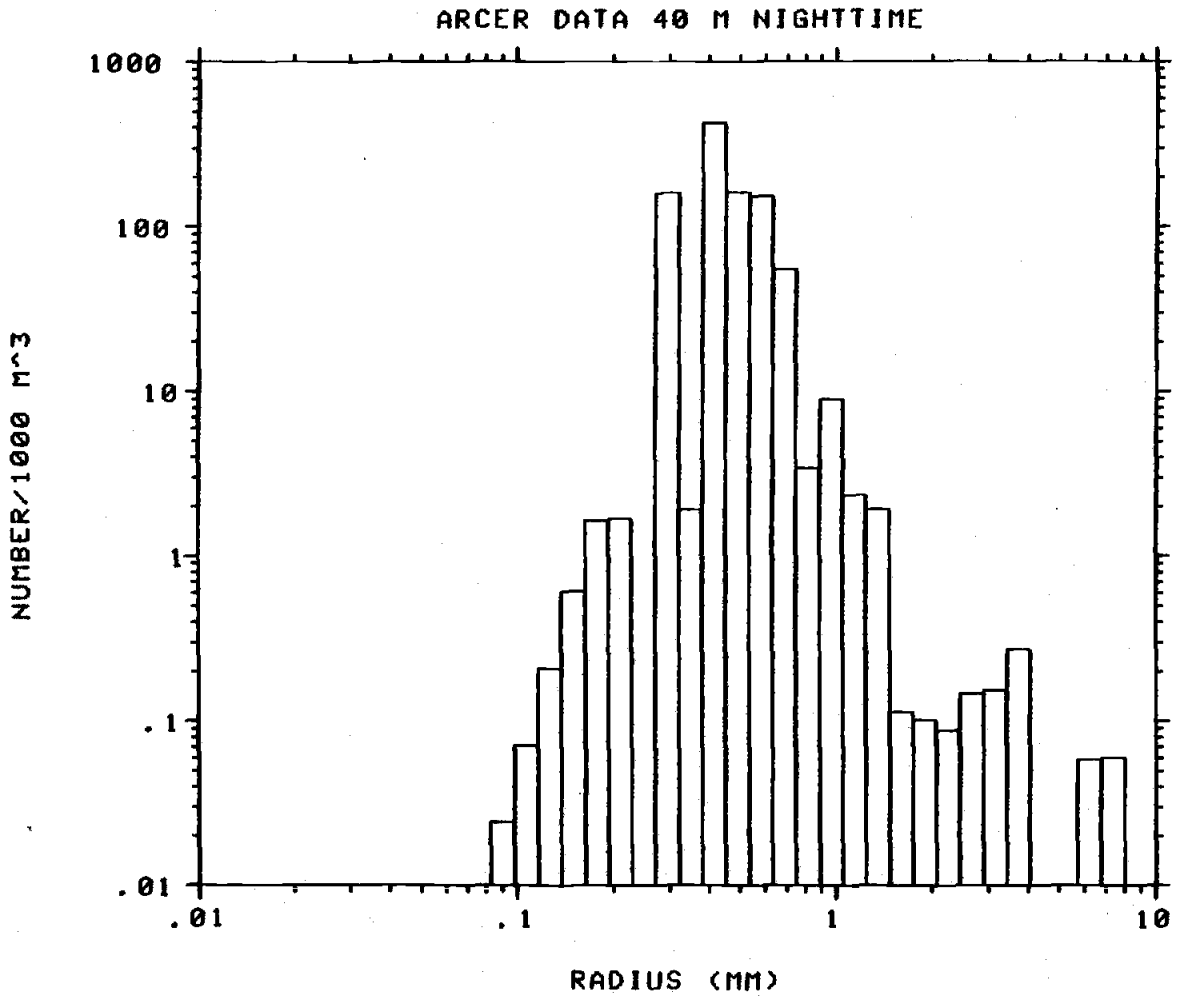

Figure 12. Acoustically estimated abundance of bubble radii measured at 40 m during the nighttime (2219 hrs.). The total estimated number of gas bubbles is 983/1000 m^3.

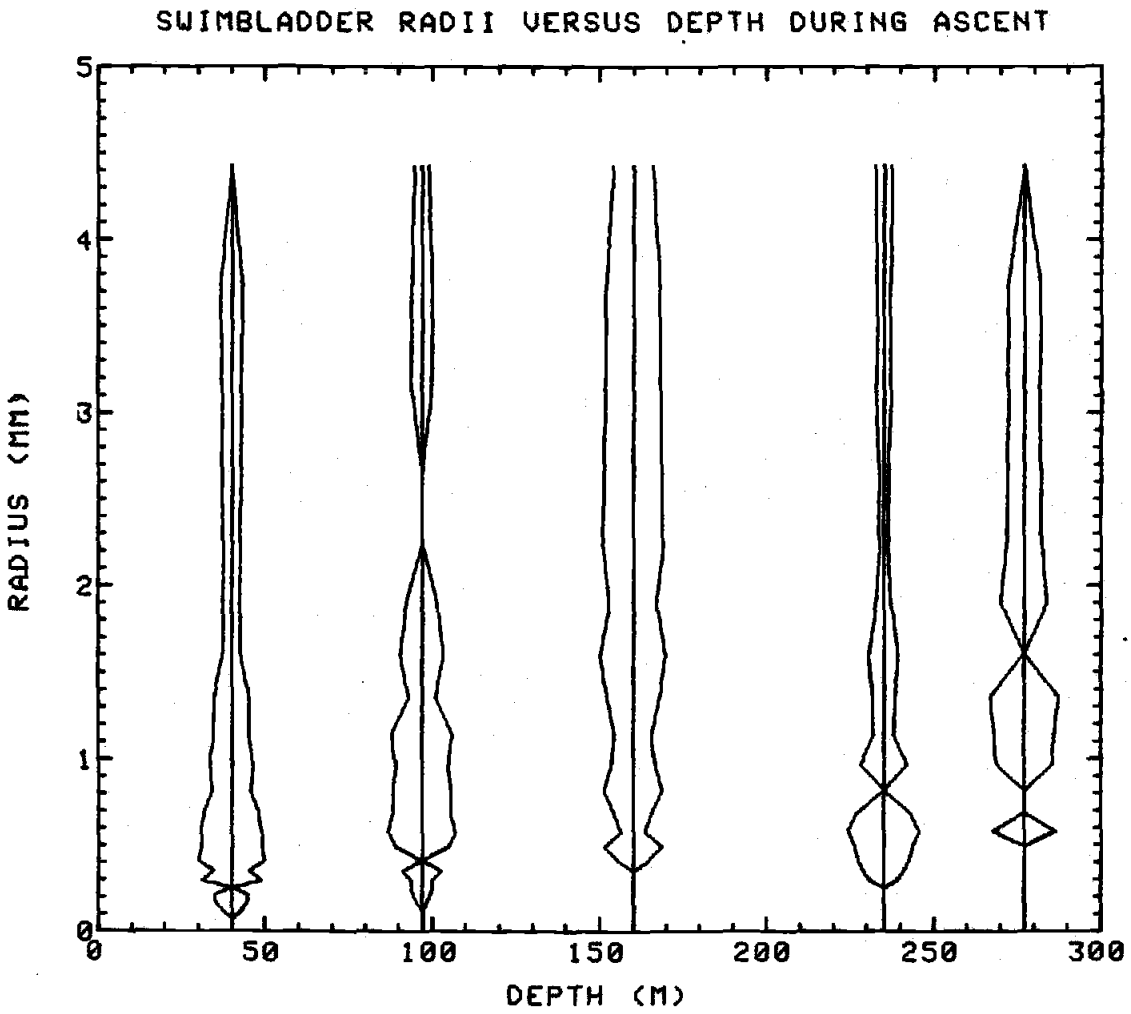

Figure 13. Acoustically estimated abundance of different bubble radii at five different depths. Acoustical measurements were made during an evening ascent period. The width of the "kite" diagrams is an indicator of the abundance of a particular radius of bubble on a log scale.

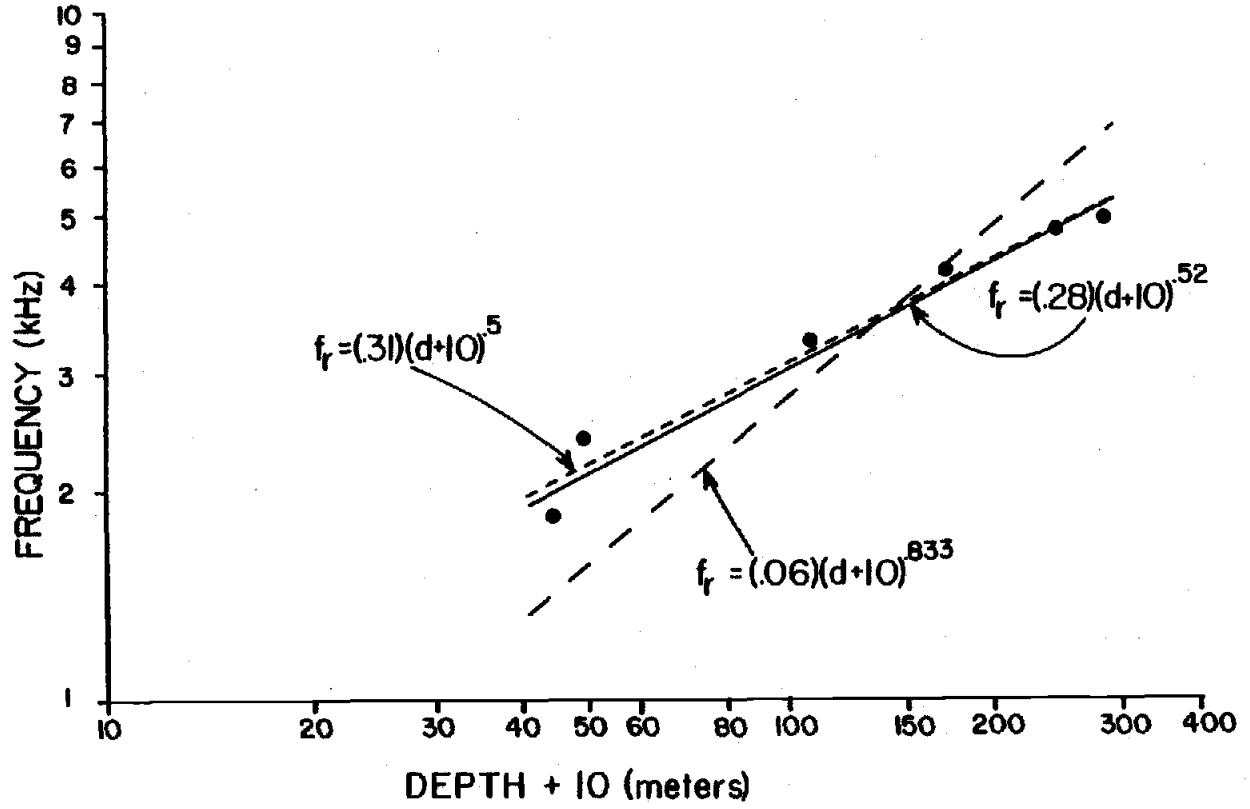

Figure 14. Plot of frequency versus depth + 10 m used to determine if swimbladders are maintained at a constant mass or regulated (constant volume) during vertical migrations. Points are lowest frequencies of peak scattering attributed to resonance at a particular depth. The solid line is the regression line for the data points (r=.98), the line made up of small dashes represents the resonant frequency shift for a constant volume migrator and the line made up of large dashes represents the shift for a constant mass migrator.

Figure 15. Mean abundance of swimbladder radii in deep daytime net collections as determined by the neutral buoyancy model (N=10). Swimbladder radii were estimated using the neutral buoyancy model for each species and size of fish. The value of α is one for all species.

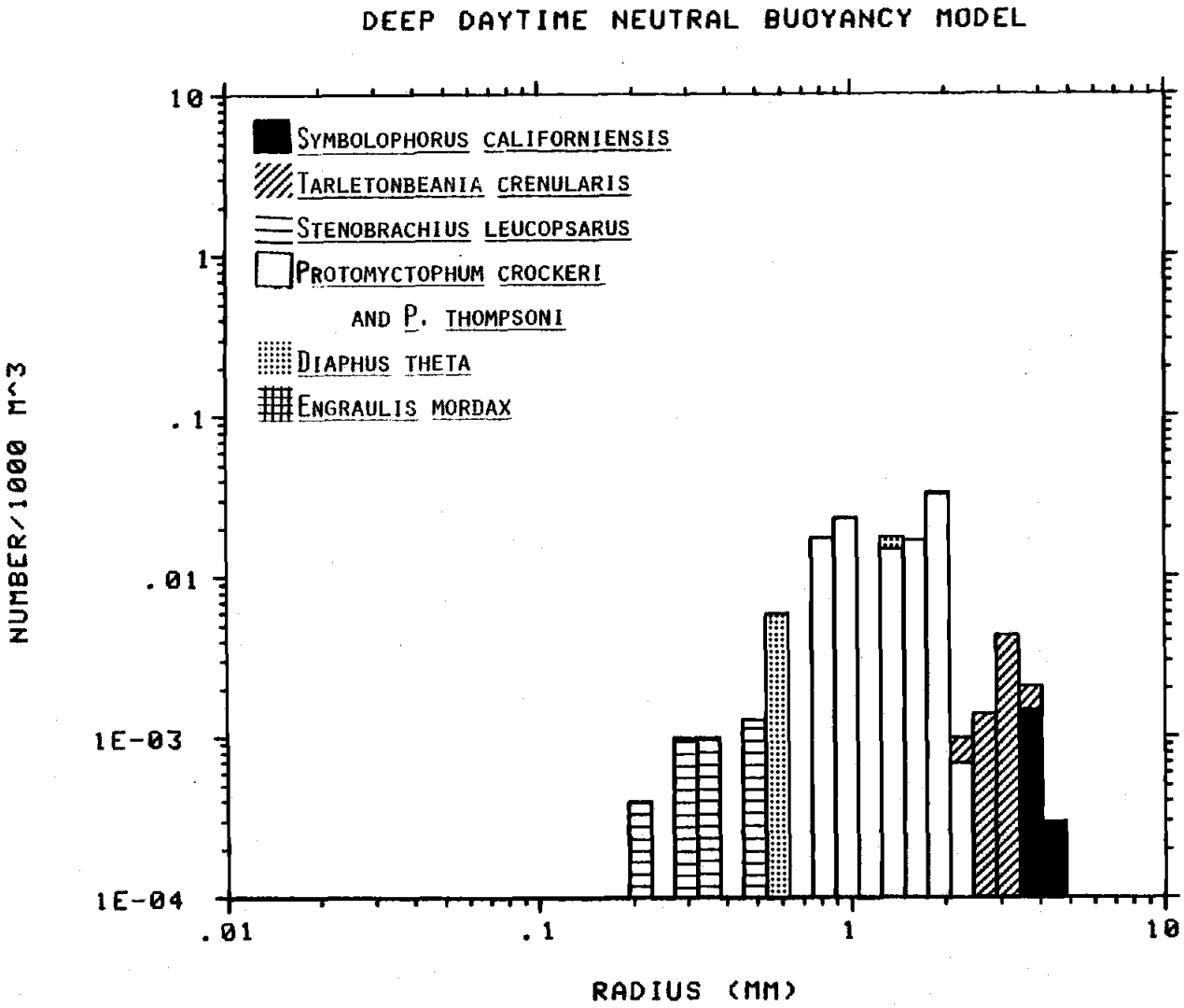
DEEP DAYTIME NEUTRAL BUOYANCY MODEL
SYMBOLOPHORUS CALIFORNIENSIS
TARLETONBEANIA CRENULARIS
STENOBRACHIUS LEUCOPSARUS
PROTOMYCTOPHUM CROCKERI
AND P. THOMPSONI
DIAPHUS THETA
ENGRAULIS MORDAX
NUMBER/1000 M^3
10
1
.1
.01
1E-03
1E-04
.01
.1
1
10
RADIUS (MM)

Figure 15.

Figure 16. Mean abundance of swimbladder radii in deep nighttime net collections as determined by the neutral buoyancy model (N=6). Swimbladder radii were estimated using the neutral buoyancy model for each species and size of fish. The value of α is one for all species.

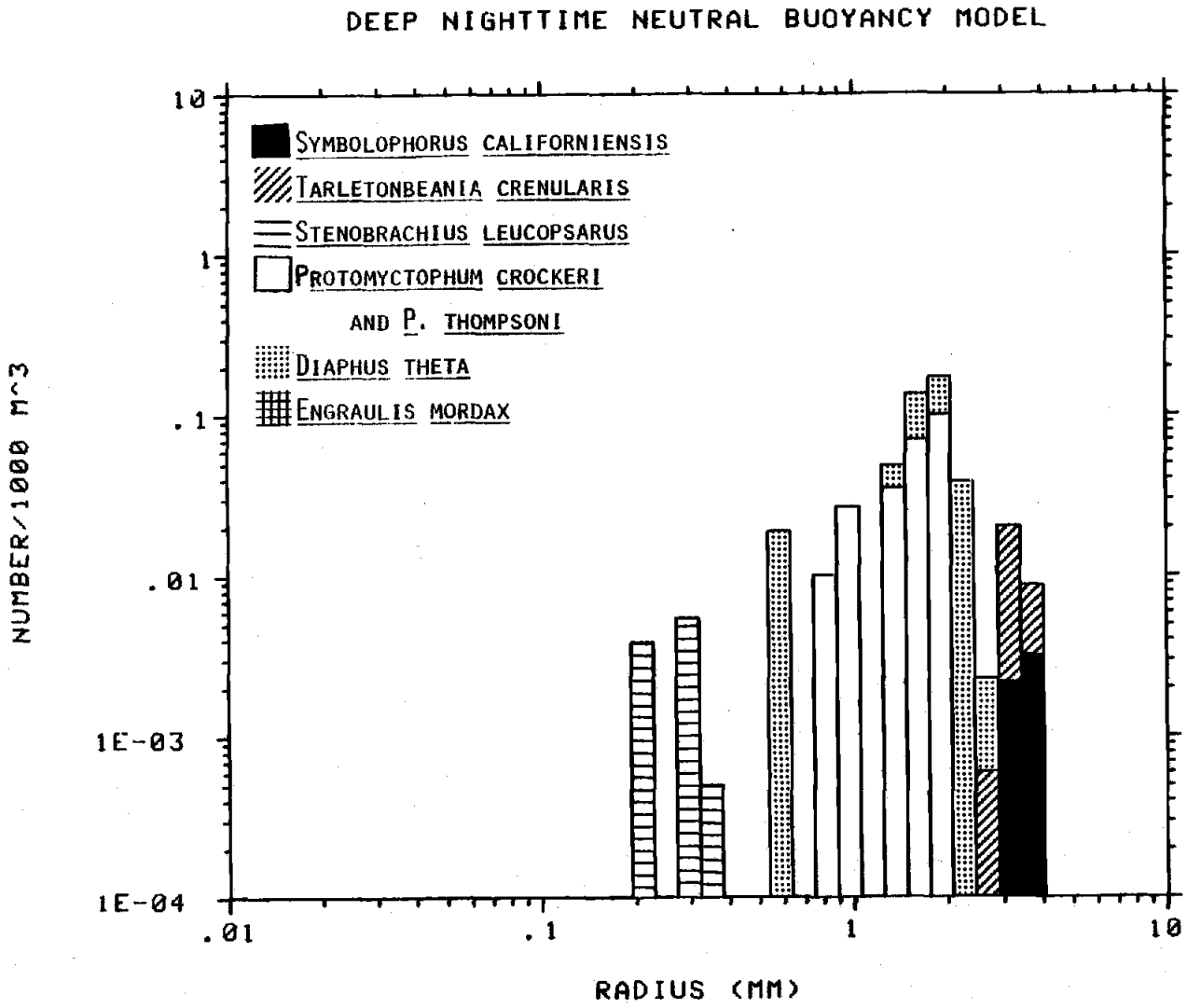
DEEP NIGHTTIME NEUTRAL BUOYANCY MODEL
SYMBOLOPHORUS CALIFORNIENSIS
TARLETONBEANIA CRENULARIS
STENOBRACHIUS LEUCOPSARUS
PROTOMYCTOPHUM CROCKERI
AND P. THOMPSONI
DIAPHUS THETA
ENGRAULIS MORDAX
NUMBER/1000 M^3
10
1
.1
.01
1E-03
1E-04
.01
.1
1
10
RADIUS (MM)

Figure 16.

Figure 17. Mean abundance of swimbladder radii in shallow night-time net collections as determined by the neutral buoyancy model (N=9). Swimbladder radii were estimated using the neutral buoyancy model for each species and size of fish. The value of α is one for all species.

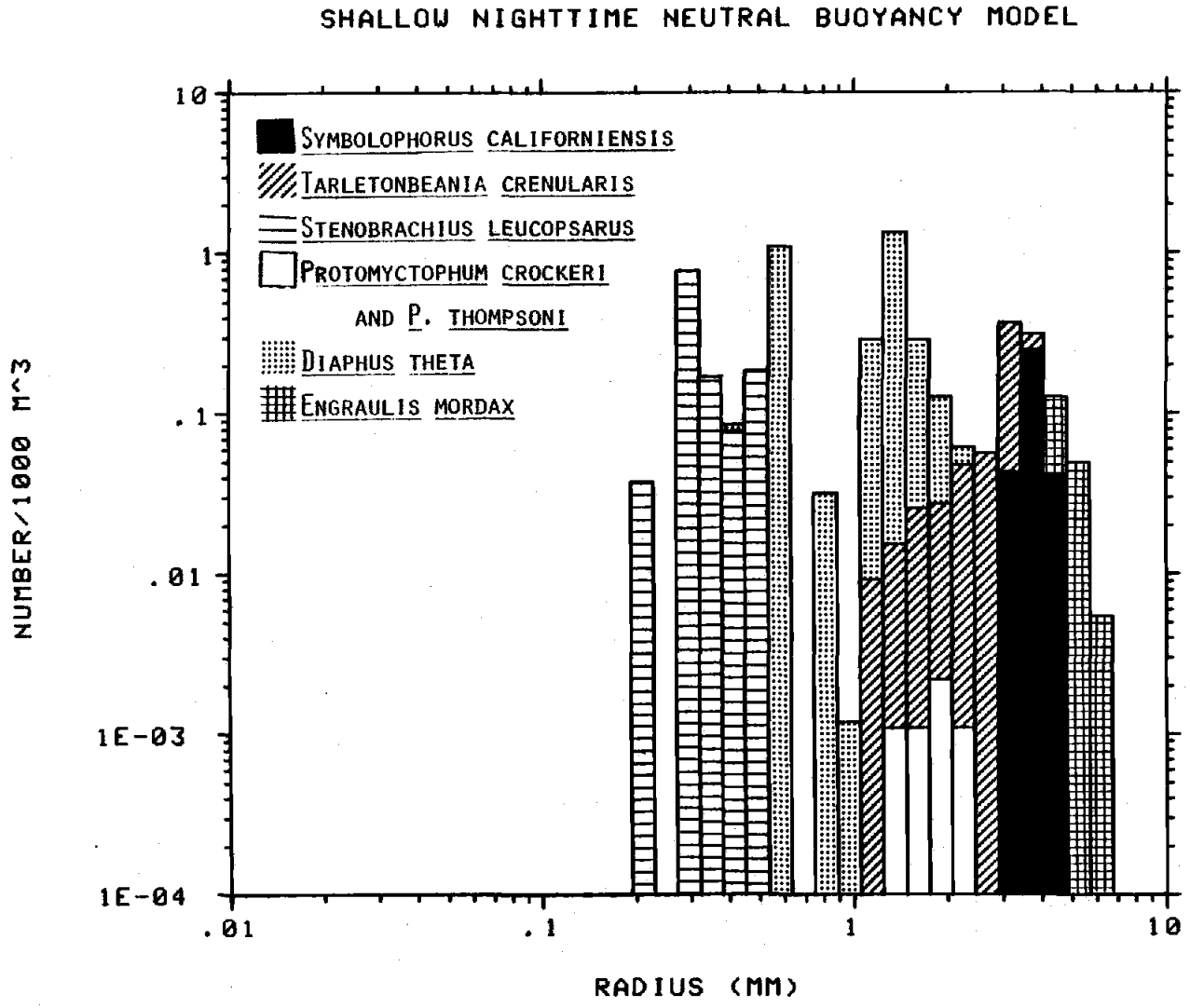
SHALLOW NIGHTTIME NEUTRAL BUOYANCY MODEL
SYMBOLOPHORUS CALIFORNIENSIS
TARLETONBEANIA CRENULARIS
STENOBRACHIUS LEUCOPSARUS
PROTOMYCTOPHUM CROCKERI
AND P. THOMPSONI
DIAPHUS THETA
ENGRAULIS MORDAX
NUMBER/1000 M^3
10
1
.1
.01
1E-03
1E-04
.01
.1
1
10
RADIUS (MM)

Figure 17.

Figure 18. Mean abundance of swimbladder radii in deep daytime net collections as determined by the model (N=10). Swimbladder radii were estimated using fractions of the neutral buoyancy model. α = .35 for Tarletonbeania crenularis and 0.9 for all other species.

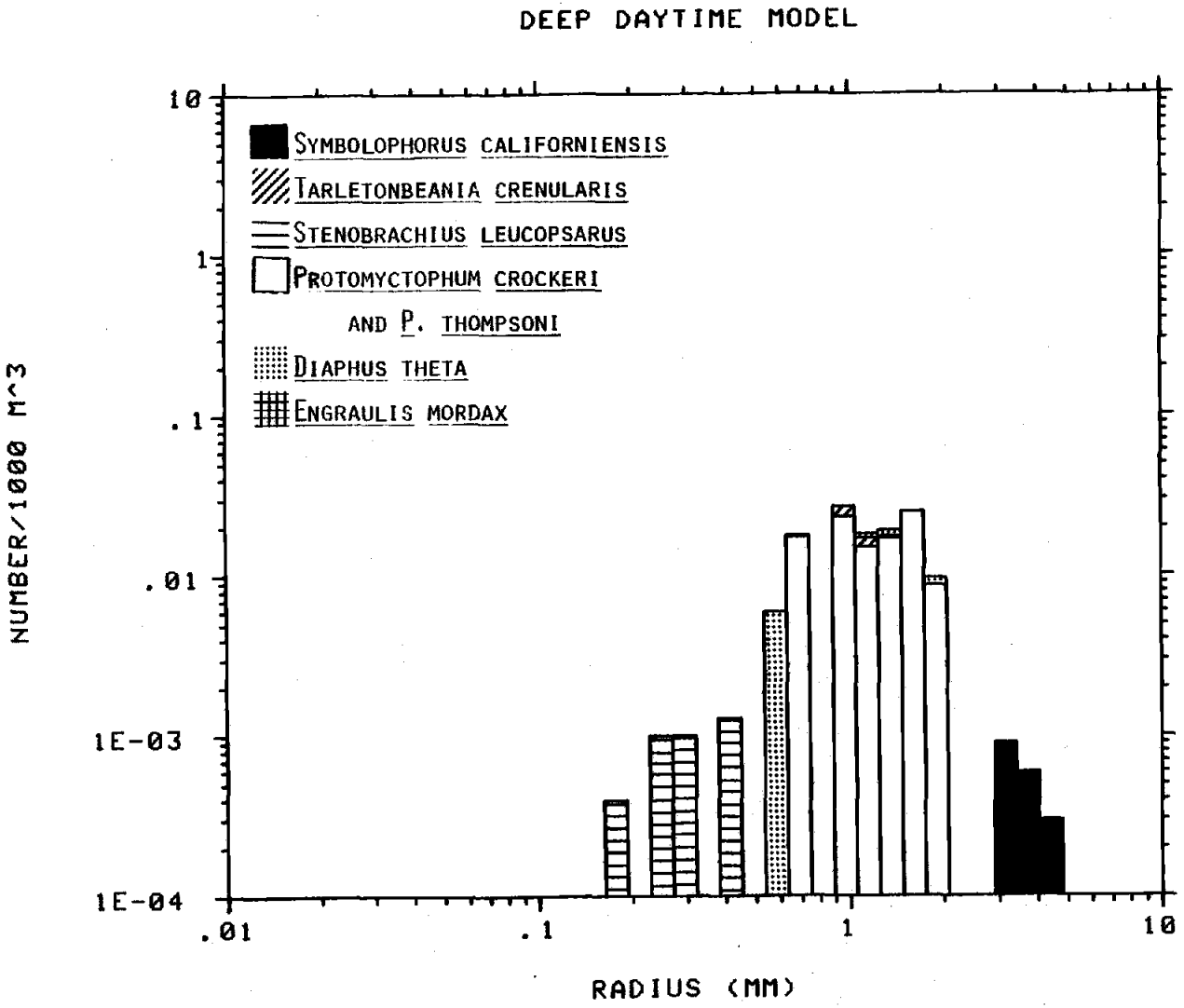
DEEP DAYTIME MODEL
SYMBOLOPHORUS CALIFORNIENSIS
TARLETONBEANIA CRENULARIS
STENOBRACHIUS LEUCOPSARUS
PROTOMYCTOPHUM CROCKERI
AND P. THOMPSONI
DIAPHUS THETA
ENGRAULIS MORDAX
NUMBER/1000 M^3
10
1
.1
.01
1E-03
1E-04
.01
.1
1
10
RADIUS (MM)

Figure 18.

Figure 19. Mean abundance of swimbladder radii in deep nighttime net collections as determined by the model (N=6). Swimbladder radii were estimated using fractions of the neutral buoyancy model. α = .35 for Tarletonbeania crenularis and 0.9 for all other species.

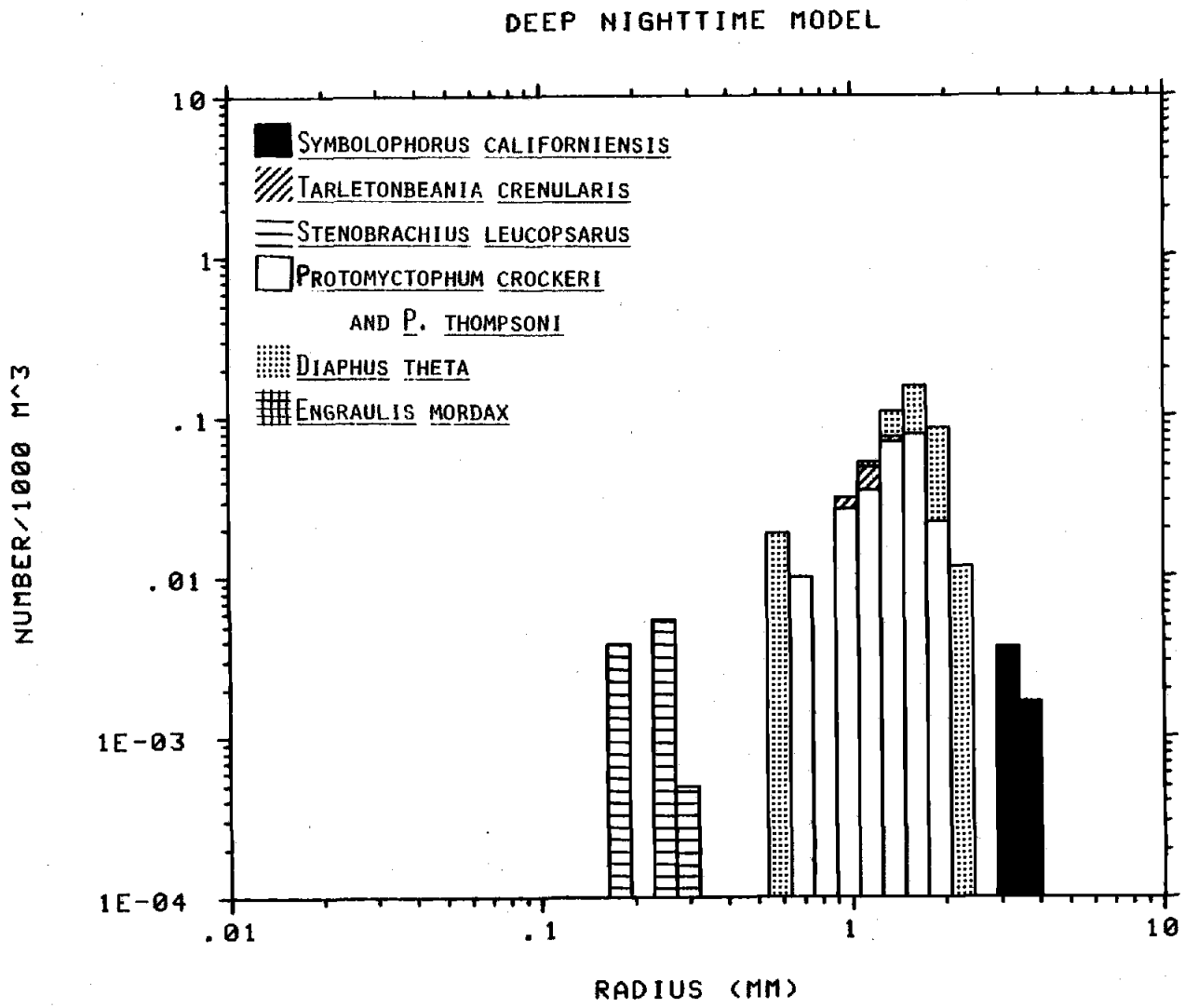
DEEP NIGHTTIME MODEL
SYMBOLOPHORUS CALIFORNIENSIS
TARLETONBEANIA CRENULARIS
STENOBRACHIUS LEUCOPSARUS
PROTOMYCTOPHUM CROCKERI
AND P. THOMPSONI
DIAPHUS THETA
ENGRAULIS MORDAX
NUMBER/1000 M^3
10
1
.1
.01
1E-03
1E-04
.01
.1
1
10
RADIUS (MM)

Figure 19.

Figure 20. Mean abundance of swimbladder radii in shallow nighttime net collections as determined by the model (N=9). Swimbladder radii were estimated using fractions of the neutral buoyancy model. $\alpha = 0.9$ for all species.

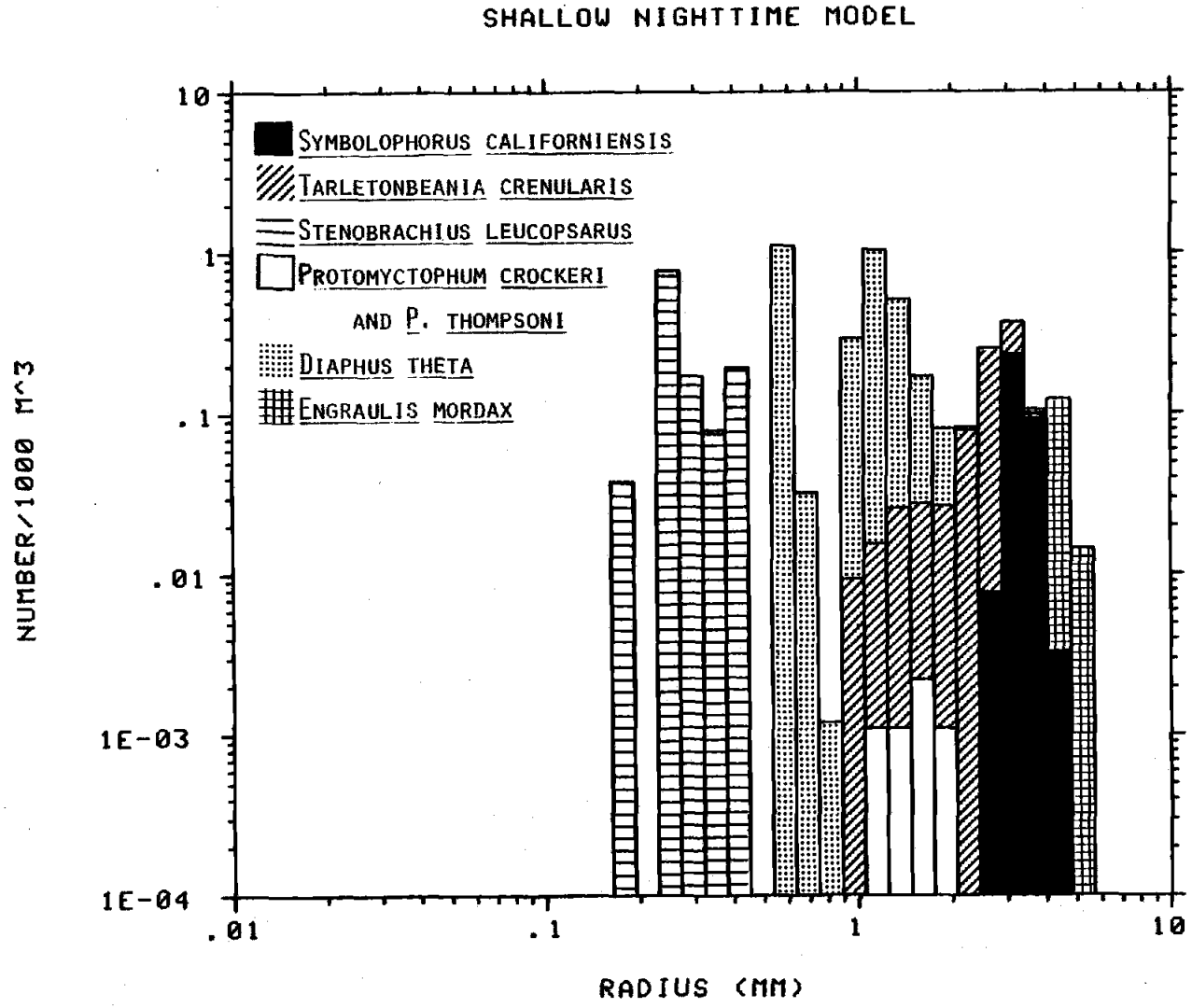
SHALLOW NIGHTTIME MODEL
SYMBOLOPHORUS CALIFORNIENSIS
TARLETONBEANIA CRENULARIS
STENOBRACHIUS LEUCOPSARUS
PROTOMYCTOPHUM CROCKERI
AND P. THOMPSONI
DIAPHUS THETA
ENGRAULIS MORDAX
NUMBER/1000 M^3
10
1
.1
.01
1E-03
1E-04
.01
.1
1
10
RADIUS (MM)

Figure 20.

REFERENCES

Alexander, R. 1971. Swimbladder gas secretions and energy expenditure in vertically migrating fishes. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Dept. of the Navy, Maury Center for Ocean Science, Washington, D.C., pp.74-81.

Alexander, R. 1972. The energetics of vertical migration by fishes. In: M.A. Sleigh and A.G. MacDonald, ed., The effects of pressure on organisms. Academic Press, N.Y.,pp.273-294.

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

Andreeva, I.B. 1964. Scattering of sound by air bladders of fish in deep sound-scattering layers. Akusts. Zh., 10:20-24(English translation in: Soviet Physics-Acoustics, 10: 17-20).

Backus, R.H., J.E. Craddock, R.L. Haedrich, D.L. Shores, J.M. Teal, A.S. Wing, G.W. Mead, and W.D. Clarke. 1968. Ceratoscopelus madarensis : Peculiar sound-scattering layer identified with this myctophid fish. Science, 160(3831): 991-993.

Badcock, J. and N.R. Merrett. 1976. Midwater fishes in the eastern North Atlantic. I. Vertical distribution and associated biology in 30 N, 23 W, with developmental notes on certain myctophids. Progress in Ocean. 7:3-58.

Baird, R.C. and D.F. Wilson. 1977. Sound scattering and oceanic midwater fishes. In: N.R. Andersen and B.J. Zahuranec, eds., Oceanic sound scattering prediction. Plenum Press, N.Y., pp.549-563.

Baker, A. De C., M.R. Clarke and M.J. Harris. 1973. The N.I.O. combination net (RMT1 + 8) and further developments of rectangular midwater trawls. J. Mar. Biol. Assoc. U.K. 53: 167-184.

Barham, E.G. 1963. Siphonophores and the deep scattering layer. Science 140(3568): 826-828.

Barham, E.G. 1966. Deep scattering layer migration and composition: Observations from a diving saucer. Science 151(3716): 1399-1403.

Barham, E.G. 1971. Deep-sea fishes: Lethargy and vertical orientation. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Washington, D.C., pp.100-116.

Batzler, W.E., W.A. Friedl and J.W. Reese. 1973. Can acoustic volume scattering be predicted from net haul data? J. Acoust. Soc. Amer. 54(1): 290.

Batzler, W.E. and G.V. Pickwell. 1971. Resonant acoustic scattering from gas-bladder fishes. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Washington, D.C., pp.168-178.

Batzler, W.E., J.W. Reese and W.A. Friedl. 1975. Acoustic volume scattering: its dependence on frequency and biological scatterers. Naval Undersea Center TP 442. 25p.

Bone, Q. 1973. A note on the buoyancy of some lantern-fishes (Myctophoidei). J. mar. biol. Ass. U.K. 53: 619-633.

Bradbury, M.G., D.P. Abbott, R.V. Bovbjerg, R.N. Mariscal, W.C. Fielding, R.T. Barber, V.B. Pearse, S.J. Proctor, J.C. Ogden, J.P. Wourms, L.R. Taylor, Jr., J.G. Christofferson, J.P. Christoferson, R.M. McPhearson, M.J. Wynne and P.M. Stromborg, Jr. 1971. Studies of the fauna associated with the deep scattering layers in the equatorial Indian Ocean, conducted on R/V Te Vega during October and November 1964. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Washington, D.C., pp.409-452.

Brooks, A.L. 1976. Swimbladder allometry of selected midwater fish species. NUSC Technical Report 4983: 44 p.

Brooks, A.L. 1977. A study of the swimbladders of selected mesopelagic fish species. In: N.R. Andersen and B.J. Zahuranec, eds. Oceanic Sound Scattering Prediction. Plenum Press, N.Y., pp.565-590.

Butler, J.L. and W.G. Pearcy. 1972. Swimbladder morphology and specific gravity of myctophids off Oregon. J. Fish. Res. Board Can. 29: 1145-1150.

Capen, R.L. 1967. Swimbladder morphology of some mesopelagic fishes in relation to sound scattering. U.S. Navy Electronics Lab. Res. Rept., 29 p.

Chapman, R.P., O.Z. Bluy, R.H. Adlington, and A.E. Robinson. 1974. Deep scattering layer spectra in the Atlantic and Pacific oceans and adjacent seas. J. Acoust. Soc. Amer. 56(6): 1722-1734.

Clarke, T.A. 1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull. 71: 404-434.

Clay, C.S. and H. Medwin. 1977. Acoustical Oceanography: Principles and Applications. John Wiley and Sons, New York. 544 p.

Ebeling, A.W., G.M. Cailliet, R.M. Ibara, F.A. DeWitt, Jr. and D.W. Brown. 1971. Pelagic communities and sound scattering off Santa Barbara, California. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Washington, D.C., pp.1-19.

Farquhar, G.B. and D.V. Holliday. 1977. Recommendations of the working group on bioacoustics. In: N.R. Andersen and B.J. Zahuranec, eds. Oceanic Sound Scattering Prediction. Plenum Press, N.Y., pp.483-491.

Foxton, P. 1963. An automatic opening-closing device for large plankton nets and midwater trawls. J. mar. biol. Ass. U.K. 43: 295-308.

Friedl, W.A., G.V. Pickwell and R.J. Vent. 1977. The MINOX program: An example of a multidisciplinary oceanic investigation. In: N.R. Andersen and B.J. Zahuranec, eds. Oceanic Sound Scattering Prediction. Plenum Press, N.Y., pp.591-618.

Greenlaw, C.F. 1977. Backscattering spectra of preserved zooplankton. J. Acoust. Soc. Am. 62: 44-52.

Greenlaw, C.F. 1979 Acoustical estimation of zooplankton populations. Limnol. Oceangr. 24(2): 226-242.

Greenlaw, C.F. and R.K. Johnson. 1983. Multiple-frequency acoustical estimation. Biol. Oceanog. 2(2-3-4): 227-252.

Hall, M. 1981. Measurements of acoustic volume backscattering in the Indian and Southern Oceans. Aust. J. Mar. Freshwater Res. 32: 855-876.

Hersey, J.B. and R.H. Backus. 1954. New evidence that migrating gas bubbles, probably the swimbladders of fish, are largely responsible for scattering layers on the continental rise south of New England. Deep-Sea Res. 1: 190-191.

Hersey, J.B. and R.H. Backus. 1962. Sound scattering by marine organisms. In: M.N. Hill, ed. The Sea: Ideas and Observations on Progress in the Study of the Seas. Volume 1. Interscience, N.Y., pp.398-439.

Hersey, J.B., R.H. Backus and J. Hellwig. 1962. Sound scattering spectra of deep scattering layers in the western North Atlantic Ocean. Deep-Sea Res. 8(3):196-210.

Hersey, J.B., H.R. Johnson and L.C. Davis. 1952. Recent findings about the deep scattering layer. J. Mar. Res. 11: 1-9.

Holliday, D.V. 1972. Resonance structure in echoes from schooled pelagic fish. J. Acoust. Soc. Am. 51(4):1322-1332.

Holliday, D.V. 1976. Technical report on exploratory development in the application of swimbladder resonance techniques to marine surveys. Tracor doc. T-76-SD-1101-0, San Diego, California.

Holliday, D.V. 1977. Extracting bio-physical information from the acoustic signatures of marine organisms. In: N.R. Andersen and B.J. Zahuranec, eds. Oceanic Sound Scattering Prediction. Plenum Press, N.Y., pp.619-624.

Holliday, D.V. 1978. MORDAX II/III/IV. Tracor doc. T-78-SD-002/3/4-U, San Diego, California. 2260 p.

Holliday, D.V. 1980. Use of acoustic frequency diversity for marine biological measurements. In: F.P. Diemer, F.J. Vernberg and D.Z. Mirkes, eds. Advanced Concepts in Ocean Measurements for Marine Biology. University of South Carolina Press, Columbia, S.C., pp.423-460.

Johnson, R.K. 1977a. Sound scattering from a fluid sphere revisited. J. Acoust. Soc. Am. 61: 375-377.

Johnson, R.K. 1977b. Acoustic estimation of scattering-layer composition. J. Acoust. Soc. Am. 61: 1636-1639.

Johnson, R.K. 1979. Gas bubble sizes for selected myctophids. School of Oceanography, Oregon State Univ., Ref. 79-6. 18p.

Kanwisher, J. and A. Ebeling. 1957. Composition of the swimbladder gas in bathypelagic fishes. Deep-Sea Res. 4: 211-217.

Kleckner, R.C. and R.H. Gibbs, Jr. 1972. Swimbladder structure of Mediterranean midwater fishes and a method of comparing swimbladder data with profiles. In: Mediterranean Biological Studies, Final Report, Vol. 1. Smithsonian Institution, Washington, D.C., pp.230-281.

Lawson, C.L. and R.J. Hanson. 1974. Solving Least Squares Problems. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Lebedeva, L.P. 1972. Sound scattering by fish. J. Ichthyol. 12: 144-149.

Love, R.H. 1975. Predictions of volume scattering strength from biological trawl data. J. Acoust. Soc. Am. 57(2): 300-306.

Love, R.H. 1977. Progress in the correlation of volume scattering strengths to biological data. In: N.R. Andersen and B.J. Zahuranec, eds. Oceanic Scattering Prediction. Plenum Press, N.Y., pp.631-646.

Love, R.H. 1978. Resonant acoustic scattering by swimbladder-bearing fish. J. Acoust. Soc. Am. 64: 571-580.

Magnuson, J.J. 1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. Fish. Bull. 71(2): 337-356.

Magnuson, J.J. 1978. Locomotion by scombrid fishes: hydromechanics, morphology, and behavior. In: W.S. Hoar and D.J. Randall, eds. Fish Physiology, Vol. 7. Academic Press, N.Y., pp.239-313.

Marshall, J.R. and R.P. Chapman. 1964. Reverberation from a deep scattering layer measured with explosive sound sources. J. Acoust. Soc. Am. 36:164-167.

Marshall, N.B. 1951. Bathypelagic fishes as sound scatterers in the ocean. J. Mar. Res. 10(1):1-17.

Marshall, N.B. 1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Discovery Reports 31:1-222.

Marshall, N.B. 1971. Swimbladder development and the life of deep-sea fishes. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Washington, D.C., pp.69-73.

Marshall, N.B. 1972. Swimbladder organization and depth ranges of deep sea teleosts. In: Society for Experimental Biology Symposium, vol. 26, pp.261-272.

McCartney, B.S. and A.R. Stubbs. 1971. Measurements of the target strength of fish in dorsal aspect, including swimbladder resonance. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Washington, D.C., pp.180-210.

Neighbors, M.A. 1980. Buoyancy in the oceanic midwaters: A comparative study of swimbladders and lipids in lanternfish (family Myctophidae). Ph.D. thesis, University of Southern California, 214pp.

Neighbors, M.A. and B.G. Nafpaktitis. 1982. Lipid compositions, water contents, swimbladder morphologies and buoyancies of nineteen species of midwater fishes (18 myctophids and 1 neoscopelid). Mar. Biol. 66: 207-215.

Nevenzel, J.C., W. Rodegker, J.S. Robinson and M. Kayama. 1969. The lipids of some lanternfishes (family Myctophidae). Comp. Biochem. Physiol. 3: 25-36.

Pearcy, W.G. 1964. Some distributional features of mesopelagic fishes off Oregon. J. Mar. Res. 22: 83-102.

Pearcy, W.G. 1975. Workshop on problems of assessing populations of nekton. Off. Nav. Res. Rep. ACR 211, pp.30.

Pearcy, W.G. 1977. Variations in abundance of sound scattering animals off Oregon. In: N.R. Andersen and B.J. Zahuranec, eds. Oceanic Sound Scattering Prediction. Plenum Press, N.Y., pp.647-666.

Pearcy, W.G., E.E. Krygier, R. Mesecar, and F. Ramsey. 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24: 223-245.

Pearcy, W.G. and R.M. Laurs. 1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13: 153-165.

Pearcy, W.G., H.V. Lorz and W. Peterson. 1979. Comparison of the feeding habits of migratory and non-migratory Stenobrachius leucopsarus (Myctophidae). Mar. Biol. 51: 1-8.

Pearcy, W.G. and R.S. Mesecar. 1971. Scattering layers and vertical distribution of oceanic animals off Oregon. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Washington, D.C., pp.381-394.

Pickwell, G.V., E.G. Barham and J.W. Wilton. 1964. Carbon monoxide production by a bathypelagic siphonophore. Science 144: 860-862.

Pickwell, G.V., R.J. Vent, E.G. Barham, W.E. Batzler and I.E. Davies. 1971. Biological acoustic scattering off southern California, Baja California and Guadalupe Island. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean, Maury Center for Ocean Science, Washington, D.C., pp.490-507.

Pieper, R.E. 1979. Euphausiid distribution and biomass determined acoustically at 102 kHz. Deep-Sea Res. 26A: 687-702.

Pieper, R.E. and B.G. Bargo. 1980. Acoustic measurements of a migrating layer of the Mexican lampfish, Triphoturus mexicanus , at 102 kilohertz. Fish. Bull. 77(4): 935-942.

Sameoto, D.D. 1982. Zooplankton and micronekton abundance in acoustic scattering layers on the Nova Scotian slope. Can. J. Fish. Aquat. Sci. 39: 760-777.

Sameoto, D.D., L.O. Jaroszynski and W.B. Fraser. 1980. BIONESS, a new design in multiple net zooplankton samplers. Can. J. Fish. Aquat. Sci. 37: 722-724.

Vent, R.J. 1972. Acoustic volume-scattering measurements at 3.5, 5.0, and 12.0 kHz. in the eastern Pacific Ocean: diurnal and seasonal variations: J. Acoust. Soc. Am. 52: 373-382.

Vent, R.J. and G.V. Pickwell. 1977. Acoustic volume scattering measurements with related biological and chemical observations in the northeastern tropical Pacific. In: N.R. Andersen and B.J. Zahuranec, eds. Oceanic Sound Scattering Prediction. Plenum Press, N.Y., pp.697-716.

Weston, D.E. 1967. Sound propagation in the presence of bladder fish. In: V.M. Albers, ed. Underwater acoustics, Vol. 2. Plenum Press, N.Y., pp.55-88.

Willis, J.M. and W.G. Pearcy. 1980. Spatial and temporal variations in the population size structure of three lanternfishes(Myctophidae) off Oregon, USA. Mar. Biol. 57: 181-191.

Zahuranec, B.J. and W.L. Pugh. 1971. Biological results from scattering layer investigations in the Norwegian Sea. In: G.B. Farquhar, ed. Proceedings of an International Symposium on Biological Sound Scattering in the Ocean. Maury Center for Ocean Science, Washington, D.C., pp.360-378.