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Diaphus taaningi Norman, the Principal
Component of a Shallow Sound-Scattering
Layer in the Cariaco Trench, Venezuela¹

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ABSTRACT

A myctophid fish, *Diaphus taaningi* Norman, is the principal component of a distinct daytime sound-scattering layer lying near 250 m, well above the anoxic, hydrogen-sulfide zone of the Cariaco Trench. The scattering layer produced strong sonar echoes at 12, 25, and 50 kHz; mean sound-scattering strength at layer depth at 25 kHz was approximately -73 dB and at 50 kHz was approximately -67 dB. *D. Taaningi* adults have a well-developed swim bladder with a mean volume of about 12 mm³. This species seems to have a restricted breeding season, and evidence suggests a one-year life cycle. Fecundity was estimated at about 1000, and egg diameters ranged from 0.5 to 0.8 mm. Acoustic evidence indicates a generally homogeneous spacing of individuals in a thin layer (approximately 30 m) over a considerable area of the Trench. Although the population was estimated at only 1.93 fish/1000 m³, total population size is large over the area studied. Volume-reverberation data from the scattering layer was used to compare estimates of fish abundance with the actual catch. The agreement between predicted and observed fish abundance in the scattering layer based on measurements at 25 kHz is considered quite close considering the formidable methodological problems involved.

INTRODUCTION. A recent study of sound-scattering layers in the Cariaco Trench, Venezuela, revealed the presence during the daylight hours of a rel-

1. Received: 8 October 1973; revised: 4 March 1974.

atively thin, distinct layer at a depth of approximately 250 m (see Wilson, 1972, Fig. 1). During morning descent, this shallow scattering layer (SSL) separated from a thicker layer that was later found (Baird, *et al.*, 1973) to consist of *Bregmaceros nectabanus* Whitley. The latter continued to migrate deep into the anoxic, hydrogen-sulfide zone before returning late in the day. The sequence of events, as determined from acoustic records, is presented elsewhere (Wilson, 1972).

While biological studies of the Cariaco Trench are few, they indicate the presence of a depauperate mesopelagic fish fauna (Mead, 1963; Pugh, 1972).

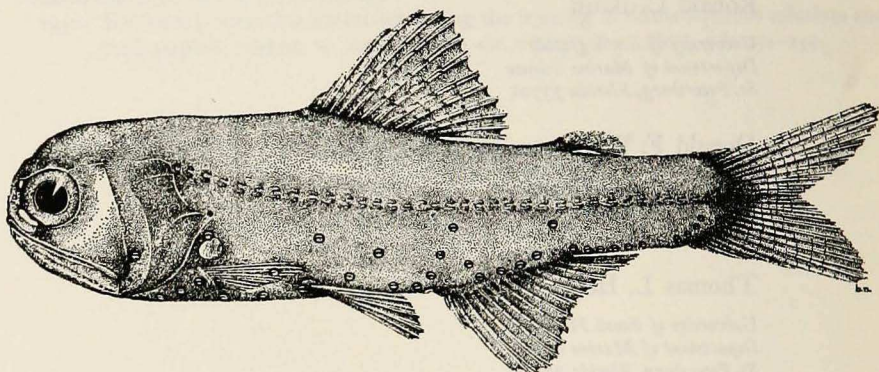


Figure 1. *Diaphus taaningi* Norman. Adult female, 58.0 mm (after Nafpaktitis, 1968).

Anoxic water below about 400 m (e.g., Richards and Vaccaro, 1956) and the presence of free H_2S below about 375 m (Betzer, 1971) or 325 m (Wilson, 1972) appear to place severe limitations on faunal diversity. Identification of scattering-layer organisms and ecological factors influencing their vertical distribution should therefore be easier than in open-ocean environments. This paper presents evidence that *Diaphus taaningi* Norman (Fig. 1) is the principal component of the well-defined 250-m SSL in the Cariaco Trench. In addition, data are presented on vertical distribution, size distribution, population density, and reproduction of this species.

MATERIALS AND METHODS. In March 1972, a single station ($10^{\circ}38'N$; $65^{\circ}45'W$) was occupied for several days by USNS MIZAR (T-AGOR-11). Special equipment and procedures for acoustic observations were as previously reported (Wilson, 1972), except that an additional acoustic profiler, operating at 50 kHz, was employed and also a Sanborn Series 4500 optical oscillograph was used to provide better indications of scattering-layer depths than could be obtained from photographs of an oscilloscope display. The 50 kHz transducer was an EDO Model 311 having a beam width of 16° at the halfpower point.

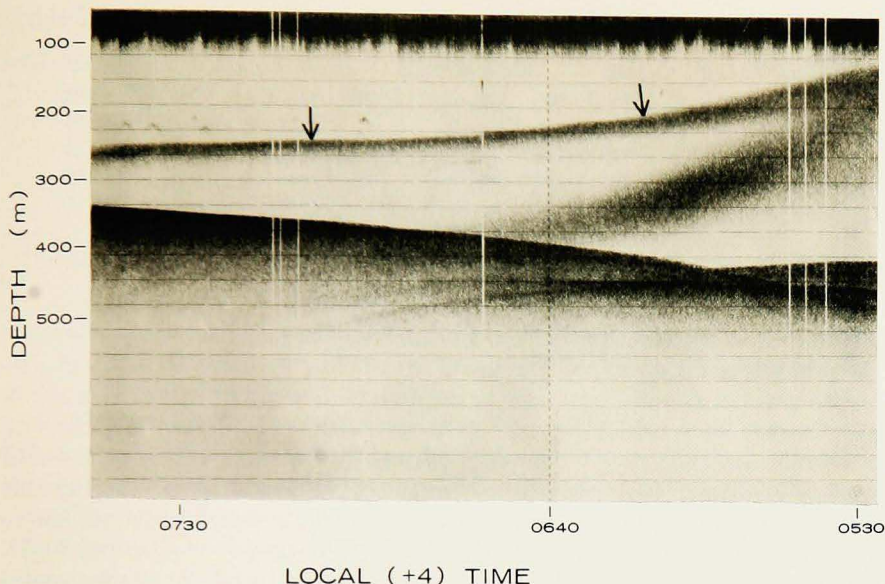


Figure 2. Photograph of 12 kHz PDR record of scattering layer (arrows) on March 10, 1972. Layer recorded at approximately 320 m is an artifact resulting from a second return from the bottom.

Repeated observations confirmed that the timing and the volume-reverberation patterns of migration reported previously (Wilson, 1972) were unchanged (Fig. 2).

Modified 6' Tucker Trawls (Hopkins, *et al.*, 1973) with messenger-actuated opening and closing mechanisms were used for biological sampling at discrete depths. Multiconductor hydro-wire was used for all trawling operations, and power was fed down to a Teledyne Taber Model 200 pressure transducer attached to the net so that depth could be monitored continuously on deck. Depth was also recorded with a Benthos Time-Depth Recorder attached below the release apparatus.

Three daytime discrete-depth samples in the vicinity of the SSL were taken together with three shallower hauls at night (Table I). Trawl No. 90 sampled well below the SSL at the depth where H_2S began to appear in water samples. Trawl No. 95 sampled primarily above the SSL, although 20 minutes were spent obliquely traversing the SSL region. Trawl No. 93 sampled the SSL proper. During the latter haul, depth was continuously adjusted so that the trawl remained in the SSL as defined by concurrent acoustic data.

Specimens from trawls were preserved in 10% formalin and later transferred to 40% isopropyl alcohol. The fish were measured to the nearest mm standard length (SL), and catches from all trawls were combined for length-frequency

Table I. Closing Tucker trawls, 8-11 March 1972 in the Cariaco Trench, Venezuela.

Trawl No.	Time	Depth (m)	No. <i>D. taaningi</i> collected
89.....	1610-1823	450-500	0
90.....	0915-1027	230-380	0
91.....	1214-1312	840-850	0
92.....	1747-1848	450	0
93.....	1542-1800	220-270	60
94.....	0230-0421	10-105	1
95.....	0841-1143	150-300	4
96.....	2015-2138	140-200	0
97.....	2227-2324	10-50	9

analysis. A random subsample of 24 individuals from two depth zones was removed, and these fish were dissected, sexed, and the females classified as to stage of gonad maturity. A single ovary was removed from one individual and all eggs greater than 0.5 mm were counted. All ovaries examined contained large, uniformly distributed, opaque yellowish eggs. Small eggs (about 0.1 mm) were often seen but were not included in the counts. No intermediate egg sizes were noted. Diameters of 30 large eggs were measured and recorded. Swim bladder measurements were made on five individuals according to the procedures outlined by Kleckner and Gibbs (1972).

RESULTS. From Precision Depth Recorder (PDR) traces made with the ship's 12 kHz sonar, the SSL by day is seen (Fig. 2) as a thin, homogeneous layer (see Wilson, 1972, Fig. 1, which is identical). Measurements with the acoustic profilers at 25 and 50 kHz also showed a relatively thin layer whose depth varied between 250 and 270 m. The SSL as seen at 25 and 50 kHz often separated into two sublayers lying at depths averaging 260 and 280 m. Separation of the layers was never seen at 12 kHz, although discrete echoes occasionally were seen above 250 m. On the basis of a few measurements made at 50 kHz with 1-msec pulses and the narrow-beam transducer, the single (combined) layer is estimated to have been about 30 m thick. When the SSL was separated into two sublayers, the layer thicknesses were approximately 25 m and 30 m for the shallower and deeper components, respectively.

Sound-scattering strength, M'_v , read on the calibrated A-scan display of the acoustic profilers, is defined as the ratio, in decibels, of the scattered intensity, I_s , at unit distance (1 m) from a unit volume (1 m³), to the incident intensity, I_0 ; thus $M'_v = 10 \log I_s/I_0$. It is related to the back-scattering coefficient, m_v , by the expression $10 \log m_v = M'_v + 10 \log 4\pi = M'_v + 11$ dB. The mean sound-scattering strengths of the SSL reported here were obtained, in the case of the separated sublayers, by measuring the peak M'_v from 15 successive pulses recorded on magnetic tape, calculating each corresponding I_s , determining the

Table II. Dimensions and volume estimates of *Diaphus taaningi* swim bladders.

Standard length	Bladder length	Bladder depth	Sex	Bladder volume**
37 mm	5.8 mm	1.7 mm	M	8.8 mm ³
43 mm*	7.0 mm	1.8 mm	F	11.9 mm ³
42 mm	7.9 mm	1.7 mm	M	11.9 mm ³
40 mm	6.8 mm	1.6 mm	M	9.1 mm ³
42 mm	7.0 mm	2.2 mm	F	17.8 mm ³

* bladder partially collapsed.

** oblate spheroid, $V = 4/3 \pi a b^2$ (Kleckner and Gibbs, 1972).

arithmetic mean of the 15 values of I_s , and converting the result back to mean M'_v in dB. The mean M'_v of the shallower and deeper components obtained in this way were -73 dB and -71 dB at 25 kHz and -67 dB and -64 dB at 50 kHz, respectively. The mean scattering strengths of the single (combined) SSL were obtained from only three (25 kHz) and five (50 kHz) oscilloscope photographic records made during Trawl 93, inasmuch as the calibration data on the tape record made during the trawl were found to be faulty. The mean M'_v from the photo records were -66 dB and -64 dB at 25 and 50 kHz, respectively.

Catch results (Table 1) strongly suggest that *Diaphus taaningi* is the principal component of the SSL. A second species, *Steindachneria argentea* Goode and Bean, was present in small numbers. Other than these, only a few juvenile *Bregmaceros nectabanus* were taken. The usual larger oceanic invertebrates, such as pelagic shrimp were absent, although smaller plankters were present in substantial numbers. The nature of the stratification pattern in the water column is indicated by the sparse fish catch in the two other trawls (Nos. 90 and 95), which sampled primarily above and below the SSL. While additional sampling is clearly needed to better delimit the distribution of both *D. taaningi* and *S. argentea* (acoustic data showed that the SSL was not separated into two component layers at the time Trawl 93 was made), acoustic and trawling evidence indicates that *D. taaningi* occupies a restricted depth range during the day corresponding to the SSL. Catches of *D. taaningi* in the upper 50 m at night indicate a diurnal migratory pattern for the species, which is supported by the acoustic evidence.

Diaphus taaningi has a large, well-developed swim bladder and gas gland (the same is true for the less common *S. argentea*, although most of the latter were smaller individuals with smaller swim bladders than *D. taaningi*). Table II summarizes data from the measurements of *D. taaningi* swim bladders and the calculated volumes. The volumes are similar to those determined for some other *Diaphus* species of similar size (Kleckner and Gibbs, 1972). No large fat deposits, gross indication of tissue investment, or atrophy of bladders were observed.

Figure 3 presents the size-frequency distribution of individuals in the pop-

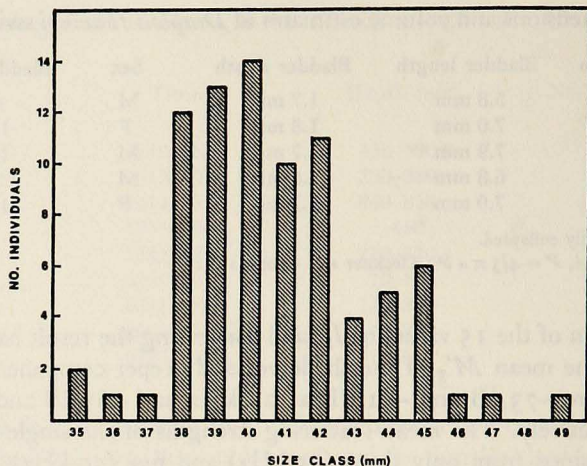


Figure 3. Size distribution (Standard lengths) of *Diaphus taaningi* collected in the Cariaco Trench ($N = 82$; $\bar{x} = 40.7$ mm; $Sd = 2.66$ mm; g (coefficient of skewness) = 0.51769 ; $t = 1.948$ ($0.10 > p > 0.05$).

ulation from all trawls combined (day and night). The distribution is statistically symmetrical and unimodal, although there is a suggestion of a second mode (43–45 mm). No juveniles or post-larvae were taken in any trawl, though these size classes were numerous for the two other midwater and several epipelagic species. Ten females and 14 males were dissected. All females were macroscopically judged to be in late stages of maturation with the smallest gravid female measuring 36 mm SL. Their ovaries were filled with large eggs corresponding to Stage IIIc of gonad maturity described by Smoker and Pearcy (1970). A set of nine individuals from a trawl sample taken at night from a depth of 10–50 m contained five females, all in gravid condition. Egg diameters ranged from 0.5 to 0.8 mm with the majority between 0.6 and 0.7 mm. The single ovary (from a 43-mm female) examined was found to contain 532 large eggs; since the ovaries were all of similar size, a fecundity of about 1000 is estimated. The male testes were lobate and whitish in color and appeared mature.

DISCUSSION. Evidence strongly indicates that the observed population of *D. taaningi* is resident in the Cariaco Trench and the thinness of the SSL may partially explain the absence of this species in other Cariaco Trench trawl samples taken during the daytime (Mead, 1963; Pugh, 1972). This evidence can be summarized as follows: 1) The station occupied is well removed from the sill (35 mi); 2) the population is large as indicated by the SSL which is continuous for at least 10 km (see below); 3) a pronounced diurnal migratory pattern is observed with daytime depths lying well above the $O_2 - H_2S$ interfaces

(albeit in oxygen deficient water with concentrations about 0.35 ml/l); 4) gravid females were common; 5) no evidence of gonadal atrophy (evidence for expatriation, O'Day and Nafpaktitis, 1967) was apparent; and 6) subsequent trawls by us in the adjacent Caribbean were negative for this species. Our results confirm the morphological distinctness (gill rakers; Ao photophores) of the Cariaco population (Pugh, 1973) from the only other known *D. taaningi* populations; the latter are found in the northern Gulf of Mexico and off West Africa (Nafpaktitis, 1968). This distribution pattern suggests that *D. taaningi* is limited to neritic mesopelagic environments.

It appears from the size distribution (Fig. 3) that a single age class is represented, although a few members of a second year class (greater than 43 mm) may also occur. The small size of *D. taaningi* at first maturity (36–40 mm) is further indication of a short life span, as is the maximum size observed (only 50 mm) for this species in the Trench (Pugh, 1973). According to Pugh, small juveniles were present in January. Apparently they were absent at the time of our cruise (in March) or perhaps were present in such low abundance that they were not sampled. All of the females examined were gravid. Thus it appears that the Cariaco population of *D. taaningi* has a restricted breeding season with a life span of about one year (with perhaps a few members surviving to the second year). Life history data presented by Gibbs *et al.* (1971) for *Diaphus mollis* from Bermuda waters indicate a similar pattern and also suggest a one year life cycle.

Data on age and growth in tropical myctophid fishes is not available. However, two sub-arctic species, *Stenobrachius leucopsarus* (Smoker and Percy, 1970) and *Benthoema glaciale* (Halliday, 1970) reach a mean size of about 32 mm after one year. Odate (1966) estimates that *Myctophum affine* from northeastern Japan attains a length of about 36 mm after a year. These data from non-tropical areas thus do not conflict with an estimate of 38–43 mm SL attained by *D. taaningi* after one year in the tropical waters of the Cariaco Trench. Additional sampling at other seasons in conjunction with another method of age determination (e.g., otoliths) are required to fully confirm these initial estimates, however.

There are several ecological characteristics of *D. taaningi* which illustrate the diversity of adaptive strategies in the genus *Diaphus*. Reproductive maturity in *D. taaningi* is reached at an early age and individuals appear to live for about one year. For many other species in the genus individuals mature at larger sizes and/or give indications of a life span covering several breeding seasons (see Nafpaktitis, 1968; Gibbs *et al.*, 1971). The adult *D. taaningi* population in the Cariaco Trench ascends to the upper 50 m at night in contrast to other diaphids in which adults, especially gravid females, do not migrate near the surface or appear to migrate very little (Nafpaktitis, 1968; Taylor, 1968). In addition the daytime depth is notably shallower than for most other species of *Diaphus* for which data are available (Table III). The productive surface waters of the

Table III. Daytime vertical distribution of various species of the genus *Diaphus*.

Species	Range	Maximum Concentration
<i>D. pacificus</i> ¹	300-400 m	300-400 m
<i>D. rafinesquei</i> ^{2,3}	450-700 m	500-700 m
<i>D. splendidus</i> ⁴	500-650 m	500-650 m
<i>D. effulgens</i> ⁴	500-700 m	500-700 m
<i>D. mollis</i> ⁴	300-600 m	500-600 m
<i>D. holti</i> ³	500-600 m	500-600 m
<i>D. theta</i> ⁵	230-365 m	320-365 m

1. Robison, 1972 (Gulf of California).

2. Badcock, 1970 (E. Atlantic, Canaries).

3. Goodyear, *et al.*, 1972 (Mediterranean).

4. Gibbs, *et al.*, 1971 (Ocean acre - Bermuda).

5. Taylor, 1968 (British Columbia).

trench may alter the photoenvironment to the extent that critical isolumes are more shallow (see Kampa, 1971) while the marked O_2 gradient and/or free H_2S may also exert an effect.

The resident midwater fish fauna in the Cariaco Trench appears to consist of only three species: *D. taaningi*, *S. argentea*, and *B. nectabanus*. The absence of other species perhaps results from an inability to adjust vertical migration patterns to avoid anoxic waters, as Mead (1963) suggests, and/or unfavorable "niche" space in waters above the anoxic interface.

Little information exists on the population structure or density of midwater fishes. However, by combining the acoustic data with that from trawl samples, one can make meaningful estimates of population size. To what extent fishes are able to avoid capture is difficult to estimate, although our specimens were well within the size range normally taken by midwater trawls (Harrison, 1967). Percy and Laurs (1966) estimate a net avoidance factor of about 12% for *D. theta* off Oregon using a 6' IKMT. Estimates of abundance from trawl samples are thus likely to be conservative. Flow meter data indicate that Trawl No. 93 (in the SSL) traversed 9600 m, and the net mouth was estimated to be 1.8 m on a side. This information in combination with catch data (60 fish; 23.1 fish per hour) gave a concentration of 1.93 fish per 1000 m³. The estimated density is in the same range as that found by Zahuranec, *et al.*, 1970, for other midwater species in the eastern Gulf and western Atlantic. Acoustic observations indicate a relatively homogeneous layer (no schools of high target strength) approximately 30 m thick. One Km² of surface area at 250 m, assuming homogeneity, should therefore contain 58,000 individuals for such a layer. Since the layer was observed continuously during the length of the tow (approximately 10 Km), it is estimated that the SSL under a disk of radius 5 Km contained approximately 4.5 million fish. Thus while *D. taaningi* individuals appear well dispersed in terms of density per 1000 m³ population size is considerable over the total area of Trench observed. This estimate is much less,

however, than the abundance of *Ceratospopelus maderensis*, a myctophid which appears in dense schools in certain areas and is associated with a peculiar sound-scattering pattern (Backus *et al.*, 1968). Their data indicate that under one Km² there were 180,000 to 2,700,000 fish (layer 3 schools deep; 25 schools/Km²; mean school dimensions of radius 25 m and 5–10 m thick).

The availability of volume-reverberation data from the SSL and its apparent near-monospecific composition provide an unusual opportunity to compare estimates of fish abundance from acoustic data with the actual catch. Unfortunately we do not have good records of the sound-scattering levels at the time of Trawl 93 (*vide supra*). Nevertheless we do have good data obtained at other times on the same station and enough information was obtained during the trawl to make a comparison attempt worthwhile. The resonant frequency (RF) of the swimbladders at depth (270 m), the acoustic scattering cross section (ASCS), and the number of scatterers per unit volume were calculated from the appropriate equations cited by Van Schuyler (1970). Comparison of the actual (all species) catch abundance (2.38 fish/1000 m³) with the fish concentration predicted from mean M'_v values obtained at the time of Trawl 93 (single layer) showed that at 25 kHz, the observed mean M'_v would have required 63 fish/1000 m³ and, at 50 kHz, 130 fish/1000 m³. On the basis of much better acoustic data taken from the magnetic tape records made when the layers were separated, at 25 kHz the shallower layer would have required 13 fish/1000 m³ and the deeper component would have required 20 fish/1000 m³, for a total of 31 fish/1000 m³. At 50 kHz, the required numbers of fish would have been 80/1000 m³ and 130/1000 m³ in the shallower and deeper layers, respectively.

A detailed discussion of the acoustic data will be treated in a subsequent paper. However, disregarding any significant net avoidance (*vide supra*), there are several factors that could be operating to make the acoustically predicted catch values greater than the actual catch. Based on the mean swimbladder dimensions obtained from only five selected *D. taaningi* (Table II), the calculated RF at 270 m is 14 kHz. However, it is not possible to determine the actual RF of the living fish at depth from our acoustic measurements, and physiological responses of swimbladders to gas metabolism may alter their size and/or shape and, consequently, their RF and ASCS. This may be particularly true here inasmuch as the SSL occurs in water of very low oxygen content. Furthermore, the RF calculations were based on *D. taaningi* only; the few *S. argentea* and juvenile *B. nectabanus* taken were, in general smaller. We know nothing about their distribution in the *D. taaningi*-dominated SSL, although their contribution appears to be small. Even so, the agreement between predicted and observed fish abundance in the SSL based on our best 25-kHz data appears good, considering the formidable methodological problems involved. It is possible that the poorer agreement with the mean M'_v at 25 kHz obtained during Trawl 93 is entirely the result of having so few acoustic measurements available.

The poor agreement at 50 kHz in both cases could be the result of the unmeasured contribution of nonresonant scattering by the substantial numbers of smaller zooplankters known to be in the layer and by the undetermined contribution to the ASCS of the fish bodies themselves as opposed to swimbladders alone (Cushing, 1973).

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