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BATHYPELAGIC FISHES AS SOUND SCATTERERS IN THE OCEAN

BY

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ABSTRACT

Investigations on the D. S. L. in oceanic waters have been considered in the light of recently acquired data on the structure of the air bladder in bathypelagic fishes. From this it has been suggested that much of the reverberation of supersonic pulses used in echo-sounding may come from layers of these oceanic fishes, particularly from those possessing an air bladder. The following evidence tends to support this:

1. An air bladder is nearly always present in species of the Gonostomatidae, the Sternoptychidae, and the Myctophidae, which are the commonest and most numerous fishes captured in deep-water nets. The dimensions of the air bladder have been listed for a number of species and the possibility of resonant scattering has been discussed.
2. Bathypelagic fishes have an ocean-wide distribution but are poorly represented in Antarctic waters where the D. S. L. has been found to be very sporadic in appearance.
3. A high proportion of species of the three above families have peaks of abundance between 150 and 450 fathoms (274 to 823 metres), the known daytime limits of the D. S. L.
4. Many of these species undertake diurnal vertical migrations.

The existence in the ocean of a deep layer which scatters sound was discovered in 1942 by Eyring, Christensen and Raitt while working for the University of California, Division of War Research. Between 1942 and 1946 a number of anonymous reports, from the Reverbera-

1 Thanks are due to Dr. G. E. R. Deacon, Mr. F. S. Russell and Dr. H. W. Parker for critically reading this paper.
tion Group and the Sonar Data Division of this research department, contained observations on this reflecting zone, now called the Deep Scattering Layer (D. S. L.) by United States workers. Certain of these findings were discussed by Sewell and Fage (1948) in a paper on the oxygen minimum layer in the ocean.

Recent papers by Raitt (1948) and Johnson (1948) deal with particular aspects of this war-time research, while those of Dietz (1948), Hersey and Moore (1948), and Tchernia (1950) present extensive data on the vertical and horizontal distribution of the D. S. L. These results seem particularly interesting in relation to a survey the writer is carrying out on the comparative biological anatomy of the air bladder in bathypelagic fishes. It is the present intention to give some details of this work and to bring together other evidence which tends to support the suggestion that much of the reverberation of supersonic pulses may be due to reflections from concentrations of bathypelagic species, particularly from those possessing an air bladder.²

Any group of organisms suggested as the main scatterers must at least conform to the following main requirements, which are implicit in the work mentioned above.

1. The group must have well defined properties of sound reflection, which includes some degree of concentration in definite strata.

2. Almost certainly, it must have a continuous and nearly ocean-wide distribution.

3. The concentrations of the scatterers must be found between 150 and 450 fathoms (274 to 823 metres) by day.

4. The organisms must show well marked powers of diurnal vertical migration.

These requirements will be discussed in turn, together with other data relevant to each heading.

Johnson (1948), who discovered the diurnal movements of the D. S. L., was the first to try to link it with concentrations of plankton, and he has presented data that show a positive correlation between the depths of the two. He has concluded, however, that this correlation "... may be partly secondary, since the more effective scatterers may be larger forms that subsist upon and migrate more or less concurrently with the plankton."

Raitt (1948), from a theoretical analysis based on oscillograph records of single scatterers obtained off Lower California, concluded that most of the total scattering was due to reflection from the larger but less numerous scatterers, with acoustical cross sections between 0.1 and 10 cm². In the discussion, after making the tentative sug-

² Chapman (1947) has discussed the possibility of tightly packed schools of such fish as louvars being the scatterers.
gestion that "... since the scatterers are probably biological organisms with density and compressibility close to that of water, their reflectivity will be low," he goes on to suggest "... the possibility of resonant scattering, caused by small gas bubbles in the scatterers or by other properties causing a large difference in compressibility with respect to water. . . ."

Dietz (1948) has also drawn attention to scattering by contained air bubbles, but as he and Johnson (1948) noted, they have not yet been found. Similarly, Hersey and Moore (1948), who have considered euphausians as likely scatterers, admit that a serious difficulty "... is their small size and the absence of any sort of swim bladder or other associated air bubble to reflect sound."

Although it is often stated that the air bladder is absent or degenerate in bathypelagic fishes, the results of this survey have shown that it is commonly present in the Gonostomatidae, the Sternopytichidae, the Astronesthidae and the Myctophidae. A list of the species so far investigated follows, together with measurements in millimetres of the standard length (S. L.) and the length times the greatest depth of the air bladder (A. B.). Clearly, the two latter measurements will not be those found in the living fish, but it is felt that they are sufficiently approximate to give some indication of the size of this reflecting body in relation to the wave lengths now used in echo-sounding.

**Gonostomatidae**

<table>
<thead>
<tr>
<th>Species</th>
<th>S. L.</th>
<th>A. B.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gonostoma denudatum</td>
<td>81.0</td>
<td>16.0 x 2.5</td>
</tr>
<tr>
<td>Gonostoma elongatum</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Gonostoma bathyphilum</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Cyclonotus signata</td>
<td>21.0</td>
<td>2.5 x 0.8</td>
</tr>
<tr>
<td>Cyclonotus microdon</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Cyclonotus braueri</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Cyclonotus livida</td>
<td></td>
<td>*</td>
</tr>
</tbody>
</table>


**Sternopytichidae**

<table>
<thead>
<tr>
<th>Species</th>
<th>S. L.</th>
<th>A. B.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Argyropelecus sladeni</td>
<td>20.0</td>
<td>1.6 x 1.7</td>
</tr>
<tr>
<td>Sternopytix diaphana</td>
<td>39.0</td>
<td>9.0 x 3.0</td>
</tr>
<tr>
<td>Polypterus laternatus</td>
<td>32.5</td>
<td>7.0 x 4.0</td>
</tr>
</tbody>
</table>

An air bladder is also present in *Argyropelecus hemigymnus* Cocco (Nusbaum-Hilarowicz [1920]).

**Astronesthidae**

<table>
<thead>
<tr>
<th>Species</th>
<th>S. L.</th>
<th>A. B.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Astronesthes niger</td>
<td>56.0</td>
<td>7.5 x 1.0</td>
</tr>
</tbody>
</table>
MYCTOPHIDAE

Electrona tenisoni (Norman) 47.0 3.5 x 1.25
Electrona antarctica (Günther) 36.0 3.0 x 1.4
Hygophum benoiti (Cocco) 41.0 6.0 x 2.0
Benthosema subrubrale (Gilbert) 24.0 4.3 x 1.3
Benthosema glaciale (Reinhardt) 45.5 5.0 x 1.5
Diogenichthys atlanticus (Taning) 25.5 3.0 x 0.6
Myctophum humboldti (Risso) 50.0 8.0 x 4.0
Myctophum affine (Lütken) 51.0 10.0 x 4.0
Diaphus dolfeini Zugmayer 32.0 6.3 x 1.5
Diaphus lütkeni (Brauer) 34.0 3.5 x 0.6
Diaphus garmani Gilbert 34.5 6.0 x 2.0
Diaphus rafinesquei (Cocco) ? 7.0 x 0.8

(data from Rauther [1922])

Notolychnus valdiviae (Brauer) 19.0 1.5 x 0.75
Lampadena chavesi Collett 75.0 9.5 x 3.5
Lampanyctus macropterus (Brauer) 65.0 20.0 x 5.5
Lampanyctus pusillus (Johnson) 22.0 3.5 x 0.5
Lampanyctus alatus Goode & Bean 57.0 9.0 x 2.5
Lampanyctus guentheri Goode & Bean 53.0 9.0 x 2.0
Lampanyctus sp. 32.0 5.0 x 1.0
Ceratoscopelus townsendi (Eigenmann and Eigenmann) 55.0 5.5 x 1.5
Gymnoscopelus nicholsi (Gilbert) 50.0 2.5 x 0.3

An air bladder is also present in Solivomer arenidens Miller. It is absent in Gonichthys cocco (Cocco) and Gymnoscopelus braueri (Lönneberg).

* Air bladder modified into a fat-storing organ in the adult. A normal gas producing bladder probably present in the young stages.
† Air bladder absent.
‡ In a freshly dissected specimen 54.5 mm long, Beebe and Vander Pyl (1944) found the air bladder to be 14.5 x 4.5 mm.
§ Data from Beebe and Vander Pyl (1944) from a freshly dissected specimen.

Thus it will be seen that an air bladder is commonly present in the Gonostomatidae (in 11 of 12 species investigated, but in five it is modified into a fat-storing structure), in the Sternoptychidae (in 4 out of 4), and in the Myctophidae (in 22 out of 24). Furthermore, from the following analysis of catches in the Atlantic (off Bermuda) and in the eastern Pacific, given by Beebe and Vander Pyl (1944), it will be seen that representatives of two of these families constitute over 90% of the specimens taken with net hauls. The Sternoptychidae are listed by Beebe (1937) as third in order of abundance from hauls made off Bermuda.
Atlantic | Pacific
---|---
Number of specimens | Number of specimens
Myctophids | 10,008 | 10,575
Relative percentage | 9.2 | 36.9
Cyclothone spp. | 95,189 | 15,500
Other fish | 10,550 | 2,200
No. of net hauls | 1,500 | 396

The Bermuda results have been well summarized by Beebe and Crane (1939) who remark "... that in number of individuals it is the plankton eaters—Cyclothone, myctophids and sternoptychids—that are numerically far ahead of eaters of fish and shrimps, such as the large-toothed stomiatoids (Stomias, melanostomiadts, Chauliodus, astronesthids, Idiacanthus), the lyomerids, large-mouthed pediculates, Chiasmodon, etc., ...". It is, in fact, these fish and shrimp eaters (except for the Astronesthidae) which have lost the air bladder, and as Beebe (1933) found, they generally live in zones which overlap but which are below those of the plankton feeders.

It is certain, however, that net hauls give only a relative conception of abundance, for it is more than likely that at least in the twilight zone of the sea (and probably in the unlighted zone according to Beebe [1934]), fish can actively escape the slow-moving nets. The only direct evidence of the absolute abundance of bathypelagic fish comes from Beebe’s (1934) bathysphere work. In comparing his underwater observations with net catches he concluded "... that a much more abundant and large-sized fish fauna exists in these waters than is in any way adumbrated by six years of trawling with the best possible oceanographic collecting outfit"; this is, as he mentioned earlier, "... in the Sargasso sea, which is accounted an arid place for oceanic life."

Concerning stratification in a scattering layer, the works of Jespersen (1935) and Leavitt (1938) have shown quite clearly that populations of bathypelagic fish have a distinct maximum of abundance between the known limits of the D. S. L. Jespersen’s analysis of horizontal hauls taken across the Pacific between the Bay of Panama and the Australian region revealed, in addition to a maximum in the upper layers, a well marked maximum corresponding to hauls with 2,000 metres of wire (probably of a depth between 600 and 1,000 metres) and an equally distinct minimum from hauls with 1,000 metres of wire. Similarly, Leavitt’s work in the deep water off the

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3 If objection is raised that the switching on of the searchlight from the bathysphere may have attracted the fish (although a number of Beebe's observations do not support this), then they must at least have been in the vicinity to be so influenced.
Woods Hole area showed a peak of abundance of fish populations at 800 metres. It must be added that both workers found that this stratification was much the same for many of the zooplankton organisms.

If bathypelagic fishes are much more abundant than is indicated by net catches, and if they are concentrated during the day in definite strata, which also seems likely from Beebe's (1934) observations, then they may well be the most likely element in the D.S.L. Dietz (1948) recorded that for 18 kc/s sound, the diameter of a resonant air bubble is from 1.5 to 2.5 mm between 150 and 415 fathoms (274 to 759 metres). It may be significant, therefore, that the depth of the air bladder of many of the species earlier recorded lies close to, or within, these limits. The degree of concentration of scatterers along the track of a moving beam (with varying lateral coverage due to the roll of the ship) necessary to produce an echogram trace has yet to be determined, but apparently it need not be of a high order, judging from Raitt's (1948) analysis.

The works of Dietz (1948), Hersey and Moore (1948) and Tchernia (1950) show clearly that any group of organisms considered to give rise to a D.S.L. must have (1) a distribution that gives the appearance of a continuous trace on the recording paper, and (2) an almost ocean-wide occurrence. Concerning the latter, the results of oceanographic expeditions, taken as a whole, do not suggest that bathypelagic fish populations have any major discontinuities in distribution (except in Arctic and Antarctic waters). For example, we may consider the station list given by Brauer (1906). The number of stations in the Atlantic and Indian oceans where midwater nets were fished was 78, of which 72 gave positive results. Of the latter, 65 contained combinations of species known to have an air bladder.

Additional evidence of the abundance of some of these fishes may be gained from an analysis of the stomach contents of their predators. Legendre (1934), who made an intensive study of the food of Germe alalunga in the Bay of Biscay area, found that, next to the amphipod Brachyscelus crusculum, the gonostomatid fish Maurolicus muelleri (Gmelin) was the most frequent and numerous in the stomach contents. He argued that the presence of hundreds of Maurolicus in Germe stomachs suggests that it is not only abundant but must live in dense concentrations. Chapman (1943) noted that the main feeding grounds of the fur seal while on the Pribilof and Komandorskie rookeries are outside the 100 fathom line and that it feeds extensively on fishes of the genus Bathylagus, which is poorly represented in collections. Davies (1949) has shown that myctophids (particularly Myctophum humboldtii) are a very important part of the food of Merluccius capensis, Zeus capensis and Brama raii in deep water off the western shores of South Africa.

Tester (1943) found that a record of herring could be obtained by echo sounder even when the fish were thinly scattered. But this was in shallow water.
Continuity in recording the D. S. L. would appear to be the stumbling block to any biological hypothesis. Even small scale patchiness would be detected on an echogram. It is because plankton populations are limited in space and time that Tchernia has criticized the plankton hypothesis.

Concerning continuity in bathypelagic fish populations, little is known. To investigate this thoroughly would mean an enormous amount of work with much more efficient catching gear than is available at present. Perhaps certain tentative conclusions may be drawn from Jespersen’s (1935) analysis of DANA stations in the Pacific. Considering only the deep-lying maximum in numbers of fish (from hauls with 2,000 metres of wire), the mean catches per one hour’s tow from stations in the eastern Pacific were five or six times greater than those obtained from the western half. Striking also is the good agreement between the different groups of stations when these two areas were considered apart. Considering the eastern Pacific, the average catch from the Bay of Panama was 523, and that from the section between Panama Bay and the Marquesas Islands was 633. From eight different sections in the western Pacific the average numbers range from 85 to 156. If bathypelagic fish populations are patchy in distribution, then these figures might be expected to differ by larger factors, particularly since the averages for each section are calculated from few hauls (eleven was the most, one the least), each haul representing only the sampling of a few miles of sea.

It may be added also that species of Cyclothone were prominent in the catches, and of these fish Beebe (1933) has stated: “Whereas Cyclothones compose four-fifths of all the fish trawled above 400 fathoms, yet I am convinced that they do not live in schools; there is too great a uniformity of numbers in each net drawn.” Furthermore, he did not observe large schools of hatchet fish or myctophids during his bathysphere dives. Thus there is some evidence (but admittedly insufficient) to show that certain bathypelagic fish do not occur in dense aggregations. If they are the scatterers and are concentrated in a layer about 100 metres thick during the day, a record which appears continuous on an echogram may not be impossible.

However, the D. S. L. is not found everywhere in deep oceanic water. Dietz (1948) records that it disappeared after crossing the Antarctic Convergence “... and was rarely ever well developed in Antarctic waters.” Tchernia (1950) also found the D. S. L. to be absent in Antarctic waters, but his records suggest that it disappeared at the northern limit of pack ice and not at the Antarctic Convergence. If euphausians or squid are the main scatterers, as suggested by Hersey and Moore (1948) and Lyman (1948) respectively, this dis-
continuity is rather surprising, for these organisms are known to be very abundant in the Antarctic area.

At first it seemed possible that this sudden disappearance of the D. S. L. could be simulated by a sharp change in the vertical distribution of the scatterers, that is, by those south of the Convergence living at sufficiently higher levels to be undetected due to masking of echoes by the outgoing signal trace. But if macroplankton organisms are the scatterers, this does not seem likely from the results of Mackintosh's (1937) report. During the summer months he found the greatest concentrations of macroplankton between the surface and 250 metres, north as well as south of the Antarctic Convergence.

Dietz (1948) has tended to link the nonformation of the D. S. L. in the Antarctic with the almost permanent daylight during summer. It is difficult to see how the one can be related to the other, for if daytime conditions are extended one might expect a parallel extension of the time the scattering layer is recorded. Even if the bulk of the macroplankton live between the surface and 250 metres, some indication of part of these relatively abundant populations might be expected, if they have scattering properties.

If fish are considered to be the scatterers, these findings seem less puzzling. There are few species of bathypelagic fishes in Antarctic waters, about 20 being recorded, mostly from the extensive surveys of the Discovery Committee's research ships. Of these, Bathylagus antarcticus, Paralepis coaesi, Gymnoscopelus braueri, Cyclothone microdon, Electrona antarctica and E. tenisoni are the most common, and only the three latter possess an air bladder.

Actually there is no marked decrease in the number of species on entering Antarctic water, for this decrease is spread over latitudes 40° to 60°, being most pronounced between latitudes 50° to 60°. Those species which do extend into the Antarctic are by no means abundant. For example, about 150 specimens of Electrona antarctica (the commonest species in net hauls, except perhaps for Cyclothone microdon) have been taken from over 2,000 DISCOVERY stations south of 50° S. This may be compared with the catches of Myctophum affine from the eastern tropical Pacific, listed by Beebe and Vander Pyl (1944); here only 31 stations yielded 3,706 fish. Thus there would appear to be some degree of correlation between the distribution of the D. S. L. and that of bathypelagic fishes. If they are the main scatterers, a sporadic development of the D. S. L. in Antarctic waters might be expected.6

6 On this reasoning, one would similarly expect the D. S. L. to be sporadically recorded in Arctic and Subarctic water, which are similarly lacking in numbers of species and individuals of bathypelagic fishes.
The third requirement may be discussed more briefly, since, in considering the stratification of deepsea fish populations, mention has already been made of the findings of Jespersen (1935) and Leavitt (1938), which show peaks of abundance between the known daytime limits of the D. S. L. Murray and Hjort (1912) found that the abundant fishes, such as *Cyclothon e signata* and certain species of Sternoptychidae and Myctophidae, have centres of concentration between 200 and 500 metres.

This is further substantiated by an analysis of the catches from the Discovery Committee’s vessels; a part of these catches was studied by Norman (1930). Nine out of ten myctophids, and all six of the gonostomatids investigated, all being common in the catches, have centres of abundance between 200 and 1,000 metres. Many of the myctophids taken by the *Arcturus* and reported by Beebe and Vander Pyl (1944) show populations living between the surface and the daytime levels of the D. S. L.

Finally there is the well marked vertical migration of this reflecting layer. Brauer (1906, 1908) mentions a number of fishes which live by day in the twilight zone between 200 and 400 metres but which appear in the upper layers at night. Murray and Hjort (1912) gave evidence suggesting a vertical migration in such fish as *Gonostoma elongatum*, *Photostomias guerni*, *Astronesthes* and *Idiacanthus*. For the sternoptychid fishes *Argyropelecus hemigymnus* and *A. olfersi*, taken in the Mediterranean and the Atlantic, Jespersen (1915) found a maximum of abundance between 300 and 600 metres by day, but at night both species were taken comparatively near the surface. Tåning (1918), while noting an obscuring factor in the avoidance of nets by scupelid fishes during the day, tentatively concluded that they are twilight fishes, with limited day and night migrations; he suggests, for example, a migration of 500 metres for *Benthosema glaciale*. Beebe and Vander Pyl (1944) concluded that numerous myctophids are nocturnal surface swimmers, descending to deeper layers during the hours of daylight.

More precise information on the vertical migrations of bathypelagic fishes is certainly needed. The time of ascent and descent of the D. S. L. seems to be only an hour or less before sunset and sunrise, from which data it might be possible to get some indication of the nature of the scatterers. For example, these times of movement do not fit very well with what is known of the migrations of oceanic zooplankton organisms. For instance, the investigations of Waterman, et al. (1939) on diurnal movements of deep-water plankton show that “Before sunrise most of the animals had already descended about half their total downward distance, and several such as *Boreomysis*,

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This page is from a scientific paper discussing the vertical stratification of deepsea fish populations, with specific emphasis on the bathypelagic fishes as sound scatterers. The text delves into the findings of previous researchers like Jespersen and Leavitt, highlighting the abundance and migration patterns of species such as *Cyclothon e signata* and various myctophids and sternoptychids. It also references the work of Brauer, Murray, and Hjort, among others, who studied the vertical migration of these fish populations. The discussion notes the limitations of current data and the need for more precise information on these migrations.
Eucopia and Parapasiphae, had reached the deepest point in their migration by sunrise."

For bathypelagic fishes, the closely spaced hauls made during the Arcturus expedition in the eastern Pacific seem to be the only ones ever taken with some purpose of studying vertical migrations in this group. Discussing the data for the very abundant Myctophum coccoi, Beebe and Vander Pyl (1944) stated: "This slender-tailed lantern fish comes up from rather shallow depths just after dark on the equator and rapidly reaches its greatest abundance, or perhaps at this time 8–9.30 p.m., keeps in very dense, compact schools. Throughout the night its numbers in the nets decrease, probably from a general scattering in search of food and the last individual dives into darker levels at 6.30 a.m. at the very latest." They also remarked on the suddenness with which this downward migration began. The correspondence with the movements of the D. S. L. appears quite good, but clearly more data are desirable before any firm conclusions can be drawn.

The speed of the upward and downward migrations of the D. S. L. has been considered previously as a possible pointer to groups of organisms which may give rise to it. Johnson (1948), obtaining a maximum rate of 8 feet per minute, concludes that some of the larger more active zooplankton organisms can swim quite comfortably at this speed. Dietz (1948) obtained rather higher rates of movement but decided that they were "... more suggestive of the general zooplankton than of faster swimming fish." Yet the more common fish have to contend with an air bladder, and in migrating upwards they must limit the rate of climb in order to avoid excessive expansion of the gases in the air bladder. Conversely, in moving downwards, the rate of descent must be slow enough to enable equilibrium to be reached with the increasing hydrostatic pressure.

Parr (1937) has considered the functioning of the air bladder in the deepsea environment, and from calculations made from the energy of compression equation, \[ E = RT \log e P2/P1 \] (where \( P2/P1 \) is the ratio of partial pressures), he found that the energy required to attain an equivalent degree of buoyancy at 1,000 metres is 300 times the amount needed at 10 metres.

Assuming 50 metres per 15 minutes as the rate of descent, and assuming the scatterers to be fish, we have the following relationships. In moving downwards from 10 to 60 metres during the first 15 minutes the increase in energy necessary to attain equivalent buoyancy at 60 metres is about 10 times that required at 10 metres. After half an hour the fish will be at 110 metres, and here the factor-of-energy increase relative to that at 60 metres must be 2.2. After three-
quarters of an hour the fish will be at 160 metres, and now only 1.6
times as much energy is required compared to the amount necessary at
110 metres; and so the factor gradually decreases. The physical
limitations may thus be less serious than Parr supposed.\(^7\)

However, it is clear that the greatest energy increase is needed
during the first part of the descent; conversely, during the latter part
of the ascent the relative decrease in hydrostatic pressure will be
greatest. Thus it may be possible that there is a slowing up of the
rate of migration in the upper reaches of the sea. A graph drawn by
Hersey and Moore (1948), plotting time against the depth of the D.
S. L. around sunset, does show some flattening at the upper levels, but
clearly it will be best to leave the discussion of this possibility until
more observations are available.

Finally it may be mentioned that the depths at which bathypelagic
fishes are found are probably dependent on local, seasonal and lati-
tudinal variations in illumination parallel to those found by Dietz
(1948) and Hersey and Moore (1948) for the variations in depth of the
D. S. L. No emphasis has been placed on this, however, as it also
applies to at least certain macroplanktonic organisms with well
developed eyes.

DISCUSSION

The measurements of air bladders of a number of bathypelagic fishes
(see p. 3–4) may now be amplified further. In any species the diameter
of the air bladder will increase in size from a fraction of a milli-
metre in the post-larvae to its full growth in the adult. At what
particular stage in the life history it begins to function is not known,
but De Jong (1936) found in post-larval cod (6.5 mm) that the nuclei
of the gas gland had a peculiar appearance. From this he assumed
that it had begun to function. In young stages of *Cyclothone microdon*
(8 mm) the air bladder is about 0.5 mm in length, is oval in outline,
and has what appears to be a relatively large gas gland fed by well
defined retia mirabilia. In the adult these are quite degenerate and,
as already indicated, the tissues of the bladder are charged with fat.
Probably in all adult *Cyclothone* spp. with a fat-charged air bladder
there is a period during the post-larval life when the air bladder
contains gases; this may well mean that the younger stages are more

To this may be added the fact that presumably more energy can be diverted to
the gas-secreting structures during the descent, since less is required in muscular
effort. Furthermore, compared to fishes living above the continental shelf, the
retia mirabilia and gas glands are extremely well developed in bathypelagic fishes;
also, in general their air bladders are relatively smaller compared to the size of the
body cavity.
effective sound scatterers than the adults. It should also be added that adult *Cyclothone* do not appear to undertake diurnal vertical migrations. Perhaps this may not apply to advanced post-larvae which have means for regulating their specific gravity.

However this may be, it is known that during growth the post-larval stages begin to move downwards, and at the metamorphosis from post-larva to adolescent there appears to be a rapid migration much nearer to adult levels (see Jespersen and Tåning [1926]). Perhaps differences from adult behavior during the adolescent phase may be the explanation of multiple scattering layers.

Thus we may conclude that within the limits of the scattering layers there is, as it were, a population of air bladders in any one species with the smaller sizes more numerous than the larger, owing to the differential mortality during the life history. Equally, there will be variations from species to species. Such an assemblage of sound scatterers might be expected to give a good return of echoes for a range of frequencies.

Merriman (1949) has suggested, however, that the bulk of the scatterers are likely to be zooplankton organisms, since minute particles are known to scatter high-frequency sound. If he is referring to the experiments of Dietz (1948) with clouds of sand grains, the writer would like to suggest that such a conclusion is not yet justified. The experiments only prove that sand grains, with very different values of compressibility and density from living organisms, can act as scatterers. Furthermore, it is possible that the particles may drag down with them a certain amount of air which would greatly enhance their powers of returning echoes. However, should bathypelagic fishes prove to be the main scatterers, Merriman's conclusions concerning echo-sounding and the discovery of major fishery resources in deep waters need hardly be modified.

It is unfortunate but understandable that such a technique for exploring the oceans should find the marine biologist with so incomplete a knowledge of the quantity of life in the deep sea and hence without some estimate of the numbers of organisms covered by a sound beam. However, the recent work of Riley, Stommel and Bumpus (1949) has done much in advancing our understanding of this aspect of oceanography. It seems clear that the over-all production of phytoplankton in deep oceanic water may be much the same as that of coastal or bank areas, but owing to its greater vertical disposition, more energy is expended by the herbivores in feeding on it. The effects of this will be reflected in each level of the food chain, and, as these workers say, it would lead to a "progressive attenuation" of the higher members.
Most of the deepsea fishes with air bladders are but one stage removed from the herbivores, since they feed particularly on copepods.

The degree of attenuation at the higher levels of the food chain can be seen from the figures given by Beebe (1937) for his Bermuda hauls, although allowance must be made for the greater ease with which some of the fish-eaters escape from nets. Starting with the families which feed particularly on copepods, the Gonostomatidae, Myctophidae, and Sternoptychidae (some of which are known to eat fish), and then following with families which prey on fish (and prawns), we have the following numbers caught: smaller Gonostomatidae (including the Maurolicidae): 95,624; Myctophidae: 10,008; Sternoptychidae: 2,464; Chauliodontidae: 793; ceratioid angler fish: 337; Melanostomatidae: 239; Malacosteidae: 141; Alepocephalidae: 128; Stomiatidae: 119; Eurypharyngidae: 84; Astronesthidae: 62; and Chiasmodontidae: 36. This gives a rough figure of 50 smaller plankton-eating fish to one large fish-eater, although the ratio is no doubt smaller than this due to the differential escape factor mentioned above and to the fact that only the more important fish-eating families have been listed. This ratio looks remarkably small, but it should be noted also that very few of these higher members of the food chain reach a length greater than 250 mm, although it is likely that in general they range to rather larger sizes than net catches indicate.

That there is a considerable degree of attenuation at the higher trophic levels may be reasonably inferred. As previously mentioned, nearly all fishes at these levels have lost the air bladder and few appear to undertake vertical migrations.

Returning to the smaller vertically-migrating plankton-feeding fishes with air bladders which, if bathypelagic fish are the scatterers, must be the main source of echoes, these take advantage of the greater concentrations of zooplankton in the surface layers, but in order to do so they must expend considerable energy in reaching the upper 100 metres and then must expend more in order to obtain sufficient food, since the concentrations must preclude efficient filter feeding. However, Riley, Stommel and Bumpus (1949) have figures showing that the mean volume of crustacean plankton in the upper 100 metres of the Sargasso Sea is about one-third that in the coastal area from the surface to the bottom. It seems not unreasonable to conclude that these waters may support a fairly numerous population of small fishes.

In conclusion, it hardly needs to be emphasized that the foregoing is no more than an attempt to substantiate an hypothesis, but it is hoped that enough evidence has been brought forward to justify consideration of bathypelagic fishes as scattering organisms. Perhaps varying combinations of these fishes with other oceanic organisms may
prove to be responsible for the D. S. L. Owing to the limited catching power of deepsea gear it will not be easy to test this; none the less, combined biological and physical observations over a period of time may be expected to give some indication through a process of elimination. At all events it is to be hoped that the nature of the scattering layers will soon be found so that full use can be made of this valuable technique for exploring the ocean.

SUMMARY

Investigations on the D. S. L. in the ocean have been considered in relation to recently acquired data on the structure of the air bladder in bathypelagic fishes. From this it has been suggested that much of the reverberation of supersonic pulses used in echo-sounding may come from concentrations of these oceanic fishes. The following evidence tends to support this:

1. It has been found that an air bladder is nearly always present in species of the Gonostomatidae, the Sternoptychidae, and the Myctophidae, which are the commonest and most numerous fishes taken in net hauls. Furthermore, it is highly likely that they are much more numerous than is indicated by collecting gear.

The presence of an air-filled structure should make these organisms strong scatterers of supersonic sound. In relation to the wave lengths now used in echo-sounding, the dimensions of the air bladders are listed.

2. Bathypelagic fishes have an ocean-wide distribution but are poorly represented in Antarctic waters. The latter may explain why the D. S. L. is rarely found south of the Antarctic Convergence. Little is known concerning the continuity of deep-living fish populations, but there is some evidence to indicate that they are fairly uniformly distributed over wide areas.

3. A high proportion of species of the three families mentioned earlier are known to have peaks of abundance between 150 and 450 fathoms (274–823 metres), the known day-time limits of the D. S. L.

4. Many of these species undergo diurnal vertical migrations. The little evidence available suggests that the timing of these movements coincides with those of the scattering layer. The rate of migration is considered in relation to the functioning of the air bladder, this indicating that the physical limitations of hydrostatic pressure change are less serious than might be supposed but that the rate of migration, whether upward or downward, may be slower in the upper layers of the sea.
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