

## Swimbladder Morphology and Specific Gravity of Myctophids off Oregon

JOHN L. BUTLER AND WILLIAM G. PEARCY

Department of Oceanography  
Oregon State University, Corvallis, Ore. 97331, USA

BUTLER, J. L., AND W. G. PEARCY. 1972. Swimbladder morphology and specific gravity of myctophids off Oregon. *J. Fish. Res. Bd. Canada* 29: 1145-1150.

Three general types of swimbladders were found in the eight species of myctophids studied: gas-filled, fat-invested, and atrophied or reduced. Small specimens of all species had thin-walled, gas-filled swimbladders. Large specimens of *Stenobrachius leucopsarus* had fat-invested swimbladders and large *Diaphus theta* had either gas-filled or atrophied swimbladders, as found by other workers. Large *Tarletonbeania crenularis* had either gas-filled or reduced swimbladders, large *Lampanyctus ritteri* and *L. regalis* had reduced swimbladders, and large *Stenobrachius nannochir* had fat-invested swimbladders. *Protomyctophum thompsoni* and *P. crockeri* retained gas-filled swimbladders.

High body lipid content was found in *S. leucopsarus*, *S. nannochir*, *L. ritteri* and *D. theta*, and low lipid content was found in the other four species. Myctophids with high lipid content had specific gravities close to that of sea water (1.026-1.030). *Tarletonbeania crenularis* with a reduced swimbladder had a specific gravity of 1.088. *Lampanyctus regalis* had a lower specific gravity (1.040) due to high water content of the tissue.

The swimbladder to body volumes in *S. leucopsarus* and *D. theta* were inversely related to body size and lipid content, indicating that lipids assume the primary buoyancy function as the gas-filled swimbladder regresses with age. This change may eliminate the physiological constraints imposed by a gas-filled swimbladder and permit the more extensive diel vertical migrations of adults.

BUTLER, J. L., AND W. G. PEARCY. 1972. Swimbladder morphology and specific gravity of myctophids off Oregon. *J. Fish. Res. Bd. Canada* 29: 1145-1150.

Nous avons identifié trois types généraux de vessie gazeuse chez huit espèces de Myctophidae: remplie de gaz, revêtue de graisse et atrophiée ou réduite. Les petits individus de toutes les espèces ont une vessie à paroi mince, remplie de gaz. Les grands spécimens de *Stenobrachius leucopsarus* ont une vessie gazeuse recouverte de graisse, et les grands *Diaphus theta* ont une vessie soit remplie de gaz, soit atrophiée, comme l'ont remarqué d'autres chercheurs. Les *Tarletonbeania crenularis* de grande taille ont une vessie remplie de gaz ou réduite, les grands *Lampanyctus ritteri* et *L. regalis* ont une vessie gazeuse réduite, alors que les grands *Stenobrachius nannochir* ont une vessie gazeuse recouverte de graisse. *Protomyctophum thompsoni* et *P. crockeri* conservent une vessie remplie de gaz.

Nous avons observé une haute teneur en lipides chez *S. leucopsarus*, *S. nannochir*, *L. ritteri* et *D. theta*, et une faible teneur dans les quatre autres espèces. Les Myctophidae à haute teneur en lipides ont un poids spécifique qui se rapproche de celui de l'eau de mer (1.026-1.030). *Tarletonbeania crenularis*, qui a une vessie gazeuse réduite, a un poids spécifique de 1.088. *Lampanyctus regalis* a un poids spécifique plus faible (1.040) à cause de la haute teneur en eau de ses tissus.

Le volume de la vessie gazeuse par rapport à celui du corps est en relation inverse de la taille et de la teneur en lipides de *S. leucopsarus* et de *D. theta*, ce qui démontre que les lipides assument graduellement la fonction primaire de flottabilité, à mesure que la vessie remplie de gaz s'atrophie avec l'âge. Ce changement peut éliminer les contraintes physiologiques qu'impose une vessie remplie de gaz, et permet des déplacements nyctéméraux plus étendus chez les adultes.

Received September 14, 1971

MYCTOPHIDS have an euphysoclistous swimbladder which is often gas-filled (Marshall 1960). Because they have gas inclusions that may effectively scatter and resonate sound and because they are common oceanic animals that are known to undertake diel vertical migrations, myctophids have been considered sources of scattering layers in the ocean (Marshall 1951, 1960; Tucker 1951; Hersey and Backus 1961; Taylor 1968).

The two most common myctophids (lanternfishes) off Oregon, *Stenobrachius leucopsarus* and *Diaphus theta*, are known to migrate vertically within 12 kHz scattering layer depths (Pearcy and Laurs 1966; Pearcy 1964; Pearcy and Mesecar 1971). These species were reported to lack a gas-filled swimbladder (Ray 1950; Jollie MS 1954; Barham MS 1956), but Capen (1967) found that small specimens of *S. leucopsarus* had gas-filled swimbladders and suspected that small specimens of *D. theta* also may have gas in their swimbladders. Thus, adults of these abundant species, lacking gas-filled swimbladders, may not scatter sound as effectively as juveniles of these species or other less common species with gas-filled swimbladders.

This study was conducted on the morphology of swimbladders to learn which species and sizes of myctophids off Oregon contain gas-filled swimbladders and which species lack gas-filled swimbladders. Such knowledge is needed to correlate the depth distribution of effective sound scattering organisms collected in nets with the depths of sonic scattering layers. Lipids and specific gravity were also studied because of their interrelation with swimbladders and buoyancy.

### Materials and Methods

Fishes were collected off Oregon with an Isaacs-Kidd midwater trawl equipped with a 5-mm mesh liner and a  $\frac{1}{2}$  m diameter codend of a 0.571 mm mesh. Preserved specimens were fixed at sea in 10% formalin and stored in 36% isopropyl alcohol. Standard length was measured to the nearest millimeter.

Swimbladder volume was studied in 123 preserved specimens of eight species of myctophids. The major and minor external axes of the swimbladder were measured with an ocular micrometer and a stereo dissecting scope. For collapsed swimbladders, one half of the circumference was measured. Total swimbladder volumes were estimated by the formula for an oblate spheroid,  $V = 4/3\pi ab^2$  (Capen 1967), where  $a$  is the minor and  $b$  the major axis. Total body volume was estimated by weighing individual fish in air and suspended in distilled water, and estimating the volume of displaced water.

For study of their structure swimbladders selected from 46 fish were embedded in paraffin, sectioned, and stained with Mallory's triple stain or hemotoxin and eosin. Certain fat-invested swimbladders were sectioned with a cryostat and stained with Sudan IV for lipids.

To determine whether or not swimbladders contained gas, fresh specimens were collected at night in mid-water trawls in the upper 50 m. Fish were dissected under water and the swimbladder was punctured to release any gas bubbles. The presence of gas in the body cavity was considered evidence for gas in the swimbladder since the swimbladder may have ruptured during the trawl ascent. One hundred thirty-nine specimens of eight species were examined in this manner.

In addition, 206 frozen specimens were analyzed for lipid content after they were dried to a constant weight at 70 C. Lipids were extracted with a two to one mixture of chloroform and methanol in a Soxhlet extractor, then each specimen was dried and reweighed. Lipid content was calculated by difference. Small individuals of the same size were grouped to provide a larger biomass. Seventy-eight extractions were made in this manner.

Specific gravity was estimated by two methods. In the laboratory intact frozen specimens were weighed in air and in distilled water, and at sea fresh specimens were suspended in a series of gum arabic solutions of known densities. Care was taken to exclude air from the gill chamber during all specific gravity measurements.

### Types of Swimbladders

The myctophids were found to have three types of swimbladders. Thin-walled, ellipsoid swimbladders (Fig. 1), were found in all small specimens of all species studied. As the fishes grow, the thin-walled swimbladder may be unmodified, or it may become fat-invested in which case the gas phase is replaced by fatty tissue (Fig. 2), or the swimbladder may be reduced in size and have thick walls (Fig. 3).

The swimbladders of *Stenobrachius leucopsarus* and *S. nannochir* becomes fat-invested with age. Fatty reticular tissue on the anterior and posterior ends of the swimbladder in small specimens (Fig. 2) stains red with Sudan IV in frozen sections indicating the presence of lipids. The reticular structure is continuous with a layer of the swimbladder wall and is bounded by the outer layer, indicating that the fatty cells form inside the wall of the swimbladder, not outside as described by Capen (1967). As the fish grows larger, the fatty tissue increases and the size of the swimbladder is reduced until only a tube of fatty tissue remains in large individuals. The volume of the entire swimbladder decreased from about 4-5% of total body volume in small specimens of 20 mm to about 0.4% in large specimens (>70 mm) of *S. leucopsarus* (Fig. 4A) and also in *S. nannochir*.

The swimbladders of *Lampanyctus ritteri* and *L. regalis* regress with increasing size of fish but, unlike *Stenobrachius* spp., they do not become invested with fat. The volume of the swimbladder decreased from about 2% of body volume in small individuals (<25 mm) to 0.01% or less in large individuals (>80 mm). The swimbladder wall is

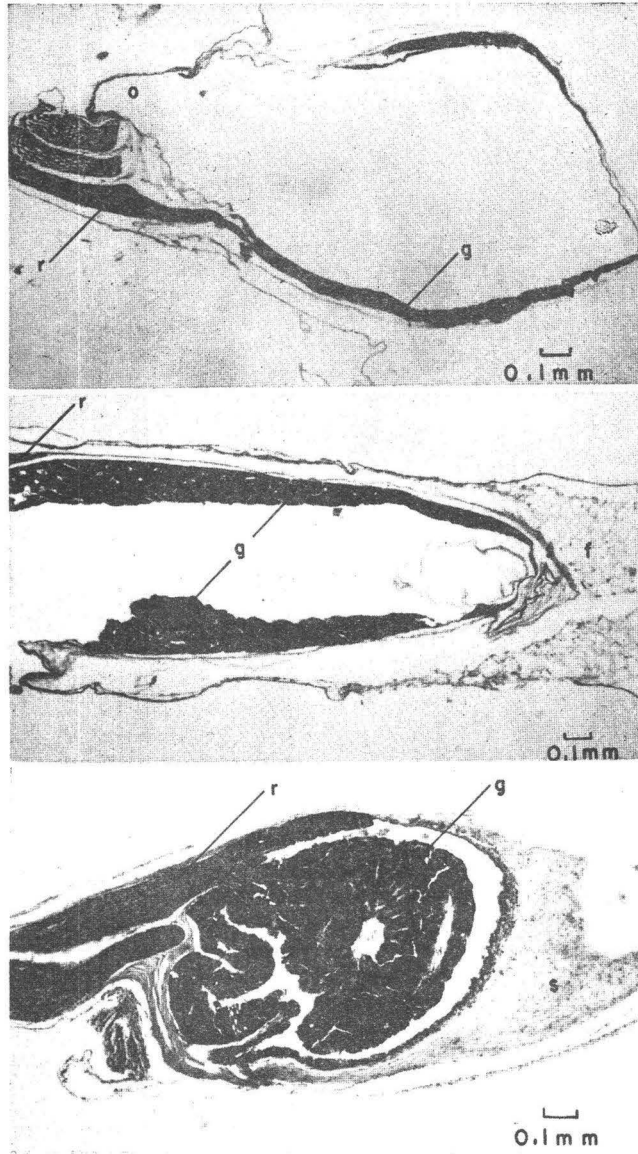


FIG. 1. (Top) Swimbladder of *Diaphus theta*, 23 mm standard length. g = gas gland, o = oval, r = rete mirabile.

FIG. 2. (Center) Fat-invested swimbladder of *Stenobranchius leucopsarus*, 36 mm. f = fat-filled tissue, g = gas gland, r = rete mirabile, s = submucosa.

FIG. 3. (Bottom) A reduced swimbladder of *Diaphus theta*, 38 mm. g = gas gland, s = submucosa, r = rete mirabile.

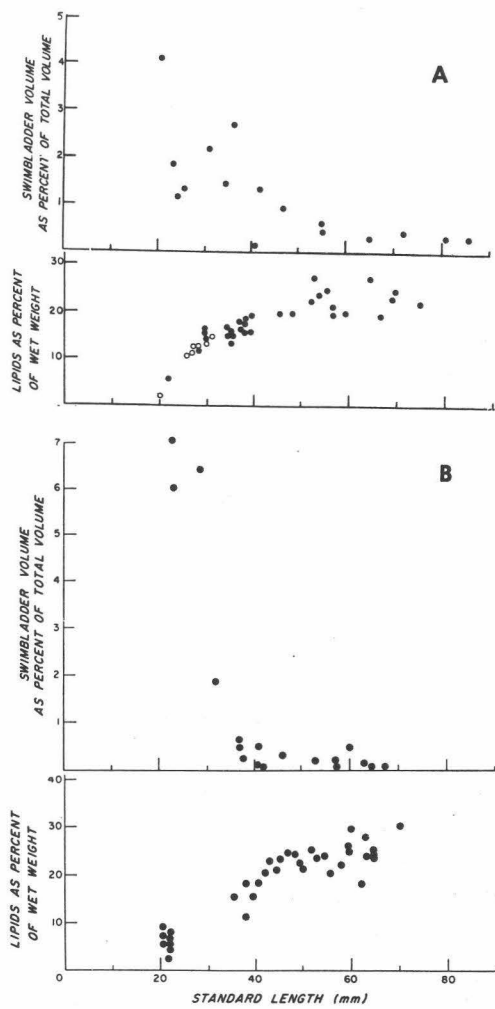


FIG. 4. Swimbladder volume and lipid content versus length of *Stenobranchius leucopsarus* (A) and *Diaphus theta* (B).

thickened with connective tissue and the lumen is occluded by the gas gland in large individuals.

The swimbladders of *Diaphus theta* do not grow proportionally with the rest of the fish and are sometimes reduced in large specimens. The swimbladder volume in small individuals was about 6–7% of the body volume (Fig. 4B). In large specimens (>25 mm) the swimbladder volume averaged only 0.3% of body volume. There was considerable variability in the large specimens, however. Some had reduced, thick-walled swimbladders with the lumen occluded by the gas gland (Fig. 3), but other adults of the same size had small, thin-walled swimbladders that were not occluded.

Swimbladders of large *Tarletonbeania crenularis*, like *D. theta*, also have two distinct forms. Small, reduced swimbladders were present in some specimens while thin-walled, capacious swimbladders were present in others. The swimbladder to body volume was 0.5% or less in reduced forms and greater than 6% in thin-walled forms. Thin-walled swimbladders predominated (9 of 13) in specimens less than 40 mm; reduced swimbladders predominated (15 of 20) in larger specimens.

All sizes of both *Protomyctophum thompsoni* and *P. crockeri* had thin-walled swimbladders. However, estimated volumes of the swimbladders in both species varied, irrespective of size, from 5.5% to less than 1.0% of the body volume. The swimbladders appeared collapsed in those specimens with small volumes, but the lumen was not occluded by an enlarged gas gland as in the reduced swimbladders of the other species.

Gas was found in small *S. leucopsarus* and *L. regalis*, in both small and large *D. theta* and *T. crenularis*, in large *P. thompsoni*, and in small *P. crockeri* (Table 1). All of the gas-filled swimbladders had thin walls. Gas was never found in the fat-invested swimbladders of large *S. leucopsarus* or in the reduced swimbladders of large *L. ritteri*. Some of the large *T. crenularis* and *D. theta* had gas inclusions; but other individuals of both species had reduced swimbladders without gas. Thus, the presence of gas in thin-walled swimbladders and the absence of gas in fat-invested or reduced swimbladders corroborated our findings based on the morphology of preserved specimens. The absence of gas in large *S. nannochir* and *L. regalis* and the presence of gas in small *P. thompsoni* and large *P. crockeri* are inferred on the basis of the swimbladder morphology and the presence or absence of gas found in their congeners.

### Lipid Contents and Specific Gravities

In large individuals the highest fat content occurred mainly in those species which lack a gas-filled swimbladder as adults, i.e. *S. leucopsarus*, *S. nannochir*, and *L. ritteri*; the lowest fat content occurred mainly in species which retain gas-filled swimbladders, i.e. *P. thompsoni* and *P. crockeri*. Exceptions were *D. theta*, which has either a small gas-filled swimbladder or a reduced swimbladder, but a high fat content; *T. crenularis*, which has either a gas-filled or a reduced swimbladder, but a low lipid content; and *L. regalis*, which has a reduced swimbladder and a low fat content.

TABLE 1. Occurrence of swimbladder gas in fresh myctophids.

Species	Gas present		Gas absent	
	No.	Length (mm)	No.	Length (mm)
<i>Stenobranchius leucopsarus</i>	27 S <sup>a</sup>	22–39	5 L <sup>b</sup>	48–72
<i>S. nannochir</i>	S	<35 <sup>c</sup>		L>35 <sup>c</sup>
<i>Lampanyctus ritteri</i>	S	<50 <sup>c</sup>	8 L	50–120
<i>L. regalis</i>	1S	<50		L>50 <sup>c</sup>
<i>Diaphus theta</i>	11 S	17–22	2 S	22–24
	9 L	34–62	30 L	29–70
<i>Tarletonbeania crenularis</i>	9 S	23–33	5 S	29–34
	4 L	30–47	15 L	36–70
<i>Protomyctophum thompsoni</i>	S	<35 <sup>c</sup>		
	13 L	35–50		
<i>P. crockeri</i>	2 S	19–26		
	L	>30 <sup>c</sup>		

<sup>a</sup>Small individuals.

<sup>b</sup>Large individuals.

<sup>c</sup>Inferred from morphology.

The total lipid contents of *S. leucopsarus* and *D. theta* were directly related to the size of the individual (Figs. 4A and B). The lipid content of small individuals (<25 mm) was less than 10% of wet weight. Large individuals (>30 mm) had a more variable lipid content which averaged 18.7 and 22.1% of wet weight, respectively (Table 2). Hence, lipid content and swimbladder volume were inversely related in these species (Fig. 4A and B), suggesting that lipids assume the buoyancy function of the gas-filled swimbladder as it regresses with age.

The values for lipid content of *T. crenularis* were plotted against fish size, but the slope of a regression line for 22 specimens (22–70 mm) did not differ significantly from zero ( $t = 0.4$ , 21 df). Moreover, the mean lipid contents of fish with gas and fish without gas were not significantly different ( $t = 0.4$ , 15 df). Apparently, lipids do not have a major role in buoyancy of this species even when the swimbladder is reduced.

The specific gravities of large *S. leucopsarus*, *S. nannochir*, *L. ritteri*, and *D. theta* that were frozen at sea and weighed in air and water were near the density of sea water (1.026–1.030) (Table 2). All the specimens of these sizes had fat-invested or reduced swimbladders without a gas phase. All of the specimens lost scales during capture so live animals may be denser than these results indicate.

Estimates of specific gravity of fresh specimens with gum arabic solutions were similar to those based on weights. The specific gravities of 17 fresh *S. leucopsarus* with gas and three without gas were less than 1.030, and those of two specimens with gas and two without gas were between 1.030 and 1.042. Those of three fresh *L. ritteri* were between 1.030 and 1.048. Specific gravity estimates of individuals which had gas-filled swimbladders are of questionable value since gas could either expand during ascent from depths of capture or escape from ruptured swimbladders.

Thawed specimens of *T. crenularis* were considerably denser than sea water (1.088, Table 2), as were seven fresh specimens without gas-filled swimbladders (1.086). The average specific gravity of eleven fresh specimens with gas-filled swimbladders was lower (1.056), but the expansion of gas during ascent from depth of capture may have produced these low values. We conclude from these results that without a gas-filled swimbladder *T. crenularis* would have to swim constantly to maintain position.

Although the specific gravity of a fresh specimen of *L. regalis* with gas (50 mm) was less than 1.030, large thawed specimens without gas (Table 2) were denser than seawater but not nearly as dense as *T. crenularis*. The body was flaccid and contained 86% water (on a weight basis) compared to 72% in *L. ritteri*. *Lampanyctus regalis* is a lower mesopelagic species (Pearcy 1964) that appears to have achieved neutral buoyancy in the same way as bathypelagic fishes by reduction of skeletal and muscular tissues (Denton and Marshall 1958; Marshall 1960).

## Discussion

The swimbladders found in all juvenile myctophids, in the adults of *P. thompsoni*, and *P. crockeri*, and in some adults of *D. theta* and *T. crenularis* were thin-walled and gas-filled, morphologically similar to those that Marshall (1960) characterized for the family.

The situation in *D. theta* and *T. crenularis*, in which both thin-walled and reduced swimbladders occurred, is curious. Capen (1967) also noted two types of swimbladders in *D. theta* but did not find gas in fresh specimens. We found no relation between type of swimbladder in these species and season of the year or sex of individuals. Thus, the ecological significance of this biphasic swimbladder system in the adults of these species is unknown. Conceivably fishes with different swim-

TABLE 2. Average specific gravities of thawed myctophids frozen at sea. All individuals lacked gas-filled swimbladders.

Species	No.	Standard Length (mm)	Specific Gravity
<i>S. leucopsarus</i>	5	58–80	1.027(1.025–1.031) <sup>a</sup>
<i>S. nannochir</i>	2	90–102	1.026
<i>L. ritteri</i>	2	73–90	1.026(1.023–1.030)
<i>D. theta</i>	4	40–64	1.038(1.025–1.062)
<i>L. regalis</i>	2	84–85	1.040(1.040–1.041)
<i>T. crenularis</i>	2	41–59	1.088(1.088–1.089)

<sup>a</sup>Range.

bladder types could have different patterns of vertical migration and behavior.

Fat-invested swimbladders were found in large *S. leucopsarus*, confirming the earlier findings of Capen (1967), and in *S. nannochir*. Reduced swimbladders occurred in all large *L. ritteri* and *L. regalis* and in those *D. theta* and *T. crenularis* which lacked thin-walled swimbladders. In general, body lipid content was high in fishes that lacked gas-filled swimbladders (with the exception of *L. regalis*). Similarly, Nevenzel et al. (1969) found larger amounts of lipids in *L. ritteri*, *S. leucopsarus*, and *D. theta* than in *T. crenularis*.

Specific gravity measurements indicate that those fishes with high lipid content (*S. leucopsarus*, *S. nannochir*, *D. theta*, and *L. ritteri*) approach neutral buoyancy. Yet the observed lipid content is not as great as Taylor (1921) predicted for neutral buoyancy. His theoretical value, based on specific gravities of 1.076 for fat-free tissue and 0.925 for lipids (cod liver oil), is 29.23% of the wet weight. Our highest observed lipid value, however, was only 22.1% of wet weight (Table 3). Thus a lower tissue density and/or lipid specific gravity is required to explain the low specific gravity of these fishes.

The lipids found in myctophids may, in fact, be lighter than Taylor's value. Nevenzel et al. (1969) reported waxy esters (chain length 30–38) as the principal lipids in *S. leucopsarus*, *L. ritteri*, and *D. theta*. These lipids may be less dense than cod liver oil, which is composed of lipids with chain lengths of 18–20 (Morrison and Boyd 1966). Nevenzel et al. (1966) cite a specific gravity of 0.86 for

oleyl oleate, a wax ester. Using this value for lipids and 1.076 for fat-free tissue, a lipid content of 19.4% of wet weight produces a specific gravity of 1.026. This value compares favorably with the observed lipid contents (Table 2) for *S. leucopsarus*, *S. nannochir*, *D. theta*, and *L. ritteri*. Thus low-density lipids may provide neutral buoyancy for these species. Lee et al. (1971) found that triglycerides were metabolized rapidly while wax esters were utilized more slowly in starved *Gaussia princeps* (Scott), a large mesopelagic copepod. Accumulating wax esters may have two advantages over triglycerides: a stable buoyancy fraction and a long-term energy reserve.

The presence of a gas phase in swimbladders is related to the vertical distribution and migration of myctophids and their importance in producing sound scattering layers in the ocean. Of the four common myctophids that Taylor (1968) caught in his study off British Columbia, *S. leucopsarus* and *D. theta*, species with fat-invested swimbladders as adults, made the most extensive vertical migrations and were most numerous below the main sonic scattering layer during the day. *Protomyctophum thompsoni*, a species with a gas-filled swimbladder, made less extensive migrations and was often found at scattering layer depths. Barham (1971) observed from submersible dives that immature myctophids, with potentially resonant gas-filled swimbladders, are sometimes concentrated at scattering layer depths while large individuals were concentrated at deeper levels. Studies with opening-closing nets (W. G. Percy unpublished data) indicated that large *S. leucopsarus*, without gas-filled swimbladders, have a greater vertical range of diel migration than juveniles, which have gas-filled swimbladders. However, small *S. leucopsarus* were also found in a 350–420 m scattering layer during both day and night periods, indicating that some juveniles of this species probably migrate little if at all. (Percy and Mesecar 1971).

Maintaining a constant volume of gas in a swimbladder during rapid, extensive vertical migrations is no mean physiological feat. It requires impressive capabilities of gas secretion and resorption (Jones 1951, 1952; Kanwisher and Ebeling 1957; D'Aoust 1971; Alexander 1971). These constraints may limit vertical movements of fishes with gas-filled swimbladders. Therefore replacement of gas by lipids as the main buoyancy regulator, as in large *S. leucopsarus* and *D. theta*, may permit more extensive vertical migrations in these myctophids.

#### Acknowledgments

This research was supported by the Office of Naval Research through contract N00014-67-A-0369-0007 under

TABLE 3. Average lipid contents of large individuals of the various myctophids.

Species	No.	% Wet Wt.	% Dry Wt.
<i>D. theta</i> (> 35 mm)	28	22.1±0.7	63.6±1.2
<i>S. leucopsarus</i> (> 30 mm)	28	18.7±4.0 <sup>a</sup>	59.8±4.0
<i>S. nannochir</i> (> 85 mm)	5	18.9±2.5	56.8±1.0
<i>L. ritteri</i> (> 58 mm)	10	16.0±0.3	57.8±2.0
<i>P. thompsoni</i> (> 25 mm)	19	4.9±0.37	24.1±1.0
<i>P. crockeri</i> (23 mm)	2	4.2	19.2
<i>T. crenularis</i> (> 23 mm)	25	4.2±0.2	19.2±0.8
<i>L. regalis</i> (> 50 mm)	5	2.2±0.7	16.6±4.6

<sup>a</sup>One standard deviation of mean.

- project NR 083-102, and the Atomic Energy Commission Contract AT (45-1) 2227, Task Agreement No. 12, RL0-2227-T12-25.
- ALEXANDER, R. M. 1971. Swimbladder gas secretion and energy expenditure in vertically migrating fishes. Proc. Int. Symp. on Biological Sound Scattering in the Ocean. U.S. Dep. Navy, MC Rep. 005: 74-85.
- BARHAM, E. G. MS 1956. The ecology of sonic scattering layers in the Monterey Bay area, California. Ph.D. thesis. Stanford Univ., Stanford, Calif. Univ. Microfilms Publ. No. 21, 564; Ann Arbor, Mich.
1971. Deep-sea fishes: Lethargy and vertical orientation. Proc. Int. Symp. on Biological Sound Scattering in the Ocean. U.S. Dep. Navy, MC Rep. 005: 100-118.
- CAPEN, R. L. 1967. Swimbladder morphology of some mesopelagic fishes in relation to sound scattering. U.S. Navy Electron. Lab. Res. Rep. 29 p.
- D'Aoust, B. G. 1971. Physiological constraints on vertical migration of mesopelagic fishes. Proc. Int. Symp. on Biological Sound Scattering in the Ocean. U.S. Dep. Navy, MC Rep. 005: 86-99.
- DENTON, E. J., AND N. B. MARSHALL. 1958. The buoyancy of bathypelagic fishes without a gas-filled swimbladder. J. Mar. Biol. Ass. U.K. 37: 753-69.
- HERSEY, J. B., AND R. H. BACKUS. 1954. New evidence that migrating gas bubbles, probably the swimbladders of fish are largely responsible for the scattering layers on the continental rise south of New England. Deep-Sea Res. 1: 190-191.
- JOLLIE, M. T. MS 1954. The general anatomy of *Lampanyctus leucopsarus* (Eigenmann and Eigenmann). Ph.D. thesis. Stanford Univ., Stanford, Calif. 239 p. Univ. Microfilms Publ. No. 10, 376; Ann Arbor, Mich.
- JONES, F. R. H. 1951. The swimbladder and the vertical movement of teleostean fishes. I. Physical factors. J. Exp. Biol. 28: 553-566.
1952. The swimbladder and the vertical movement of teleostean fishes. II. The restriction to rapid and slow movements. J. Exp. Biol. 29: 94-109.
- KANWISHER, J., AND A. EBELING. 1957. Composition of swimbladder gas in bathypelagic fishes. Deep-Sea Res. 4: 211-217.
- LEE, R. F., J. HIROTA, AND A. M. BARNETT. 1971. Distribution and importance of wax esters in marine copepods and other zooplankton. Deep-Sea Res. 18: 1147-1165.
- MARSHALL, N. B. 1951. Bathypelagic fishes as sound scatterers in the ocean. J. Mar. Res. 10: 1-17.
1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Discovery Rep. 31: 1-122.
- MORRISON, R. T., AND R. N. BOYD. 1966. Organic chemistry. Allyn and Bacon Inc., Boston. 1204 p.
- NEVENZEL, J. C., W. RODEGKER, J. F. MEAD, AND M. S. GORDON. 1966. Lipids of the living coelacanth, *Latimera chalumnae*. Science 152: 1753-1755.
- NEVENZEL, J. C., W. RODEGKER, J. S. ROBINSON, AND M. KAYAMA. 1969. The lipids of some lantern fishes (family Myctophidae). J. Comp. Biochem. Physiol. 31: 25-36.
- PEARCY, W. G. 1964. Some distributional features of mesopelagic fishes off Oregon. J. Mar. Res. 22: 83-102.
- 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., AND R. S. MESECAR. 1971. Scattering layers and vertical distribution of oceanic animals off Oregon. Proc. Int. Symp. Biological Sound Scattering in the Ocean. U.S. Dep. Navy, MC Rep. 005: 381-394.
- RAY, D. L. 1950. The peripheral nervous system of *Lampanyctus leucopsarus*. J. Morphol. 87: 61-178.
- TAYLOR, F. H. C. 1968. The relationship of midwater trawl catches to sound scattering layers off the coast of northern British Columbia. J. Fish. Res. Bd. Canada 25: 457-472.
- TAYLOR, H. F. 1921. Airbladder and specific gravity. Bull. U. S. Fish. 38: 121.
- TUCKER, G. H. 1951. Relation of fishes and other organisms to the scattering of underwater sound. J. Mar. Res. 10: 215-238.