

AN ABSTRACT OF THE THESIS OF

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Swimbladder Morphology and Buoyancy  
of Northeastern Pacific Myctophids

Abstract approved:

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Of the common adult lanternfishes found off Oregon, two species have fat-invested swimbladders (Stenobranchius leucopsarus Eigenmann and Eigenmann 1890 and Stenobranchius nannochir Gilbert 1891), two species have reduced swimbladders (Lampanyctus ritteri Gilbert 1915 and Lampanyctus regalis Gilbert 1891), two species have gas-filled swimbladders ((Protomyctophum thompsoni (Chapman 1944)) and (Protomyctophum crockeri (Bolin 1939))). Adult Diaphus theta Eigenmann and Eigenmann 1891 and adult Tarletonbeania crenularis Jordan and Gilbert 1880, however, have either gas-filled or reduced swimbladders. Small individuals of all the above species have gas-filled swimbladders.

The primary buoyancy mechanism is lipids for large S. leucopsarus, S. nannochir, L. ritteri and D. theta, is reduction of dense material for large L. regalis, and is gas for all juveniles and for P. thompsoni, P. crockeri and some adult T. crenularis and D. theta.

Swimbladder Morphology and Buoyancy  
of Northeastern Pacific Myctophids

by

John Lawton Butler

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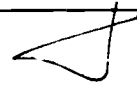
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# Swimbladder Morphology and Buoyancy of Northeastern Pacific Myctophids

## INTRODUCTION

Myctophids are mesopelagic fishes which undergo diel vertical migrations. Vertical movement may affect the buoyancy of fishes with gas filled swimbladder. The objective of this study was to determine the buoyancy mechanisms of these fish.

Buoyancy is an important ecological factor for fishes in the open ocean. Primary production only occurs in surface waters, and there food is most abundant. For a fish to remain near the food source it must be neutrally buoyant or spend considerable energy swimming to produce hydrodynamic lift (Alexander, 1966).

Swimbladders of teleosts function in buoyancy, respiration, detection of pressure changes and the production of sound (Jones and Marshall, 1953 and Alexander, 1966). The principal function is buoyancy (Taylor, 1921). Although fat may also provide lift, a gaseous inclusion is the most efficient buoyancy compound because of its low specific gravity.

The buoyancy of a gas-filled swimbladder is unstable, however. Since the walls of the swimbladder are not rigid, the gas conforms to Boyle's Law. If, for example, a fish moves upward the pressure decreases, and the gas expands. The increased volume produces more lift, which will raise the fish farther if not counteracted. If the swimbladder is filled at depth the rate of upward movement will be limited by the fish's ability to resorb gas. Jones (1951, 1952) and Kanwisher and Ebeling (1957) argue on physiological evidence that it is unlikely that fishes can maintain buoyancy during an

extensive vertical migration. Alexander (1970) concludes from energy considerations that a gas-filled swimbladder may be economical to maintain for a shallow migrating fish, but that it is prohibitively costly to an extensively migrating fish.

Because of the acoustical properties of the swimbladder, fishes are often cited as causes of deep scattering layers (Marshall, 1951 and Tucker, 1951). Hersey and Backus (1954) and Hersey, Backus, and Hellwig (1961) analyzed the frequency shift of migrating scattering layers. These shifts suggested that gas bubbles (probably swimbladders of fishes) were responsible for most of the scattering. The relationship between frequency and depth also indicated that the swimbladder volume of some fishes may be constant during migration, while the swimbladders of others are filled at nighttime depths only and volumes conform to Boyle's Law.

Fishes of the family Myctophidae, because they are often abundant and migrate vertically, are cited as possible causes of scattering layers. Marshall (1951) proposed criteria which an organism must fulfill to be considered as a cause of a deep scattering layer. The organism must: have a continuous world wide distribution, be concentrated at 274-823 meters, and migrate vertically. Marshall felt that fishes of the families Gonostomiatidae, Sternoptychidae and Myctophidae best fit these criteria. Tucker (1951), Barham, (1957) and Taylor (1967) have associated net collections of myctophids with scattering layers. Barham (1967) observed organisms in the vicinity of two scattering layers from a submersible. Physonect siphonophores were associated with one



layer, myctophids with the other layer. From a submersible Backus et al. (1968) observed an unusual parabolic scattering layer caused by aggregations of Ceratoscopelus maderensis Lowe 1839, a myctophid.

Marshall (1960), who examined the swimbladders of many mesopelagic fishes, characterized the swimbladders of myctophids as thin walled sacs with three unipolar retia mirabilia and a well developed oval. However, three species of myctophids have been reported with fat-invested or occluded swimbladders (Ray, 1950; Jollie, 1954; Barham, 1957; and Capen, 1967). Barham (1970) feels that the type of swimbladder may be correlated with myctophid behavior as observed from a submersible. Myctophids with fat-invested or occluded swimbladders and wide caudal peduncles are lethargic and negatively phototactic by day, while myctophids with or without gas-filled swimbladders and with thin caudal peduncles are active and positively phototactic.

## MATERIALS AND METHODS

Fishes used in this project were collected by the Oregon State University Department of Oceanography over a period of eight years. Collections were made with an Isaacs-Kidd midwater trawl (Isaacs and Kidd, 1953) equipped with a 5 mm mesh liner and a 0.571 mm mesh 1/2 m cod end. Preserved specimens were fixed at sea in 10 percent formalin and stored in 36 percent isopropyl alcohol. Standard length of all individuals was measured to the nearest millimeter.

Swimbladder morphology was studied in 123 preserved specimens. A series of specimens, selected to cover the largest size range for each species, was examined under a stereo dissection scope. The major and minor axes of the swimbladder were measured with an ocular micrometer. For collapsed swimbladders, one half of the circumference was measured. Since myctophid swimbladders are ellipsoid sacs, volumes of swimbladders were estimated by the formula for an oblate spheroid,  $V = 4/3\pi ab^2$  where  $a$  is the minor and  $b$  the major axis. Total body volume was measured so that the swimbladder volumes could be expressed as a function of body size. The fish were weighed suspended in air and in distilled water. The volume was estimated by the weight of water displaced.

Swimbladders selected from 46 fish were sectioned after parafin embedding and were stained with Mallory's triple stain or hemotoxin and eosin. Certain fat-invested swimbladders were sectioned with a cryostat and were stained with Sudan IV for lipids.

Preserved specimens can provide, at best, only negative evidence for the presence of gas. Therefore fresh specimens were collected at night in midwater trawls to shallow depths. The fish were separated from the rest of the catch and placed in sea water. Individuals were then measured and dissected under water. 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 rupture during the ascent if the fish is captured at depth. One hundred thirty-four specimens were examined in this manner.

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 for analysis. Seventy-eight extractions were made in this manner.

Specific gravity was estimated by two methods. Intact frozen specimens were weighed in air and in distilled water. Specific gravity was calculated from the weight and the volume of water displaced. Fresh specimens collected at sea were also 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.

## RESULTS AND DISCUSSION

### Morphology

The morphology of the swimbladders investigated was similar to that described by Marshall, (1960). Myctophid swimbladders are thin-walled ellipsoid sacs. Three unipolar retia mirabilia enter anteriorly and supply three corresponding lobes of the gas gland. The retia appear in longitudinal section as parallel tubes (Figure 1) or in cross section as bundles of tubes (Figure 2). The retia are usually filled with red blood cells. Blood vessels from retia anastomose through the gas gland, a thickening of the epithelium which lines the lumen (Figure 3). The cells are large, glandular and stain darkly (Figure 4). The oval is separated from the lumen by a sphincter which regulates gas resorption. The thin walls are richly supplied with blood vessels (Figure 2). The structure of the swimbladder wall has been compared to the structure of the intestinal tract by Fange (1953). Because of the thinness of the walls (Figure 2) the layers described by Fange were not discernible. The thickening in the wall by connective tissue in reduced swimbladders, however, has a structure similar to that described by Fange (1953) for the submucosa (Figures 1, 5 and 6).

The typical thin-walled swimbladder was found in all of the small individuals (Figure 2) and some of the adults investigated. Swimbladders of some large fishes departed from this typical structure and were either fat-invested or reduced. Table 1 summarizes the types of swimbladders found in the eight species studied.

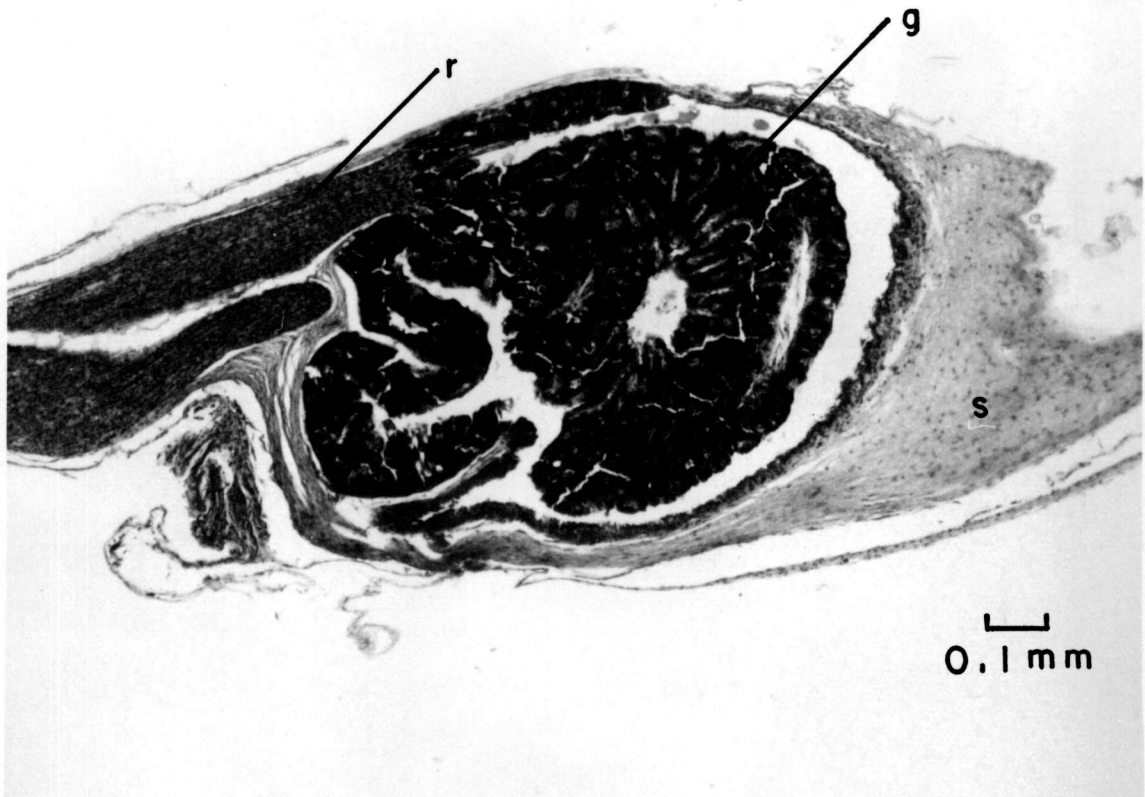


Figure 1. *Diaphus theta*, 38 mm. g = gas gland, s = submucosa,  
r = retia mirabilia

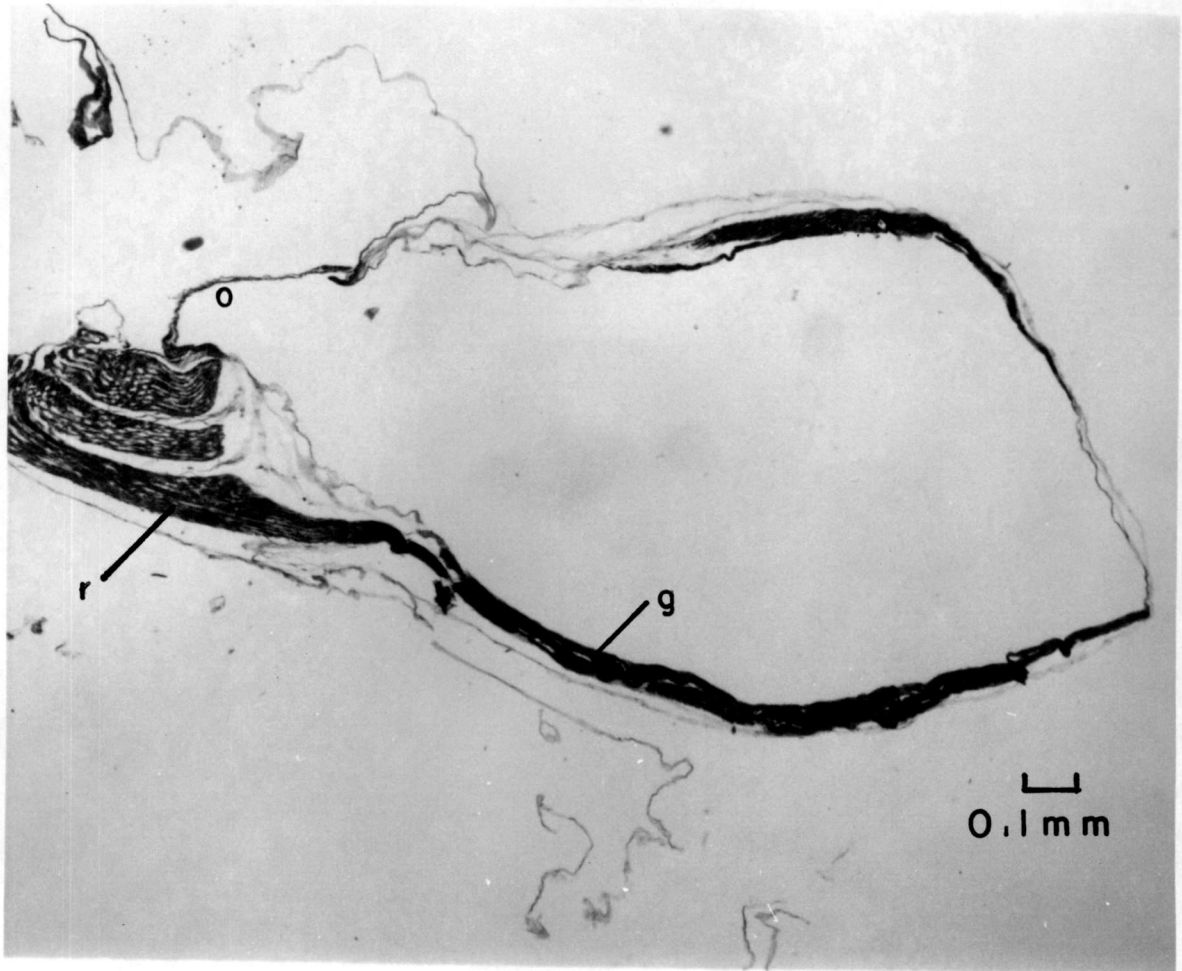


Figure 2. Swimbladder of Diaphus theta, 23 mm. g = gas gland, o = oval, r = retia mirabilia

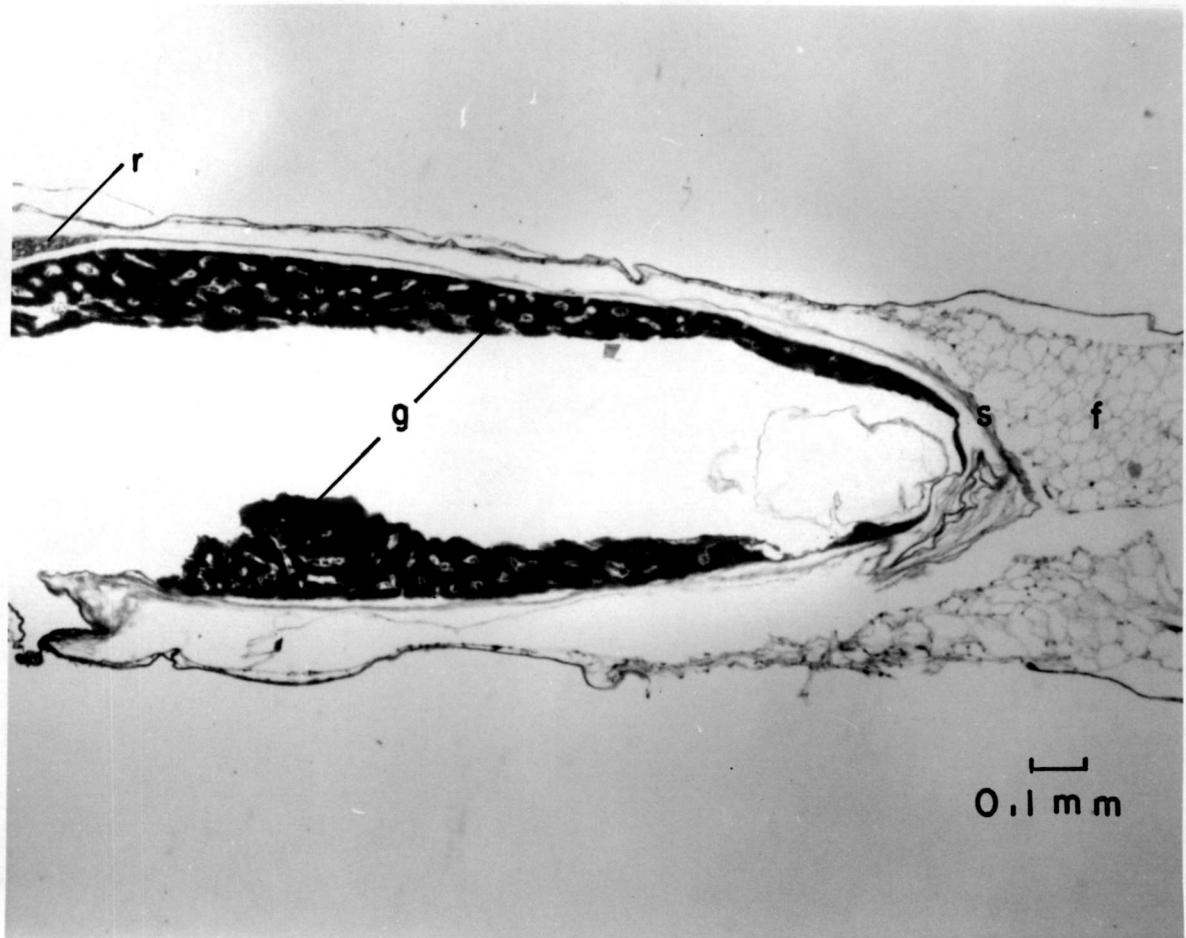


Figure 3. Fat invested swimbladder of Stenobranchius leucopsarus, 36 mm. e = tunica externa, f = fat-filled tissue, g = gas gland, r = retia mirabilia, s = submucosa

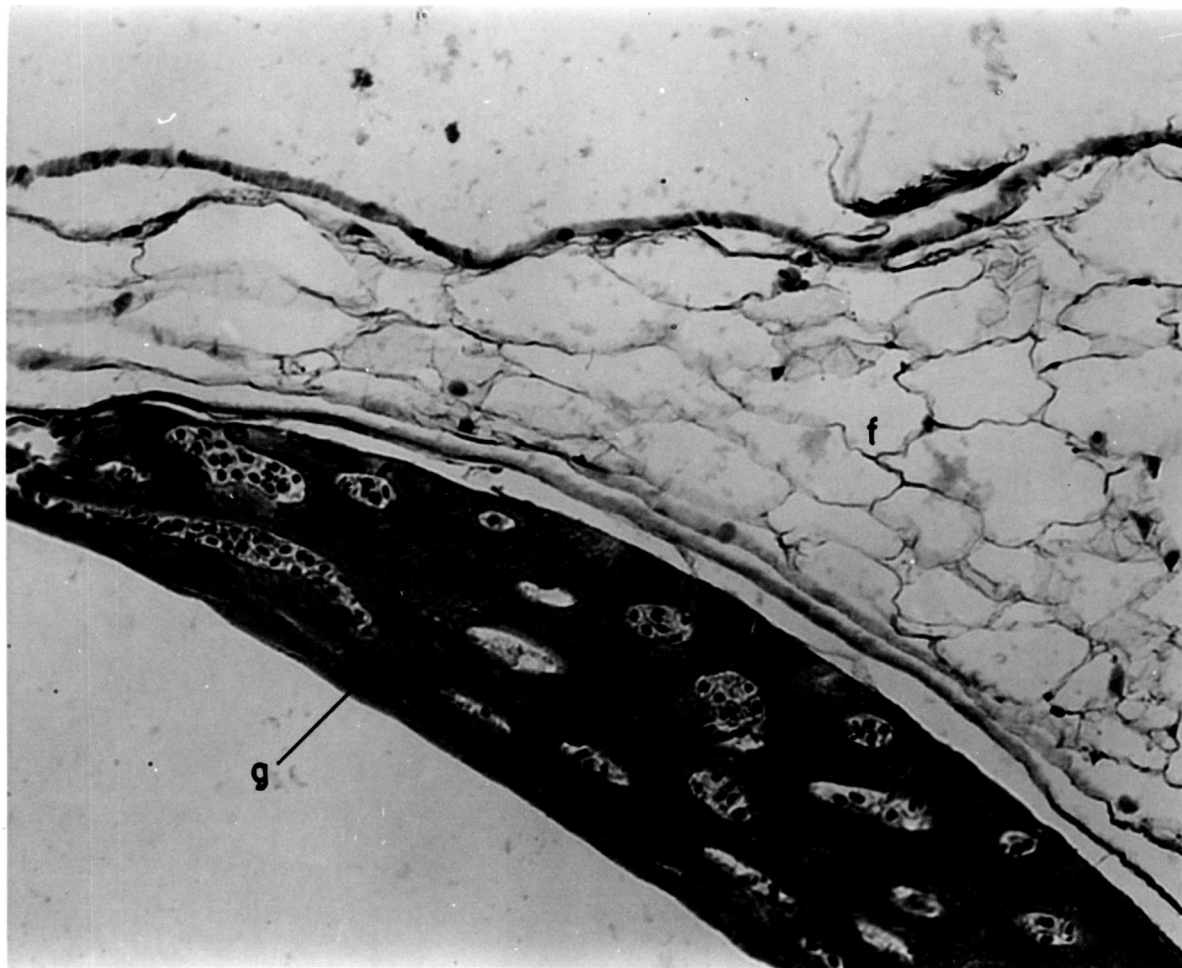


Figure 4. Fat-filled, reticular tissue of S. leucopsarus, 41 mm.  
f = fat-filled tissue, g = gas gland



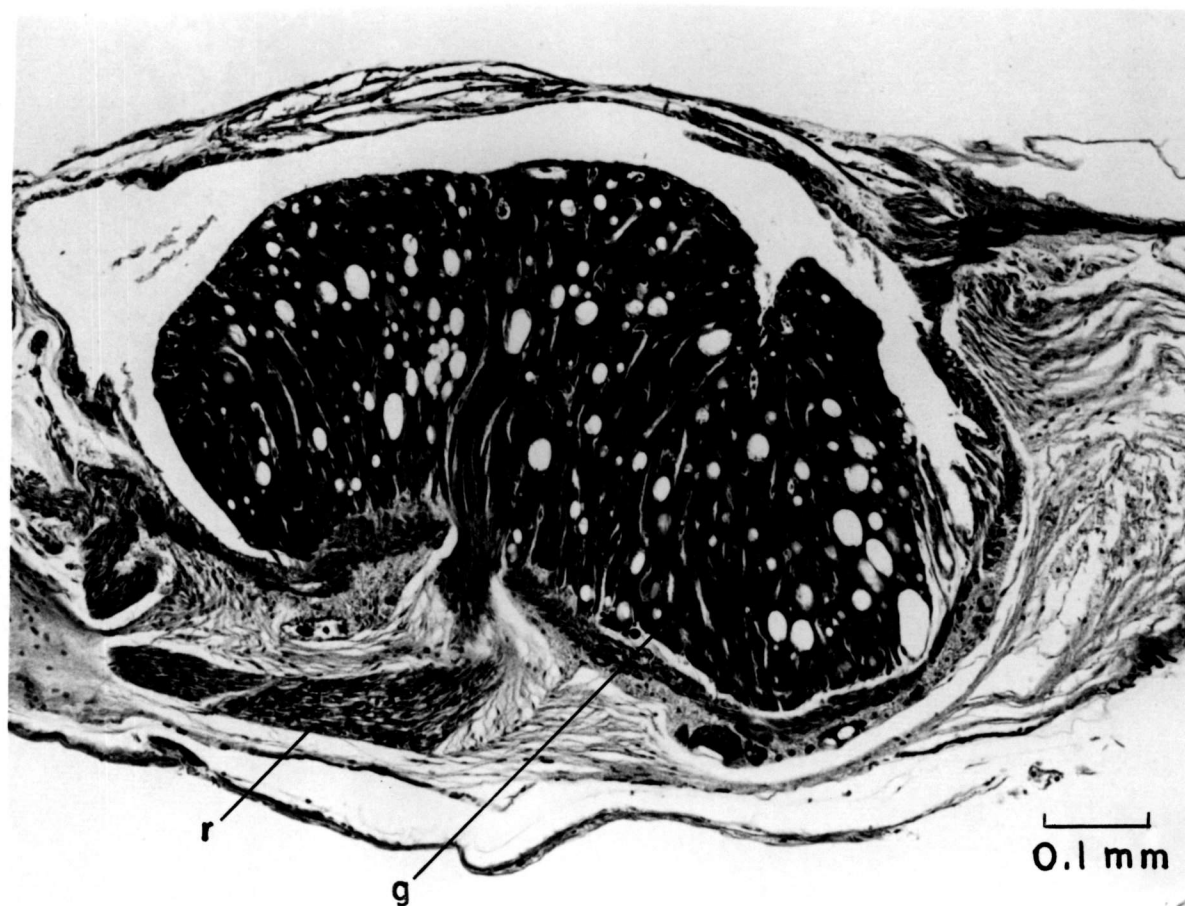


Figure 5. Reduced swimbladder of *L. ritteri*, 89 mm. r = retia mirabilia, g = gas gland

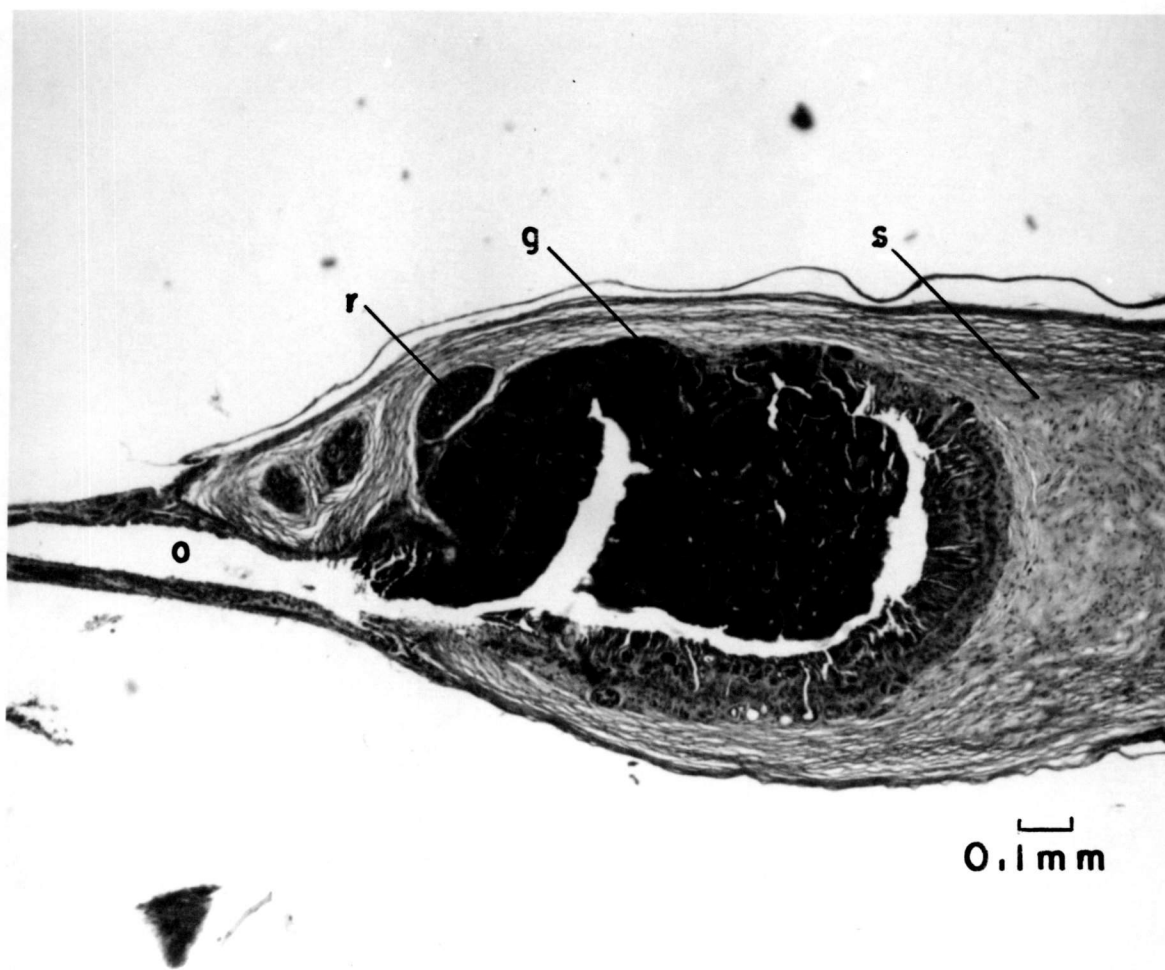


Figure 6. *Tarletonbeania crenularis*, 53 mm. g = gas gland, r = retia mirabilia, s = submucosa, o = oval

Table 1. Swimbladder Morphology

<u>Species</u>	<u>Thin walled</u>	<u>Fat invested</u>	<u>Reduced</u>
<u>Stenobranchius leucopsarus</u> Eigenmann and Eigenmann 1890	S	L	
<u>Stenobranchius nannochir</u> Gilbert 1891	S	L	
<u>Lampanyctus ritteri</u> Gilbert 1915	S		L
<u>Lampanyctus regalis</u> Gilbert 1891	S		L
<u>Diaphus theta</u> Eigenmann and Eigenmann 1891	S L		L
<u>Tarletonbeania crenularis</u> Jordan and Gilbert 1880	S L		L
<u>Protomyctophum thompsoni</u> (Chapmann 1944)	S L		
<u>Protomyctophum crockeri</u> (Bolin 1939)	S L		

S small individuals

L large individuals

The swimbladders of the two Stenobranchius, S. leucopsarus and S. nannochir, undergo similar transformations with age. Fat is deposited in a reticular tissue on the anterior and posterior ends of the juvenile swimbladder (Figures 3 and 4). This tissue 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 bound by the outer layer (Figure 3). It may represent a modification of the connective tissue in the submucosa layer. As the fish grows longer, the fatty tissue increases while the juvenile swimbladder is reduced. In large adults only a tube of fatty tissue remains. The volume of the swimbladder decreases from 4 to 5.6 percent of total body volume in juveniles to only 0.3 to 0.5 percent in adults (Figure 7 and Table IIa).

Capen (1967) found similar changes in S. leucopsarus off southern California. He correctly described the adult swimbladders as fat-invested rather than fat-filled as reported by earlier authors (Ray, 1950; Jollie, 1954; and Barhan, 1957). However, the fatty cells do not form outside the swimbladder as Capen described, but within the wall itself (Figure 3).

The swimbladders of L. ritteri and L. regalis regress as the fishes grow longer but they do not become invested with fat. The size of the swimbladder decreases from 1 to 2 percent in small individuals to 0.01 percent or less of body volume in large adults (Tables IIb and IIc). With age the swimbladder wall thickens with connective tissue, and the lumen is occluded by the gas gland (Figure 5).

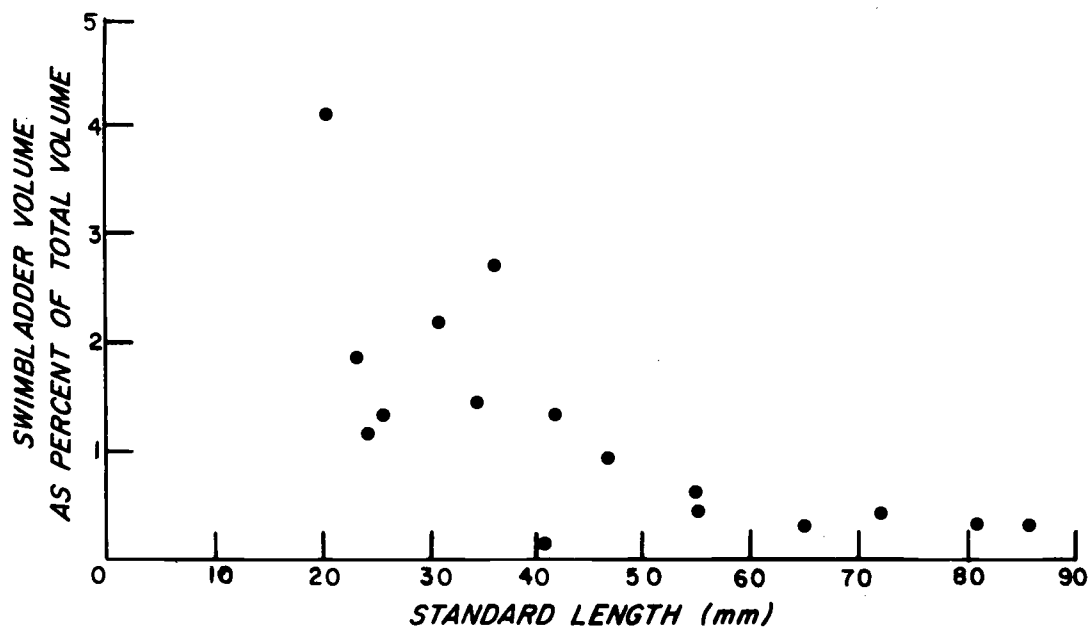


Figure 7. Swimbladder volume versus length of *Stenobranchius leucopsarus*

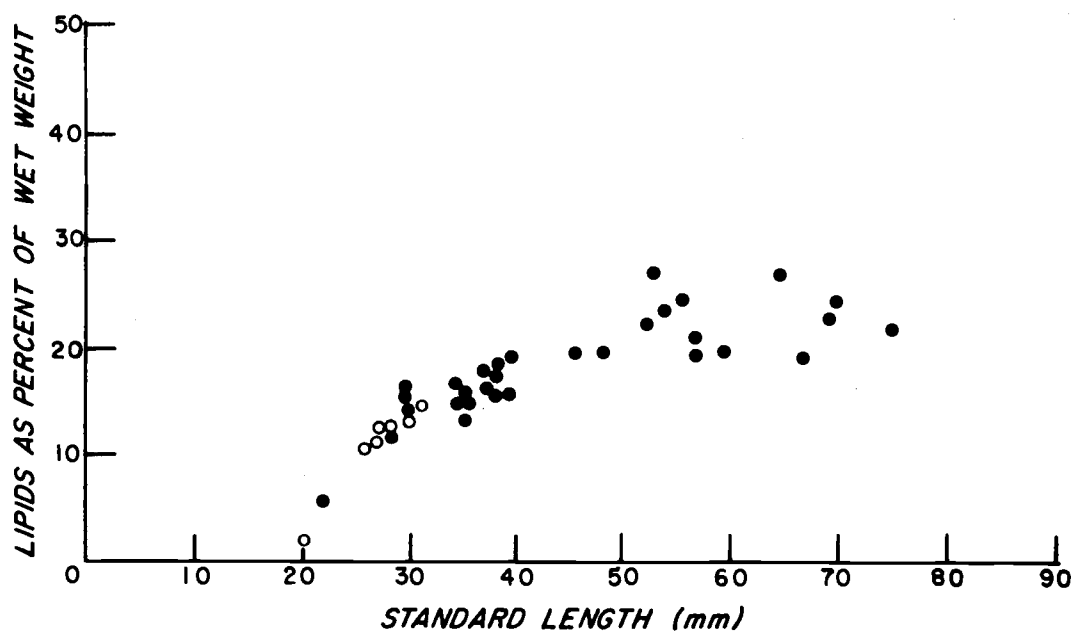


Figure 8. Lipid content versus length of *Stenobranchius leucopsarus* ● = individual ○ = >10 individuals

Table IIa

Estimated Swimbladder Volume of Stenobranchius nannochir

<u>Standard Length mm.</u>	<u>Swimbladder Volume mm.<sup>3</sup></u>	<u>Percent of Total Body Volume</u>
23	3.1	5.6
29	1.8	1.4
30	1.0	0.8
35	0.1	0.1
40	6.8	2.1
41	5.5	1.4
44	4.8	0.9
47	4.2	0.6
54	7.9	0.7
59	7.6	0.7
64	16.4	0.8
68	12.3	0.9
72	14.1	0.4
82	31.3	0.6
93	41.1	0.6
98	52.0	0.6
104	53.3	0.5
109	47.2	0.4

Table IIb

Estimated Swimbladder Volume of Lampanyctus ritteri

<u>Standard Length mm.</u>	<u>Swimbladder Volume mm. <sup>3</sup></u>	<u>Percent of Total Body Volume</u>
22	1.2	2.2
29	0.7	0.6
33	1.0	0.5
37	0.3	0.1
41	0.5	0.1
49	0.6	0.1
53	0.4	0.03
58	0.2	0.02
64	0.5	0.02
66	0.7	0.02
71	0.9	0.03
84	0.5	0.01
89	1.2	0.02
99	1.4	0.02
107	0.1	0.001

Table IIc

Estimated Swimbladder Volume of Lampanyctus regalis

<u>Standard Length mm.</u>	<u>Swimbladder Volume mm. <sup>3</sup></u>	<u>Percent of Total Body Volume</u>
30	1.2	0.8
34	1.7	0.5
38	4.3	1.5
40	4.5	1.4
50	1.1	0.1
53	3.6	0.4
59	3.3	0.2
62	0.6	0.03
68	1.1	
73	2.7	0.07
80	1.0	0.02
83	0.5	0.01



The swimbladders of D. 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 9 to 22 mm<sup>3</sup> or about 6 to 7 percent of the total body volume (Table IIId). In large specimens the swimbladder volume was as low as 3 to 9 mm<sup>3</sup>, only 0.1 to 0.5 percent of body volume. There was considerable variability in the large specimens, however. Some specimens had reduced, thick-walled swimbladders with the lumen occluded by the gas gland (Figure 1), but other adults of the same size had small swimbladders that were not occluded. Barham (1957) reported that the swimbladders of D. theta were partially or wholly occluded by fatty material, while Capen (1967) found that all adult swimbladders were filled with a "cottony tissue" outgrowth from the gas gland.

The swimbladders of large T. crenularis also had two forms. Small reduced swimbladders were present in some specimens (Figure 6), while thin-walled, capacious swimbladders were present in others. The volume was 0.5 percent or less of total volume in reduced forms or greater than 6 percent in thin-walled forms (Table IIe). Thin-walled swimbladders predominated in specimens less than 40 mm; reduced swimbladders predominated in larger specimens.

Both P. thompsoni and P. crockeri had thin-walled swimbladders in all sizes. In both species, however, the volume of the swimbladder was not great and in some specimens it was quite small

Table IIId

Estimated Swimbladder Volume of Diaphus theta

Standard Length mm.	Swimbladder Volume mm. <sup>3</sup>	Percent of Total Body Volume
23	9.1	6.8
23	8.6	6.0
29	22.0	6.4
32	8.2	1.8
37	5.6	0.7
37	4.4	0.5
38	2.2	0.3
39	0.3	0.02
41	1.4	0.2
41	5.9	0.6
42	1.5	0.1
46	3.9	0.3
53	5.1	0.2
57	2.0	0.03
57	51.1	1.68
57	3.6	0.1
63	9.1	0.2
64	4.1	0.1
64	2.7	0.1
67	4.3	0.1

Table IIe

Estimated Swimbladder Volume of Tarletonbeania crenularis

<u>Standard Length mm.</u>	<u>Swimbladder Volume mm.<sup>3</sup></u>	<u>Per cent of Total Body Volume</u>
24	5.8	6.8
28	7.5	4.0
34	7.0	2.3
37	1.1	0.2
40	0.6	0.1
42	13.7	2.3
44	3.6	0.5
45	3.0	0.4
46	28.1	3.4
52	74.4	5.8
53	5.7	0.4
56	6.6	0.5
62	160.3	7.3
66	2.8	0.1
75	333.6	6.9

(Tables II<sub>f</sub> and II<sub>g</sub>). In these specimens the swimbladder appeared collapsed, but the lumen was not occluded by an enlarged gas gland as in the reduced swimbladders of the above species.

### Swimbladder Gas

The occurrence of swimbladder gas for individual species is noted in Table III. Gas was found in small S. leucopsarus and L. regalis, in small and large D. theta and T. crenularis, in large P. thompsoni, and in small P. crockeri. All of these gas-filled swimbladders conformed to the thin-walled capacious swimbladders described above. Gas was never found in the fat-filled swimbladders of large S. leucopsarus nor the reduced swimbladders of large L. ritteri. Some but not all large T. crenularis and D. theta had gas inclusions; those without gas had reduced swimbladders. The presence of gas in thin-walled swimbladders and the absence of gas in fat-invested or reduced swimbladders corroborates the findings based on the morphology of preserved specimens. Therefore the absence of gas in large S. nannochir and L. regalis and the presence of gas in both small and large P. crockeri may be inferred on the basis of the swimbladder morphology and the presence or absence of gas found in their congeneric species pair.

### Lipid Content

The highest fat content was found in those species which lack a gas-filled swimbladder as adults; the lowest fat content occurred in species which retain a gas-filled swimbladder (Table IV).

Table II<sub>f</sub>Estimated Swimbladder Volume of Protomyctophum thompsoni

<u>Standard Length mm.</u>	<u>Swimbladder Volume mm.<sup>3</sup></u>	<u>Percent of Total Body Volume</u>
18	0.8	1.3
23	5.8	4.5
25	2.3	1.2
34	20.0	3.5
35	5.2	0.9
36	7.1	1.0
38	3.4	0.6
42	12.8	1.3
42	39.5	4.0
44	61.1	5.5
48	24.9	1.6
51	5.8	0.3

Table IIg

Estimated Swimbladder Volume of Protomyctophum crockeri

<u>Standard Length mm.</u>	<u>Swimbladder Volume mm.<sup>3</sup></u>	<u>Percent of Total Body Volume</u>
21	6.6	3.4
24	1.4	0.6
26	0.9	0.4
30	12.8	2.9
34	2.1	0.5
35	15.6	2.5
35	3.2	0.6
37	18.0	2.6

Table III. Swimbladder Gas

<u>Species</u>	<u>Presence</u>		<u>Absence</u>	
	<u>No.</u>	<u>Size</u>	<u>No.</u>	<u>Size</u>
<u>S. leucopsarus</u>	27	S 22-39mm	5	L 48-72mm
<u>S. nannochir</u>	(S)	<35mm	(L)	>35mm
<u>L. ritteri</u>	(S)	<50mm	8	L 50-102mm
<u>L. regalis</u>	1	S 50mm	(L)	>50mm
<u>D. theta</u>	11	S 17-22mm	2	S 22-24mm
	9	L 34-62mm	30	L 29-70mm
<u>T. crenularis</u>	8	S 23-33mm	2	S 29-34mm
	4	L 30-47mm	15	L 36-70mm
<u>P. thompsoni</u>	(S)			
	13	L 35-50mm		
<u>P. crockeri</u>	1	S 26mm		
	(L)			

S = Small

L = Large

( ) inferred from morphology

Table IV. Lipid Content

<u>Species</u>	<u>No.</u>	<u>% Wet Wt.</u>	<u>% Dry Wt.</u>
<u>S. leucopsarus</u> (>30 mm)	28	18.7 ± 4.0	59.8 ± 4.0
<u>S. nannochir</u> (>85 mm)	5	18.9 ± 2.5	56.8 ± 1.0
<u>L. ritteri</u> (>58 mm)	5	15.4 ± 1.6	54.1 ± 3.5
<u>L. regalis</u> (>50 mm)	5	2.2 ± 0.7	16.6 ± 4.6
<u>D. theta</u> (>35 mm)	11	11.5 ± 4.8	47.5 ± 11.5
<u>T. crenularis</u> (>23 mm)	20	4.1 ± 1.1	19.3 ± 4.4
<u>P. thompsoni</u> (>25 mm)	7 18	4.2 ± 1.7 4.9	24.6 ± 4.6 23.5
<u>P. crockeri</u> (23 mm)	1	1.4 -	11.4 -



Diaphus theta, which has a small gas-filled swimbladder or a reduced swimbladder, had a high fat content. However, T. crenularis, which also had a gas-filled or reduced swimbladder, and L. regalis, which had a reduced swimbladder, had low fat contents.

Nevenzel et al. (1969) also analyzed the lipid content of S. leucopsarus, L. ritteri, D. theta and T. crenularis. My values for lipid content agree with theirs, except I found that small S. leucopsarus had low lipids.

The lipid content of S. leucopsarus is directly related to the size of the individual (Figure 8). The lipid content of 12 small individuals (19-21 mm) was only 2.1 percent of wet weight (22.1 percent of dry weight), while adults (>30 mm) had an average lipid content of 18.7 percent of wet weight (59.8 percent of dry weight) (Table IV). The lipid content increased rapidly between 20 mm to 40 mm in length. Variability of values also increased with size. The inverse relationship between lipid content and swimbladder size (Figures 7 and 8) suggests that lipids assume the buoyancy function of the swimbladder as it regresses.

The lipid content of T. crenularis was low and did not increase with growth (Table IV). The slope of a regression line fitted to length versus lipid content as a percent of wet weight for 22 specimens (22-70 mm) was 0.06 and did not differ significantly from zero. The difference in lipid content between fish with gas and fish without gas was also not significant ( $t=0.42$ ,  $d.f.=15$ ). The unchanging

lipid content indicates that lipids do not become a major buoyancy mechanism, even when the swimbladder is reduced in this species.

### Specific Gravity

The specific gravities of thawed S. leucopsarus, S. nannochir, L. ritteri, and D. theta that were frozen at sea are within or near the density of sea water (1.026 - 1.030) (Table V). All specimens, however, with the exception of T. crenularis were without scales. The live animals are probably denser than the results indicate.

Bracketing the specific gravity of fresh specimens in gum arabic solutions produced similar results for S. leucopsarus and L. ritteri. The specific gravity of 17 fresh S. leucopsarus with gas and three without gas was less than 1.030. The specific gravity of two specimens with gas and two without gas was between 1.030 and 1.042. The specific gravity of three fresh L. ritteri was between 1.030 and 1.048.

Since gas was not present in the frozen specimens or in some of the fresh specimens the low specific gravity can only be attributed to the fat content. Although many specimens appear to have neutral buoyancy without gas, the fat content is not as great as Taylor (1921) predicted for neutral buoyancy. The theoretical value, based on a specific gravity of 1.076 for fat free tissue and 0.925 for lipids is 29.23 percent of the wet weight. The highest observed lipid values, however, were only 18.9 percent (Table IV). A lower density for either material would explain the low specific gravity of the fishes with the observed fat content.

Table V. Specific Gravity of Thawed Fishes Frozen at Sea

<u>Species</u>	<u>Standard Length</u>	<u>Specific Gravity</u>
<u>S. leucopsarus</u>	58	1.028
	58	1.028
	73	1.031
	73	1.025
	80	1.026
<u>S. nannochir</u>	90	1.026
	102	1.026
<u>L. ritteri</u>	73	1.023
	90	1.030
<u>L. regalis</u>	84	1.041
	85	1.040
<u>D. theta</u>	40	1.039
	57	1.025
	58	1.026
	64	1.062
<u>T. crenularis</u>	41	1.089
	59	1.088

The type of lipids found in myctophids suggests that this material is, in fact, 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 are less dense than cod liver oil, which is composed of lipids with chain lengths of 18 to 20 (Morrison and Boyd, 1966). Thus low density lipids may provide neutral buoyancy for S. leucopsarus, S. nannochir and L. ritteri and for D. theta in conjunction with a small gas-filled swimbladder.

Thawed specimens of T. crenularis were denser than sea water (Table V). Fresh specimens with gas-filled swimbladders were somewhat lighter, but without gas-filled swimbladders they were about the same specific gravity as thawed specimens (Table VI). These high densities correlate with a low fat content (Table IV). Without a gas-filled swimbladder T. crenularis must swim constantly to maintain position. The thin caudal peduncle and migrations to the surface at night are consistent with an active existence.

Although the specific gravity of a fresh specimen of L. regalis with gas (50 mm) was less than 1.030, large specimens without gas were denser than sea water but not as dense as T. crenularis. The broad caudal peduncle and flacid body (water is 86 percent of the wet weight in L. regalis, 72 percent of the wet weight in L. ritteri) suggest a less active life than T. crenularis. In fact large L. regalis without a gas-filled swimbladder may approach neutral buoyancy by the reduction of skeletal and muscular tissue in the same manner as bathypelagic fishes (Denton and Marshall, 1958).

Table VI

Presence of Swimbladder Gas Determined by Dissection at Sea  
 and Specific Gravity of Fresh Tarletonbeania crenularis  
 Determined Using Gum Arabic Solutions at Sea

<u>Standard Length (mm)</u>	<u>Gas</u>	<u>Specific Gravity</u>
23	yes	1.042 - 1.048
27	yes	1.042 - 1.048
28	yes	1.048 - 1.054
30	yes	1.061 - 1.067
31	yes	1.042 - 1.048
31	yes	1.054 - 1.061
33	yes	1.042 - 1.048
36	yes	1.048 - 1.054
37	yes	1.067 - 1.072
40	yes	1.054 - 1.061
41	no	1.083 - 1.092
45	no	1.083 - 1.092
46	no	1.083 - 1.092
47	no	1.083 - 1.092
47	yes	1.083 - 1.092
49	no	1.083 - 1.092
51	no	1.083 - 1.092
64	no	
70	no	1.073 - 1.083

Although no specific gravity measurements were made for P. thompsoni and P. crockeri, the low fat content and presence of gas-filled swimbladder in adults suggests that gas remains the important buoyancy mechanism throughout the life of these species. Gas is of course the principal buoyancy mechanism in small individuals of all species.

The change from gas to fat as a buoyancy mechanism may be related to the migratory habits of some myctophids. Of the species with a well developed gas-filled swimbladder, P. thompsoni has been reported from a non-migratory scattering layer, while S. leucopsarus is reported to make extensive vertical migrations (Taylor, 1967). If a gas-filled swimbladder does restrict vertical migration, juveniles may make less extensive migrations than adults of the same species without a gas-filled swimbladder. Since the juveniles may be resonant sound scatterers, a differential migration of juveniles and adults would explain Taylor's (1967) catches of larger individuals below daytime scattering layers.

Of the mechanisms available to teleosts a gas-filled swimbladder is the most efficient method of maintaining neutral buoyancy. However, a non-compressible material such as lipids may be more efficient for mesopelagic fishes which make extensive migrations. Bathypelagic fishes may have lost the swimbladder because there is insufficient potential energy in the environment to support the 'extra' tissue that can be carried by this organ (Marshall, 1960). Myctophids off Oregon have adopted all of these modes of existence.

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