

SWIM-BLADDER STATE AND STRUCTURE IN RELATION TO BEHAVIOR AND MODE OF LIFE IN STROMATEOID FISHES

MICHAEL H. HORN¹

ABSTRACT

Fourteen of the 15 genera of stromateoid fishes possess a relatively small (0.6-3.4% of body volume), euphysoclistous swim bladder which forms early in life (3-5 mm standard length) and regresses in all genera except possibly *Nomeus* before maturity (150-200 mm standard length) is reached. The organ is thus an almost exclusive characteristic of the juveniles which occupy surface layers (upper 100-150 m) in coastal and oceanic waters.

The gas gland of the swim bladder consists of cuboidal to irregularly shaped cells 6-46 μ m in greatest dimension. The retia mirabilia range in length from 0.4 to 2.0 mm and in diameter of individual capillaries from 4 to 10 μ m. The area of the gas gland and the length of the retia relative to the size of the swim-bladder lumen are great compared to the same in other epipelagic fishes and are similar to those of deeper living, mesopelagic fishes. The relatively large gas-secreting complex is considered to be an adaptation for rapid and efficient gas secretion in maintaining hydrostatic equilibrium as the juvenile fishes swim in the surface layers, frequently in association with floating objects, where pressure changes are greatest with depth.

Swim-bladder loss accompanies changes in behavior and mode of life and is part of the transition from the juvenile to the adult stage of life. Hovering and high maneuverability as principal components of locomotor behavior in juveniles give way to continuous swimming in adults which are generally independent of floating objects and occupy a greater depth range. The relative length of the paired fins changes with age and varies among the species. *Peprilus triacanthus* and *P. simillimus*, negatively buoyant, active swimmers, have long pectoral fins as adults whereas *Schedophilus medusophagus*, a neutrally or nearly neutrally buoyant, slow-moving fish, has short pectoral fins. Both *P. simillimus* and *S. medusophagus* have high levels of lipid which may serve to replace the swim bladder in a buoyancy function when the fishes are adults.

The swim bladder (or gas bladder), a gas-filled organ unique to bony fishes, has its greatest functional significance as a hydrostatic device, i.e., one that provides neutral or nearly neutral buoyancy to the fish. It is one of the most plastic of vertebrate organs (Marshall 1960) and occurs in a great diversity of fishes from a variety of habitats. The swim bladder is not necessary for life as it is absent in many fishes, but according to Fänge (1966) about one-half of the 20,000 existing species have it as adults and even more as larvae or juveniles. The organ, owing to its diversity of form and widespread occurrence, should reflect in its presence or absence and structure the behavior and mode of life of the fishes possessing it. In stromateoid fishes, the swim bladder regresses in 13, possibly 14, of the 15 genera, and the regression seems to be associated with other morphological changes and changes in mode of life (Horn 1970a).

The swim bladder of stromateoid fishes has received little mention in the literature partly due to its absence or reduced state in adults. Goode and Bean (1895) and Jordan and Evermann (1896) stated that the organ was "usually absent" in the Stromateidae, and the former as well as Grey (1955) reported its absence in the Tetragonuridae. Fowler (1936) in his treatment of several stromateoid genera indicated that the swim bladder was "present or absent." Goode and Bean (1895) stated that it was present in *Nomeus* as did Haedrich (1967) for *Ariomma*. Based upon an examination of approximately one-half of the species in the group, I have found the organ to be present at some stage (larval and/or juvenile) in the life of all stromateoid genera except *Pampus*. Even in *Pampus* it may be present at an early stage since larvae or small juveniles (< 20 mm SL, standard length) were not studied.

The perciform suborder Stromateoidei consists of 6 families, 15 genera, and about 60 species (Haedrich and Horn 1972) and is characterized by toothed saccular outgrowths in the gullet and by

¹Department of Biology, California State University, Fullerton, CA 92634.

small teeth approximately unilateral in the jaws (Haedrich 1967). The larvae and juveniles occur mainly in the surface layers of the ocean and are frequently associated with animate or inanimate floating objects. The adults, ranging in maximum size from about 30 to 120 cm, form a diverse group of temperate and tropical species which variously occupy a wide range of depths in coastal and oceanic waters (including mesopelagic and bathypelagic levels). The Centrolophidae (six genera) are either coastal or oceanic, the Stromateidae (three genera) are coastal, the Amarsipidae (one genus), Nomeidae (three genera), and Tetragonuridae (one genus) are oceanic, and the Ariommidae (one genus) are benthopelagic on the continental shelf and slope.

The purposes of the present paper are to 1) describe the morphology and histology of the stromateoid swim bladder, 2) compare the dimensions and capabilities of the stromateoid swim bladder with that of other fishes of similar and different habitats, and 3) discuss the relationship of swim-bladder state and structure to the behavior and mode of life of stromateoids based upon the results of the present and other studies.

MATERIALS AND METHODS

The majority of specimens examined (Table 1) for swim-bladder structure and other morphological detail were preserved although fresh or frozen material of several species was studied. Observations on the behavior of certain species were made and are briefly described in appropriate sections of the paper.

Specimens in addition to those personally collected were obtained from the following institutions: British Museum (Natural History), London; Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; Institute of Oceanographic Sciences, Wormley, England; Natural History Museum of Los Angeles County, Los Angeles, Calif.; Scripps Institution of Oceanography, La Jolla, Calif.; Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla; Woods Hole Oceanographic Institution, Woods Hole, Mass.; and Zoological Museum, Copenhagen, Denmark.

Swim-bladder dimensions were measured with an ocular micrometer in either a dissecting or compound microscope or, in large specimens, with

TABLE 1.—Stromateoid specimens examined for swim bladder and other morphological characteristics.

Family and species	Number of specimens	Size range (mm SL)
Centrolophidae:		
<i>Hyperoglyphe antarctica</i>	4	23.4- 34.9
<i>Hyperoglyphe perciformis</i>	2	35.8, 47.7
<i>Schedophilus huttoni</i>	1	22.9
<i>Schedophilus maculatus</i>	2	70.2, 77.5
<i>Schedophilus medusophagus</i>	7	10.4-285.0
<i>Centrolophus maoricus</i>	3	15.1-127.8
<i>Centrolophus niger</i>	2	124.0, 231.0
<i>Ichthyos lockingtoni</i>	20	3.5-268.0
<i>Seriola punctata</i>	2	132.0, 162.6
<i>Seriola violacea</i>	3	12.8- 84.0
<i>Psenopsis cyanea</i>	2	94.2, 104.2
Stromateidae:		
<i>Stromateus brasiliensis</i>	7	75.7-167.3
<i>Stromateus fiatola</i>	9	12.5- 93.5
<i>Stromateus stellatus</i>	5	17.5- 99.4
<i>Peprilus burti</i>	3	57.4- 95.1
<i>Peprilus paru</i>	10	28.6-123.0
<i>Peprilus simillimus</i>	17	2.0-135.0
<i>Peprilus triacanthus</i>	10	12.0-120.4
<i>Pampus argenteus</i>	7	24.6- 49.0
<i>Pampus chinensis</i>	6	25.4- 67.3
Amarsipidae:		
<i>Amarsipus carlsbergi</i>	3	22.0- 67.5
Nomeidae:		
<i>Cubiceps caeruleus</i>	1	18.5
<i>Cubiceps carinatus</i>	1	8.5
<i>Cubiceps gracilis</i>	10	16.5-330.0
<i>Nomeus gronovii</i>	13	11.6-142.7
<i>Psenes arafurensis</i>	2	17.0, 18.0
<i>Psenes cyanophrys</i>	17	9.1-120.0
<i>Psenes maculatus</i>	1	33.6
<i>Psenes pellucidus</i>	2	26.9, 34.8
Unidentified (probably <i>Psenes</i>)	5	3.4- 12.3
Tetragonuridae:		
<i>Tetragonurus cuvieri</i>	13	4.0-242.0
Ariommidae:		
<i>Ariomma bondi</i>	7	20.9-124.3
<i>Ariomma indica</i>	1	59.7
<i>Ariomma melanum</i>	2	each 134.1
<i>Ariomma regulus</i>	3	123.3-150.0
<i>Ariomma</i> sp.	1	16.5
(either <i>A. bondi</i> or <i>A. melanum</i>)		
Total number of specimens	204	

dial calipers. Swim-bladder and body volumes were determined by displacement and/or, for the former, calculated on the assumption that the bladder was a prolate spheroid ($v = 4/3\pi ab^2$, where a and b are the major and minor semiaxes (see Capen 1967)). Volume measurements were made from swim bladders that were in most cases well expanded. Ten percent was allowed for shrinkage of preserved material.

Transverse or longitudinal serial sections of the swim bladder of 13 genera and species were cut at 8- μ m thickness and stained with haemalum and eosin.

Buoyancy determinations were made by weighing each fish in air and in water of known temperature and salinity. Results are expressed as the percentage of the air weight that each fish weighed in seawater.

RESULTS

Swim-Bladder Structure

The stromateoid swim bladder is of the physoclistous, two-chambered type usually found in perciform fishes (Horn 1970a) (Figure 1). The delicate, thin-walled sac lies in the upper part of the body cavity above the gut and below the kidney and is closely invested by the dorsal peritoneum. A muscular diaphragm (not always visible) divides the bladder into anterior and

posterior chambers (Figures 1, 2), the latter of which serves a gas-resorbing function (a euphysoclistous condition). The gas gland, associated with the anterior chamber, typically forms a U-shape and may be single or divided into two or more lobes (Figure 1). Cells composing the gland are cuboidal to irregular in shape and usually in two or more layers (Figures 2-5). Some cells appear to be either syncytial or of the giant type found widely distributed in marine euphysoclists (Fänge 1953) and in some deep-sea fishes (Marshall 1960). The retia mirabilia are unipolar,

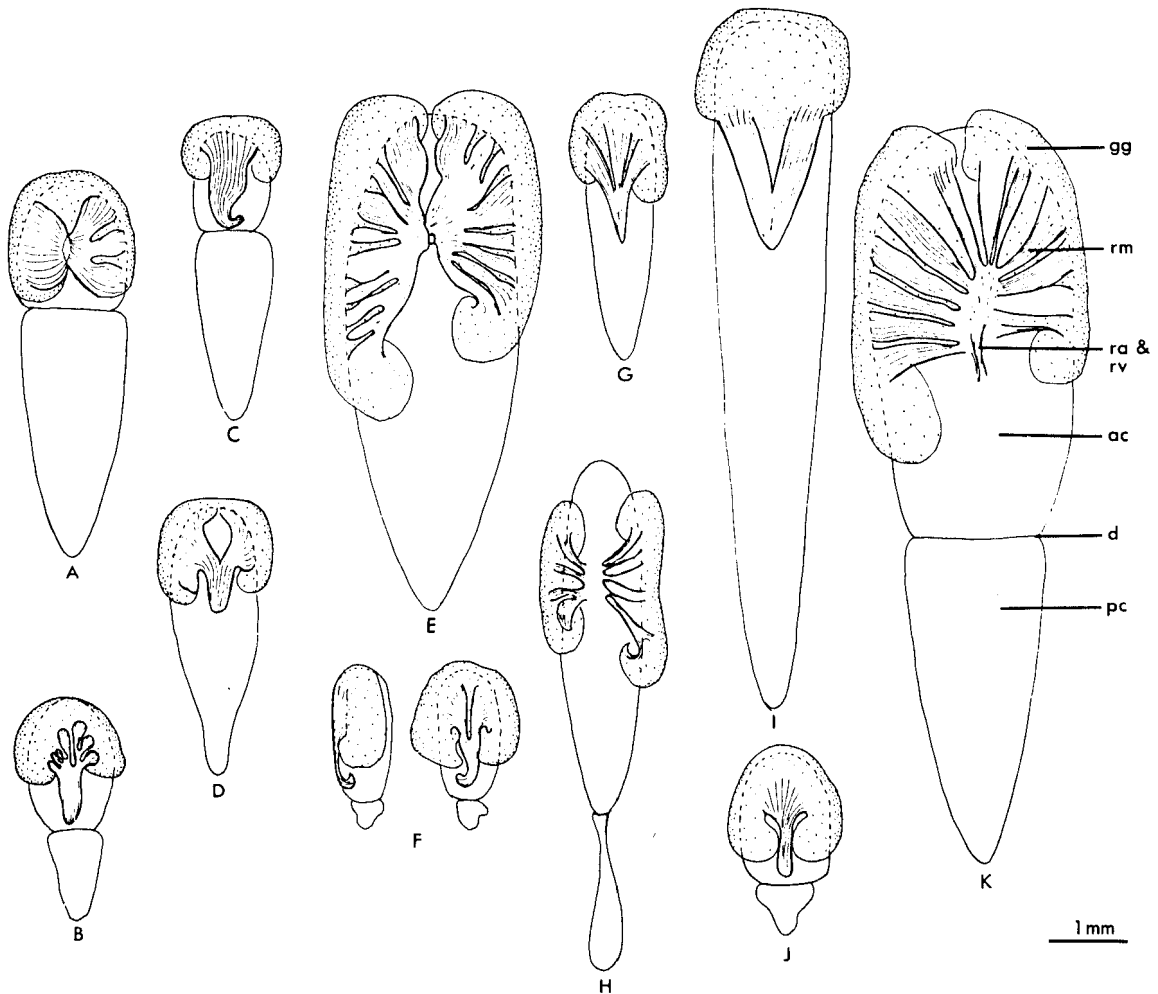


FIGURE 1.—Ventral view of the swim bladder of 11 species of stromateoids (all drawn to same scale). gg, gas gland (slightly flattened and expanded); rm, rete mirabile; ra and rv, retial artery and retial vein; ac, anterior chamber; d, diaphragm; pc, posterior chamber. A, *Ariomma bondi*, 24.2 mm SL; B, *Centrolophus maoricus*, 15.1 mm SL; C, *Tetragonurus cuvieri*, 28.8 mm SL; D, *Serirolella violacea*, 12.8 mm SL; E, *Cubiceps gracilis*, 30.5 mm SL; F, *Schedophilus medusophagus*, 17.4 mm SL (lateral and ventral view); G, *Psenes cyanophrys*, 11.5 mm SL; H, *Nomeus gronovii*, 26.4 mm SL; I, *Stromateus fiatola*, 34.1 mm SL; J, *Ichthyos lockingtoni*, 16.3 mm SL; K, *Hyperoglyphe antarctica*, 34.9 mm SL.

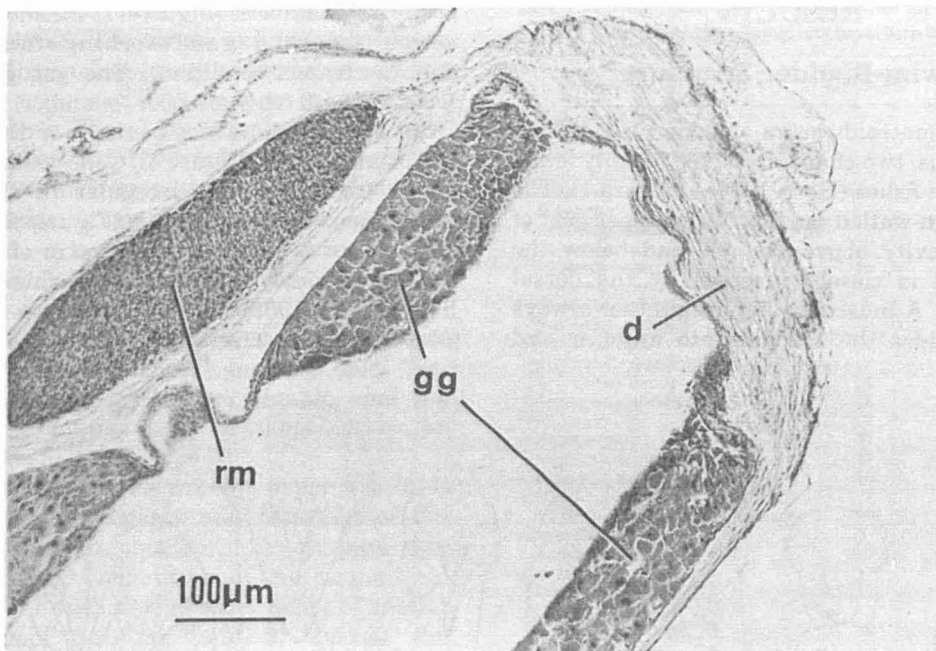


FIGURE 2.—Sagittal section of the anterior chamber of the swim bladder of *Ariomma bondi*. d, diaphragm; gg, gas gland; rm, rete mirabile. (From same specimen as Figure 1A.)

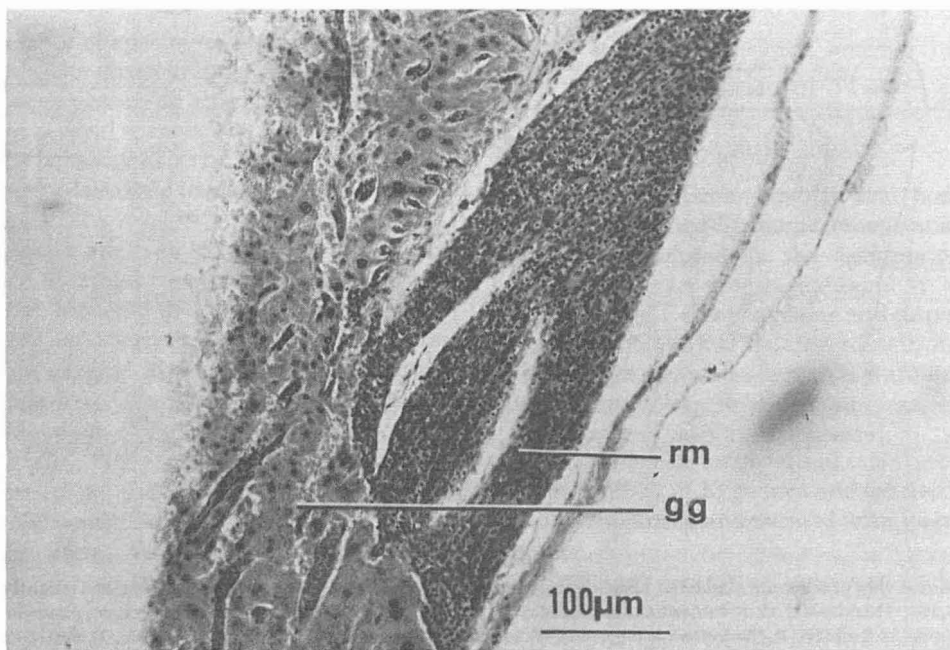


FIGURE 3.—Sagittal section of the gas secreting complex of the swim bladder of *Cubiceps gracilis*. gg, gas gland; rm, rete mirabile. (From same specimen as Figure 1B.)

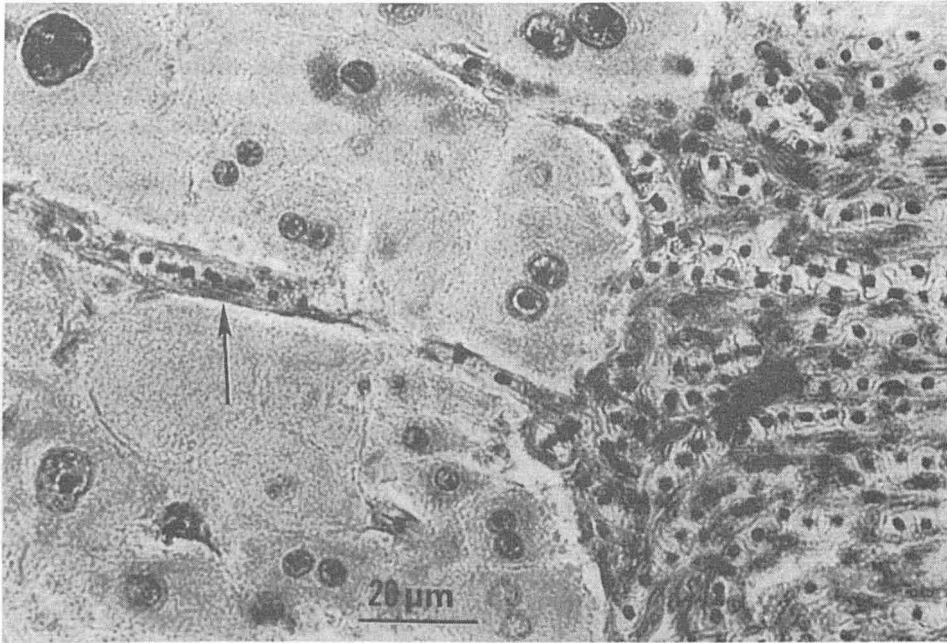


FIGURE 4.—Gas gland cells and retial capillaries of the swimbladder of *Cubiceps gracilis*. Arrow points to retial capillary between gas gland cells. (From same specimen as Figures 1E and 3.)

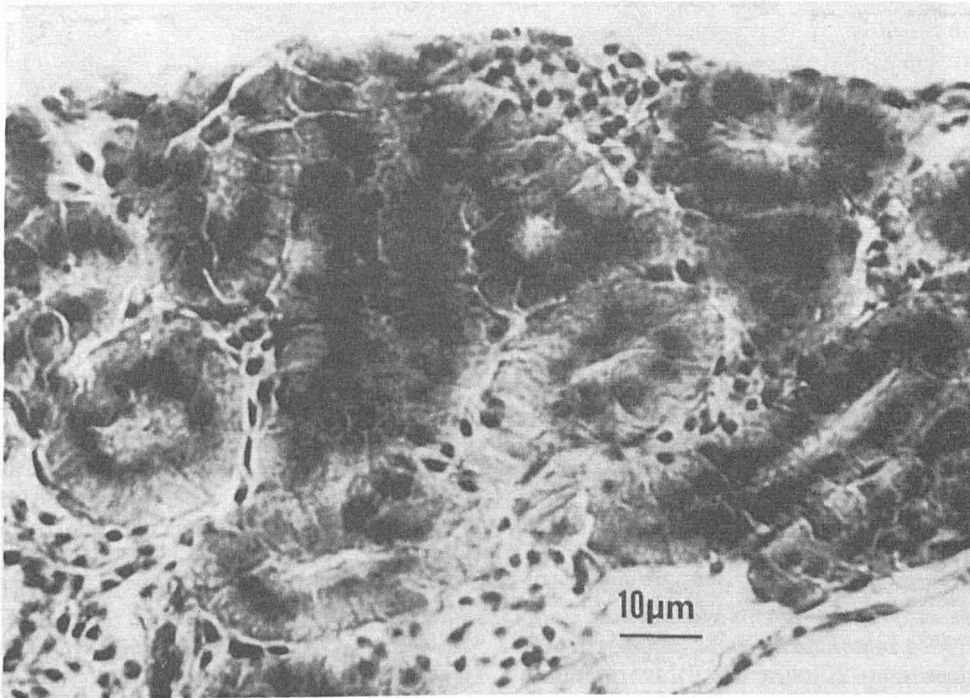


FIGURE 5.—Gas gland of *Peprilus triacanthus*, 16.5 mm SL, showing arrangement of cells. (Transverse section.)

i.e., the artery and vein subdivide to form parallel capillaries which enter the gas gland (Figures 3, 4, 6). Retial orientation varies from a position parallel to the long axis of the swim bladder to one that is perpendicular (Figure 1). Size characteristics of swim-bladder components are given in Table 2. Distinctive features of the swim bladder of the six stromateoid families are described below.

Centrolophidae

Swim-bladder volume in the fishes examined varied from less than 1% of body volume in *Schedophilus* to greater than 3% in *Hyperoglyphe*. Size (greatest dimension) of the gas gland cells ranged from 10-17 μm in *Hyperoglyphe* and *Seriolella* to 20-40 μm in *Schedophilus*. Retial length ranged from 1.1 mm in *Seriolella* to 2.0 mm

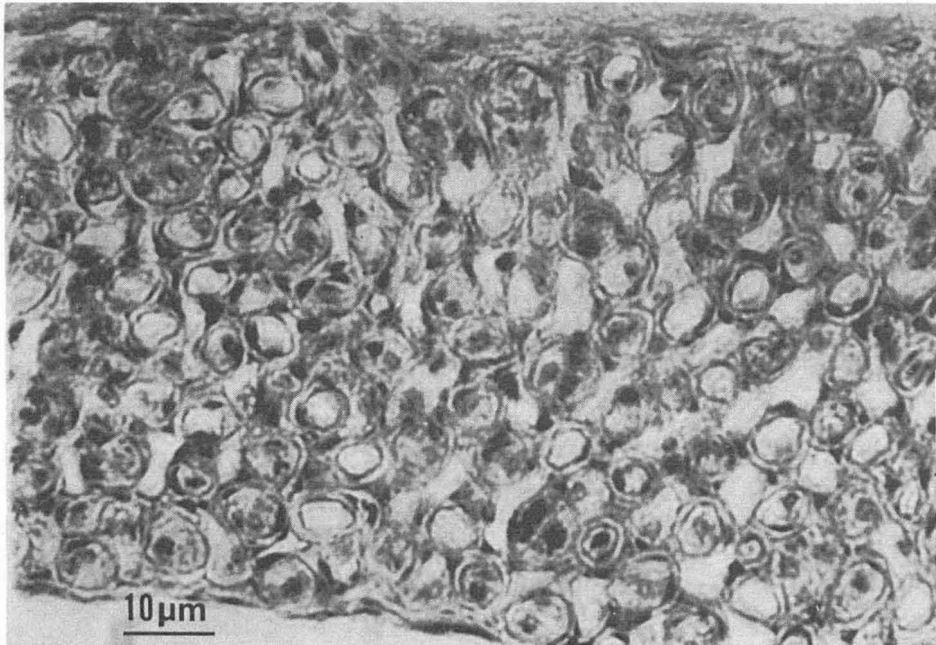


FIGURE 6.—Transverse section through the rete mirabile of the swim bladder of *Tetragonurus cuvieri*. (From same specimen as Figure 1C.)

TABLE 2.—Size characteristics of the swim-bladder lumen, gas gland, and rete mirabile in 12 species of stromateoids.

Species	Lumen				Gas gland		Rete mirabile			
	Size (mm SL)	L × W (mm)	Vol (mm ³)	Vol (%)	Area (mm ²)	Cell size (μm)	Capillary diam (μm)	Length (mm)	Total number of capillaries	Total capillary length (m)
<i>Hyperoglyphe antarctica</i>	34.9	9.8 × 2.7	37.0	3.4	5.4	10-17	7-10	1.3-2.0	2,000	2.6 -4.0
<i>Schedophilus medusophagus</i>	17.4	2.1 × 0.8	—	—	1.8	20-40	8-10	1.3	800	1.04
<i>Ichthys lockingtoni</i>	16.3	2.4 × 1.2	2.0	3.0	2.1	15-20	6-8	1.4	1,000	1.4
<i>Seriolella violacea</i>	12.8	3.5 × 1.1	—	—	1.0	10-17	4-8	1.1-1.2	1,200	1.3 -1.4
<i>Stromateus fiatola</i>	34.1	9.1 × 2.0	—	—	2.9	10-20	6-8	1.8-2.0	1,500	2.7 -3.0
<i>Peprilus triacanthus</i>	16.5	2.5 × 1.0	3.0	2.3	0.8	6-10	5-6	0.8	600	0.48
<i>Amarsipus carlsbergi</i>	22.0	2.0 × 0.8	0.7	—	1.0	8-20	4-8	0.7-0.9	1,100	0.77-0.99
<i>Cubiceps gracilis</i>	30.5	6.6 × 2.3	21.0	3.3	8.7	25-40	8-10	1.1-1.9	3,000	3.5 -5.7
<i>Nomeus gronovii</i>	26.4	6.7 × 1.0	3.5	0.7	1.6	—	—	0.4-0.6	—	—
	27.4	6.8 × 1.3	—	—	2.5	10-30	5-6	0.5-0.6	2,000	1.0 -1.2
<i>Psenes cyanophrys</i>	14.1	3.7 × 1.2	2.5	2.1	0.7	—	—	1.0	—	—
	18.6	5.1 × 1.6	—	—	6.0	25-40	5-6	0.8-0.9	1,500	1.2 -1.35
<i>Tetragonurus cuvieri</i>	28.8	3.8 × 1.0	2.0	0.6	0.6	8-20	4-10	1.3	1,000	1.3
<i>Ariomma bondi</i>	23.3	6.5 × 1.3	7.0	2.9	3.6	—	—	0.9	—	—
	24.2	5.0 × 1.4	5.0	1.7	3.7	20-46	8	0.6-0.9	2,500	1.5 -2.25

in *Hyperoglyphe*. Retial orientation was generally parallel to the long axis of the bladder, and the retial bundle either remained single anteriorly as in *Icichthys* (Figure 1J) or variously branched into smaller bundles perpendicular to the long axis as in *Hyperoglyphe* (Figure 1K). The rete bundle of *Schedophilus* had a sharp turn near the posterior end producing a sigmoid outline (Figure 1F). Swim-bladder shape which depends to a large degree upon secretory and absorptive states varied from elongate with a large posterior chamber to short and bulbous with either a small posterior chamber or no posterior chamber visible.

Stromateidae

The organ was similar in structure and shape to that of the Centrolophidae. The gas gland cells of *Peprilus triacanthus* were small (6-10 μm) and were arranged in loops and rings (Figure 5). In one *P. triacanthus* (16.5 mm SL) the retial blood vessels formed a single bundle posteriorly which expanded anteriorly over the gas gland whereas in two somewhat larger juveniles (22.2 and 33.9 mm SL) the retia were more nearly perpendicular to the long axis of the bladder and consisted of 7 or 8 distinct branches.

Amarsipidae

The swim bladder was similar to that of the Centrolophidae. The rete originated posteriorly as a single bundle and divided anteriorly into 7 or 8 distinct branches before entering the gas gland.

Nomeidae

Swim-bladder volume ranged from 0.7% in *Nomeus* to 3.3% of body volume in *Cubiceps* and gas gland size from 10-30 μm in *Nomeus* to 25-40 μm in *Cubiceps* and *Psenes*. Retial length varied from 0.4 mm in *Nomeus* to 1.9 mm in *Cubiceps*. The retia were divided into several branches and in position were more nearly perpendicular than parallel to the long axis of the bladder (Figure 1E, H). Small juvenile *Psenes cyanophrys* (9.1 and 14.1 mm SL) had retia almost parallel to the long axis of the bladder (Figure 1G) whereas larger juveniles (e.g., 60.8 mm SL) tended to have retia which were more nearly perpendicular to the long axis and more highly branched. The pattern, seen also in *Peprilus triacanthus*, may be part of the regression process that the swim bladder undergoes.

Tetragonuridae

The sac was small (0.6% of body volume) and elongate. The retial bundle was parallel to the long axis of the bladder and, as in *Schedophilus medusophagus*, had an S-shaped turn near the posterior end (Figure 1C). The gas gland was relatively small and located at the anterior end of the lumen.

Ariommidae

The swim bladder was relatively large (up to 2.9% of body volume) and elongate. The gas gland cells were in the upper range of size (20-46 μm) among the stromateoids examined, and the retia were broad, fanlike and perpendicular to the long axis of the bladder (Figure 1A).

Size at Swim-Bladder Inflation

The swim bladder becomes functional early in the life of stromateoids. Whether the larval fishes gulp air at the surface or whether gas is secreted to initially fill the bladder was not determined. Examination of larvae of four genera indicated that the organ in one species was almost completely developed at 3.0 mm SL and in three others at slightly larger sizes. Specimens of *Peprilus simillimus* as small as 3.0 mm SL had what appeared to be a fully developed swim bladder whereas in smaller individuals, e.g., 2.7 mm SL, the sac was inflated but the gas gland and retia were incomplete. The bladder was absent in a fish of 2.4 mm SL. A series of larvae, 3.4-5.0 mm SL, of an unidentified species of *Psenes* had an inflated swim bladder, and larvae of *Tetragonurus cuvieri* as small as 4.0 mm SL had a gas-filled sac which was visible through the semitransparent body wall. Individuals of *Icichthys lockingtoni*, 5.0 and 7.5 mm SL, had an inflated sac and an apparently fully developed gas gland and retial complement.

Swim-Bladder Regression

The swim bladder regresses, becomes nonfunctional, and finally disappears before the adult stage is reached in all stromateoid genera except *Pampus* in which the organ is apparently absent and possibly *Nomeus* in which the largest individual examined (142.7 mm SL) had a functional swim bladder. The regression is a

TABLE 3.—Surface area of the gas gland (mm^2) and length of the rete mirabile (mm) relative to swim-bladder volume (mm^3 or ml) or dimension (length \times width, in mm) in the European eel, certain shallow-sea and deep-sea fishes, and in 12 species of stromateoids. Total capillary length (m) = retial length \times number of retial capillaries. Retial lengths of stromateoids are means of individuals for each species.

Species	Size (mm SL)	Gas gland area \times 1,000/swim-bladder volume (mm^2)	Retial length \times 1,000/swim-bladder dimension	Total capillary length/swim-bladder volume (ml)
European eel ¹				
<i>Anguilla anguilla</i>	—	—	—	30
Shallow-sea (epipelagic): ¹				
<i>Cypsilurus cyanopterus</i>	290.0	8	0.5	—
<i>Danichthys rondelæti</i>	214.0	8	1.3	—
<i>Exocoetus volitans</i>	159.0	—	5	—
<i>Petalichthys capensis</i>	—	—	1.5	—
<i>Hyporhamphus</i> sp.	112.0	40	8	—
<i>Scomberesox saurus</i>	—	—	2	—
<i>Gadus minutus</i>	—	—	13	—
<i>Capros aper</i>	—	—	18	—
Deep-sea: ¹				
<i>Gonostoma denudatum</i>	81.0	—	76	—
<i>Pollichthys mauii</i>	43.0	—	125	—
<i>Bonapartia pedaliota</i>	67.0	—	71	—
<i>Vinciguerria attenuata</i>	43.5	140	34	—
<i>Vinciguerria nimbaria</i>	—	—	—	150
<i>Argyropelecus aculeatus</i>	23.0	140	38	50
<i>Polyipnus lateratus</i>	36.0	—	143	100
<i>Astronesthes niger</i>	41.0	250	111	—
<i>Astronesthes similis</i>	104.0	170	—	—
<i>Myctophym punctatum</i>	71.0	200	40	20
<i>Benthoosema suborbitale</i>	24.0	500	—	—
<i>Lampanyctus guntheri</i>	53.0	330	142	—
<i>Diaphus ralinæquei</i>	—	—	21	—
<i>Melamphaes megalops</i>	56.0	60	250	30
<i>Stephanoberyx monae</i>	83.5	—	63	—
<i>Chiasmodon niger</i>	104.0	250	71	—
Stromateoids:				
<i>Hyperoglyphe antarctica</i>	34.9	140	63	89
<i>Schedophilus medusophagus</i>	17.4	—	1,000	—
<i>Ichthyichthys lockingtoni</i>	16.3	1,000	500	700
<i>Serirolella violacea</i>	12.8	—	333	—
<i>Stromateus fiatola</i>	34.1	—	100	—
<i>Peprilus triacanthus</i>	16.5	250	333	167
<i>Amarsipus carlsbergi</i>	22.0	—	500	—
<i>Cubiceps gracilis</i>	30.5	500	100	214
<i>Nomeus gronovii</i>	26.4	500	77	—
<i>Psenes cyanophrys</i>	11.5	1,000	333	—
<i>Tetragonurus cuvieri</i>	28.8	330	333	650
<i>Ariomma bondi</i>	23.3	500	111	380

¹Data from Marshall (1960).

gradual process which makes difficult the determination of the exact time of loss of function. Several stages are recognizable in the process although they vary in appearance, and both the stages and the overall regression vary in duration among and within species. Estimated ranges of fish size during which regression occurs in nine stromateoid species are given in Table 4.

Early in the regression the gas gland contracts and thickens and the sac begins to decrease in size. Later the gas gland and retia mirabilia become atrophied as the cells and capillaries lose integrity (Figure 7). A yellowish-white material, possibly lipid, frequently invests the gas gland. Finally, the swim-bladder wall is resorbed, and the gas secreting and absorbing complexes become indistinct. A large stromateoid (> 100-200 mm SL, see Table 4) may have either a small irregularly

shaped mass of yellowish-white material lying in the dorsal mesentery (Figure 7) as the only remnant of the swim bladder or no visible trace at all of the organ.

DISCUSSION

Relative Dimensions and Capabilities of the Swim Bladder

Volume

Mean percentage volumes were relatively small, 0.6-3.4% (Table 2), and generally below the 3.1-5.7 range for the swim bladder calculated by Alexander (1966) to be necessary for neutral buoyancy in seawater. A number of mid-water fishes also have swim bladders of low volume

TABLE 4.—Size ranges during which swim-bladder regression occurs in nine species of stromateoids and during which the same species have been observed in association with animate (mainly coelenterate) or inanimate floating objects. Former ranges derived from data of present study and latter from sources listed.

Species	Size during regression (mm SL)	Size during association (mm SL, FL, or TL) ¹	Associated species or object	Source ²
<i>Centrolophus niger</i>	50-75	30-40 TL 103-477 SL	<i>Rhizostoma pulmo</i> <i>Mola mola</i>	Mansueti 1963 Mackay 1972
<i>Icichthys lockingtoni</i>	40-65	55 TL 16.3 SL 180.5 TL	<i>Pelagia noctiluca</i> <i>Pelagia noctiluca</i> <i>Pelagia noctiluca</i>	Mansueti 1963 Specimen label (MCZ) Mansueti 1963
<i>Stromateus fiatola</i> (including <i>S. fasciatus</i>)	50-75	10-40 TL 10-40 TL 127 TL	<i>Rhizostoma pulmo</i> <i>Cotylorhiza tuberculata</i> Unidentified medusa	Mansueti 1963 Mansueti 1963 Mansueti 1963
<i>Peprilus triacanthus</i>	75-100	12.5-28.2 SL 10-20 TL 51-64 TL 50-73 TL	<i>Cassiopeia carbonica</i> <i>Chrysaora quinquecirrha</i> <i>Cyanea capillata</i> Unidentified medusa	Specimen label (ZMC) Mansueti 1963 Mansueti 1963 Mansueti 1963
<i>Peprilus paru</i> (including <i>P. alepidotus</i>)	60-100	18-69 TL 13 TL 147 TL 28.6 SL	<i>Chrysaora quinquecirrha</i> <i>Chrysaora quinquecirrha</i> Unidentified medusa Unidentified medusa	Mansueti 1963 Mansueti 1963 Mansueti 1963 Specimen label (BMNH 1956.11.12.12)
<i>Cubiceps gracilis</i> <i>Nomeus gronovii</i>	40-75 Swim bladder present at ≥ 150 SL	42 SL 20 FL 51-76 TL 127-152 TL 142.7 SL	Unidentified medusa Drifting raft <i>Physalia pelagica</i> <i>Stomolophus meleagris</i> <i>Physalia pelagica</i>	Specimen label (BMNH 76.6.21-2) Gooding and Magnuson 1967 Mansueti 1963 Mansueti 1963 NIO specimen, HMS <i>Discovery II</i> Stn. 6688-3
<i>Psenes cyanophrys</i> (including <i>P. pacificus</i>)	110-130	15-124 FL 10-133 SL	Drifting raft Flotsam	Gooding and Magnuson 1967 Hunter and Mitchell 1967
<i>Tetragonurus cuvieri</i>	40-60	34 SL	Unidentified medusa	Specimen label (BMNH 76.6.21.23)

¹SL = standard length, FL = fork length, TL = total length.

²MCZ = Museum of Comparative Zoology, Harvard University.

ZMC = Zoological Museum, Copenhagen.

BMNH = British Museum (Natural History), London.

(Capen 1967; Kleckner and Gibbs 1972) and even a relatively small gas-filled sac provides some degree of buoyancy which may be significant depending upon what other lift or buoyancy devices are utilized. Larval and juvenile stromateoids, the stages which have the organ, have a different mode of life (see below) and are in some species at least probably less dense than adults. Only a 1% reduction in specific gravity of a fish lowers the required percentage volume for neutral buoyancy from 3.1%, the lower value in Alexander's (1966) calculated range (which was based upon specific gravities of adults), to 2.2% (Horn 1970a). Thus, even a small swim bladder would be an important contribution to buoyancy. Data on specific gravities of young stromateoids which might help to explain the range of percentage volumes found within the group are not yet available.

Gas Gland

The area of the gas gland relative to swim-bladder volume is similar to that in a number of deep-sea fishes and much greater than that of a series of epipelagic or shallow-sea ones (Table 3). Marshall (1960) stated that the large gas gland of deep-sea fishes, especially vertical migrators, may be an adaptation for rapid gas secretion as the fish de-

scends. Even though juvenile stromateoids occur only in the epipelagic, the adaptive significance of a large gas gland would be the same for them as for deep vertical migrators since stromateoids range over depths in the upper 100-150 m where pressure changes are greatest (e.g., the pressure at 10 m is 2 \times that at the surface). Maintaining association with animate floating objects as many stromateoids do requires that fishes range, even if slowly, over depths in the surface layers and in so doing secrete gas during descents if the hydrostatic advantage of the swim bladder is to be effected. Thus, the main selective value of the large gas gland may be for making fine adjustments to buoyancy. At least some of the epipelagic fishes listed in Table 3 have a narrow vertical range near the surface and would not require as large a gas gland.

The size and structure of the gas gland cells vary widely among stromateoids, a common situation in both shallow-water (Woodland 1911; Fänge 1953) and deep-sea fishes (Marshall 1960). Cells measured in stromateoids ranged from 6 to 46 μ m (Table 2), although some other cells in a few species appeared to be multinucleate and syncytial or similar to the giant cells (50-150 μ m) described by Fänge (1953) and Marshall (1960). The gland consisted of relatively large cells in a

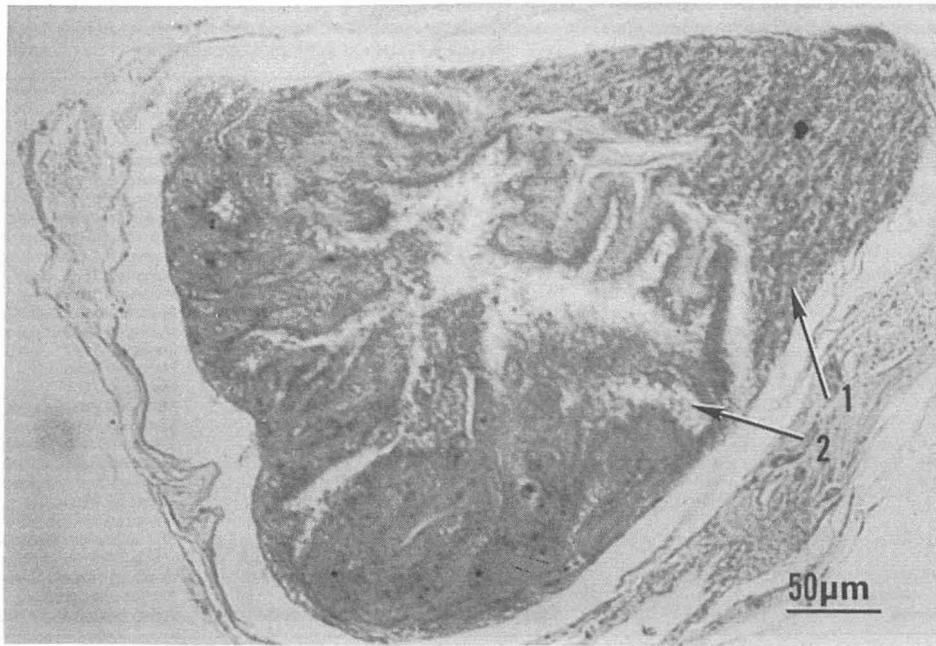


FIGURE 7.—Transverse section through the regressed swim bladder of *Ariomma indica*, 59.7 mm SL. Arrow (1) points to regressed rete mirabile, arrow (2) to regressed gas gland.

complex, multilayered arrangement as in *Ariomma bondi* (Figure 2), or, less frequently, of small cells arranged in circles or loops as in *Peprilus triacanthus* (Figure 5). The functional significance of cells of either different sizes or arrangements is poorly understood.

Rete Mirabile

Retial length in stromateoids ranged from 0.4 to 2.0 mm (Table 2), similar to the 0.75 to 2.0-mm range listed by Marshall (1972) for upper mesopelagic (200-600 m) fishes. The ratio of retial length to swim-bladder dimension (length \times width) (Table 3) as an approximation of relative development is high in stromateoids and similar to that of Marshall's (1960) deep-sea group which includes some vertical migrators. The stromateoid ratio is much higher than that of other epipelagic fishes and demonstrates that the retia, as with the gas gland, which together form the gas-secreting complex, are relatively well developed in stromateoids. In addition, the total length of the retial capillaries (retial length \times number of retial capillaries) in relation to swim-bladder volume is similar to or exceeds that for the eel, *Anguilla anguilla*, and certain deep-sea fishes (Table 3).

Marshall (1972) pointed out that the only flexible adaptation to increase the surface available for countercurrent gas exchange is an increase in length of the retial capillaries. An increase in length will not only lead to increased gas exchange but also slow the rate of bloodflow and so further enhance the efficiency of exchange (Marshall 1960). Marshall (1972) showed that the deeper the living space of a fish the greater the absolute length of the retia. On the basis of the pattern of retial length and depth of living described by Marshall, the predicted depth zone for larval and juvenile stromateoids would be the upper mesopelagic.

Besides length, the diameter of the retial capillaries of stromateoids shows a somewhat greater similarity to that of deep-sea fishes than to other epipelagic fishes. Stromateoids have capillary bores of 4-10 μm (Table 2) whereas epipelagic fishes listed by Marshall (1960) had diameters of greater than 10 μm . Deep-sea fishes with large erythrocytes have retial capillaries 7-18 μm in diameter and those with small, nonnucleated erythrocytes such as *Maurolicus* and *Vinciguerria* have retial capillaries 2-10 μm in diameter (Marshall 1972). The smaller the diameter the greater the efficiency of gaseous exchange (Marshall

1960), although decreased bore is an adaptation limited in most fish species by the size of the erythrocytes.

Swim-Bladder Regression in Relation to Behavior and Mode of Life

Data from the present study and other sources on depth distribution, association with floating objects, and locomotion and buoyancy make it possible to formulate a general outline of the changes in behavior and mode of life that accompany the regression of the swim bladder and which are part of the transition from the juvenile to the adult state.

Depth Distribution

Adult stromateoids generally occupy a wide range of depths either over the continental shelf or in the open ocean, whereas larvae and juveniles of all or nearly all species occur in the surface layers (mainly the upper 100 m) (Haedrich 1967, 1969; Horn 1970a). Larval nomeids (*Psenes* and *Cubiceps*) are important constituents of the epipelagic fauna; this is known especially for the eastern tropical Pacific (Ahlstrom 1971, 1972). The Centrolophidae and Tetragonuridae were listed by Ahlstrom (1969) as two of the principal families of deep-sea fishes which had larvae in the surface layers of the California Current region. The stromateid, *Peprilus simillimus*, occurs mainly in the upper 50 m of coastal waters off California and Baja California (Ahlstrom 1959), and ariommid larvae and juveniles apparently live in the surface layers although the adults are benthopelagic (Horn 1972). Thus, swim-bladder loss occurs as the fishes increase their range of vertical distribution.

Association with Floating Objects

Beginning at a small size (≤ 10 mm SL) and usually ending before maturity is reached (≤ 200 mm SL), stromateoids commonly associate with a wide variety of animate and inanimate floating objects (Mansueti 1963; Haedrich 1967; Horn 1970a) and during the period that the swim bladder is functional (Table 4). The associations are not obligatory but rather, as Mansueti (1963) described them, temporary ecological phenomena in which the objects (e.g., jellyfishes or flotsam) are essentially passive hosts and the fishes active op-

portunists. Scyphozoan medusae of several genera form a major group of associates particularly of stromateids and to some extent of centrolophids, nomeids, and tetragonurids (Mansueti 1963). The nomeid, *Nomeus gronovii*, and the Portuguese man-of-war, *Physalia*, form the apparently most intimate and enduring of "fish-jellyfish" associations. Certain stromateoids have also been found inside pelagic ascidians (Grey 1955), beneath the ocean sunfish, *Mola* (Mackay 1972) and beneath floating plants such as *Sargassum* (Haedrich 1967). Several species occur beneath flotsam, and the nomeid, *Psenes cyanophrys*, is one of the more abundant fishes under drifting objects (Hunter and Mitchell 1967, 1968; Gooding and Magnuson 1967). Drift associations are not well understood but probably provide one or more ecological advantages such as food, protection, or visual stimuli.

Juvenile stromateoids in their coloration and maneuverability are well adapted for life beneath floating objects, especially coelenterates. Young fish typically have a banded, mottled, or blotched pattern whereas adults are generally uniform in color or are dark above and pale below. The duration of the juvenile color pattern is similar to the period when the fishes are associated with floating objects, and the patterns according to Haedrich (1967) serve as protective coloration beneath the shifting shadows of objects, especially jellyfishes. *Nomeus* which retains its association with floating objects longer than most or all other stromateoids also retains its mottled color pattern in the largest specimens known.

Maneuverability and avoidance by the fish appear to be of primary importance in all or most stromateoid-coelenterate associations (Mansueti 1963; Horn 1970a). *Peprilus triacanthus* placed in tanks with a medusa, *Chrysaora quinquecirrha*, gradually increased the amount of time spent near the jellyfish and after 72 h remained within a 4-cm distance of the bell at least 75% of the time (Horn unpubl. data). Hovering and rapid turning were significant parts of the locomotor behavior of the fish in avoiding the tentacles of the medusa. Contact of the skin of the fish by the tentacles resulted in nematocyst firing as evidenced by the clinging of the tentacles to the fish's body causing the fish to rapidly swim away. In a two-way feeding relationship, *P. triacanthus* frequently nibbled at the manubrium and tentacles of the medusa, while weakened or otherwise slow-moving fish were captured and ingested by the medusa.

Although Lane (1960) reported that *Nomeus* can survive doses of *Physalia* toxin as much as 10 times the amount that would kill other fishes of the same size and type, *Nomeus* is stung if forced into contact with the tentacles (Lane 1960) and can be killed if touched by the tentacles according to Zahl (1952). Maul (1964) found that *Schedophilus* (= *Mupus*) *ovalis* also suffered large weals on the body from nematocysts when in contact with *Physalia* and that safety for the fish must be due in part to its ability to avoid contact with the tentacles. Mansueti (1963) concluded that in all fish-jellyfish associations the former skillfully maneuver between tentacles and generally avoid being stung but that contacts are inevitable.

Locomotion and buoyancy

The differences in locomotor behavior found between juvenile and adult stromateoids that have been observed illustrate the importance of maneuverability for juveniles and correspond to swim-bladder loss and increased independence of floating objects as maturity is reached. The paired fins are important locomotor devices among stromateoids. The pectoral fins are moved in a rotary manner for maintaining position in juveniles of *Peprilus triacanthus* and *Schedophilus medusophagus* when hovering beneath floating objects (pers. obs.) and sculled for effecting continuous swimming at less than maximum speeds in these species (Horn 1970b, unpubl. obs.) and in other stromateoids such as *Cubiceps gracilis* (Figure 8). I have observed adults of both *P. triacanthus* and *P. simillimus* in public aquaria and calculated that the pectorals are used at least 80-90% of the time as a main propulsive force at cruising speeds. The pelvic fins which may be absent (all stromateid species except one) or small (as in certain centrolophids) are well developed in juveniles of certain species. Pelvics are large in *Nomeus* and apparently important for increasing maneuverability and enhancing protective coloration for a fish living among the tentacles of *Physalia*.

The relative length of the paired fins changes with age and varies among the species (Haedrich 1967; Horn 1970b). Extremes are represented by *P. triacanthus* and *S. medusophagus* (Figures 9, 10). In *P. triacanthus* (which lacks pelvic fins) the relative length of the pectoral fin increases rapidly until the fish reaches about 75-80 mm

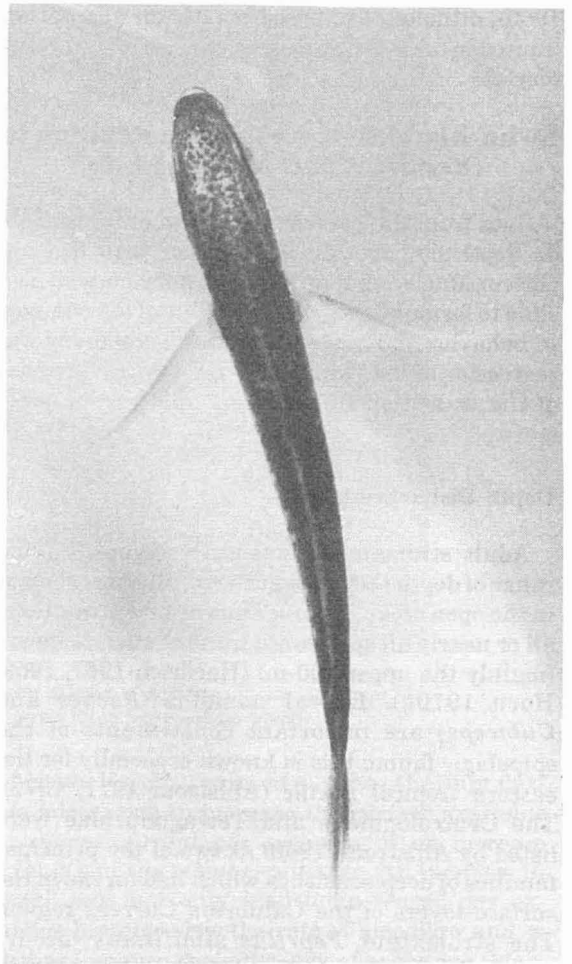


FIGURE 8.—*Cubiceps gracilis*, 68 mm SL, swimming in plastic container and using pectoral fins as principal locomotor force. Swim bladder of this fish partially regressed (see Table 4). Specimen captured at the surface in the North Atlantic.

SL beyond which the fin length ceases to increase (Figure 9). This fish size is in the range of that when the swim bladder regresses and the fish deserts its coelenterate host (Table 4). Individuals of *P. triacanthus* greater than 75-80 mm SL are negatively buoyant (see below) and swim continuously using mainly the long pectorals which also generate dynamic lift. In *S. medusophagus* the relative length of the paired fins decreases with age (Figure 10), a pattern opposite that of *P. triacanthus*. The swim bladder regresses in a size range of about 40-60 mm SL corresponding closely to the size interval during which the marked change in paired fin length occurs and apparently during which the fish deserts its coelenterate host

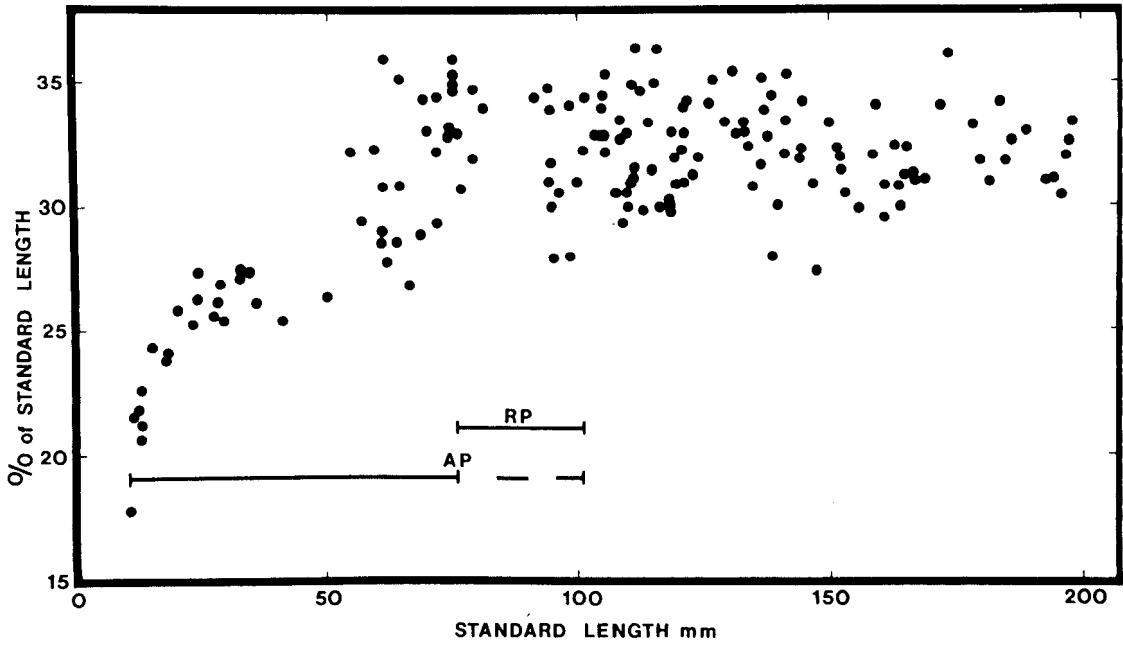


FIGURE 9.—Scatter diagram of pectoral fin length as a percentage of standard length in *Peprilus triacanthus*. RP, regression period, or size interval during which swim bladder regresses; AP, association period, or size interval during which fish associates with floating objects (dashed part of line indicates less frequent association) (see Table 4).

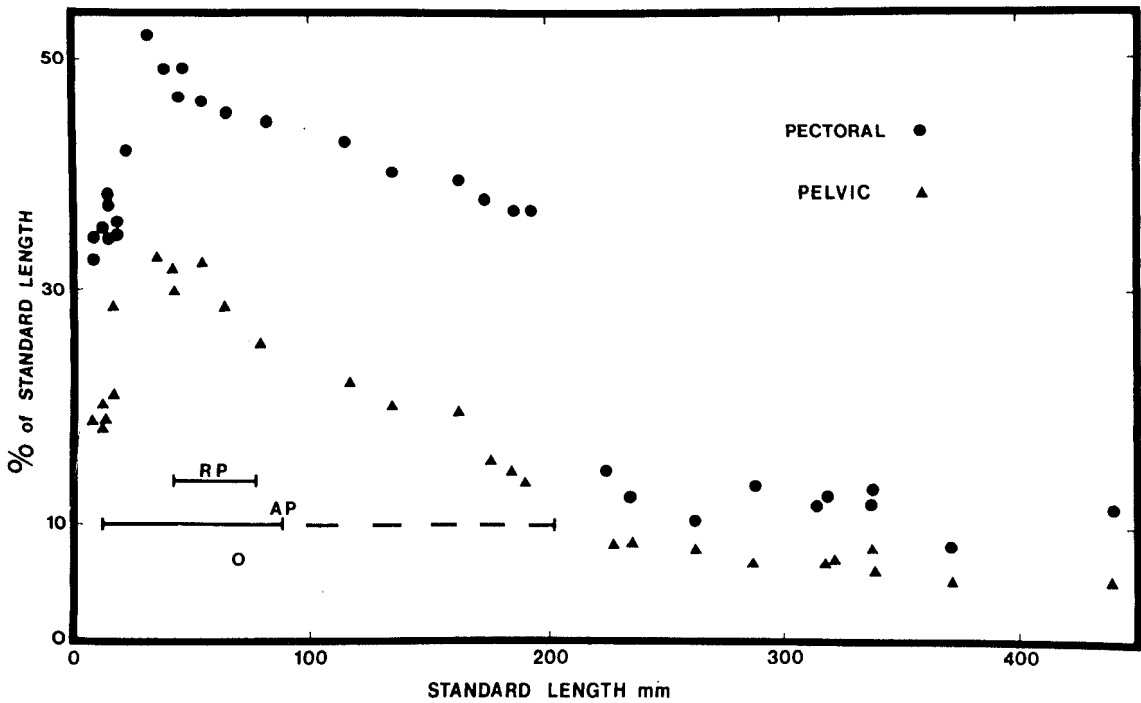


FIGURE 10.—Scatter diagram of pectoral fin and pelvic fin lengths as a percentage of standard length in *Schedophilus medusophagus*. RP and AP as in Figure 9.

(Mansueti 1963). Unlike *P. triacanthus*, *S. medusophagus* becomes neutrally buoyant or nearly so (see below) and has a poorly ossified skeleton and soft musculature (Bone and Brook 1973). Adult *S. medusophagus* swim slowly and continuously in near anguilliform manner and with only a minor part of the propulsive force provided by the small pectorals (pers. obs.). Because of the fish's low density, little or no lift is required from locomotor activity.

Changes in the level of buoyancy and in the nature of the buoyancy mechanism may coincide with swim-bladder loss and other changes occurring as stromateoids mature although the data are as yet insufficient to permit conclusions to be reached. *Peprilus triacanthus* and a closely related species, *P. simillimus*, are negatively buoyant as adults (weight in water 1.4-2.3% of weight in air) (unpubl. data). Juvenile *S. medusophagus* (85-200 mm SL) are slightly negatively buoyant (Bone and Brook 1973) whereas a larger (285 mm SL) specimen was found to be neutrally buoyant in surface seawater (unpubl. data). Large amounts of lipid have been found in adults of both *P. simillimus* and *S. medusophagus* especially in the skull and spine (Lee et al. in press). Bone and Brook (1973) found relatively low amounts of lipid in juvenile *S. medusophagus*, an indication that lipid content may increase with size in this species. Lipids may serve to partially replace the swim bladder in a buoyancy function as the organ regresses in *P. simillimus* and *S. medusophagus*, two morphologically and ecologically dissimilar stromateoids. *Peprilus simillimus*, an active, continuous swimmer with long pectoral fins, has a relatively well ossified skeleton, firm musculature, and is negatively buoyant, whereas *S. medusophagus*, a slow moving, continuous swimmer with short pectoral fins, has poorly ossified bones and soft, loosely packed muscles, and approaches or attains neutral buoyancy.

Increased lipid content as a buoyancy replacement for the swim bladder would be advantageous for *P. simillimus*, *S. medusophagus*, and probably other stromateoids that range over the upper several hundred meters of the water column since the low coefficient of compressibility of lipid compared to gas reduces the stress of pressure changes with depth. Nevenzel et al. (1969) pointed out the advantage of lipid for a vertically migrating mid-water fish, and Butler and Percy (1972) discovered that in two such species, the myctophids

Stenobrachius leucopsarus and *Diaphus theta*, swim bladder-to-body volumes were inversely related to body size and lipid content indicating that lipids assume the primary buoyancy function as the swim bladder regresses with age. An additional advantage of stored lipid, especially triglycerides, may be as an energy source (Lee et al. in press). Bone (1973) has suggested that vertically migrating myctophids can be grouped into functional types based on swim-bladder state, lipid content, density, and size of the pectoral fins. Stromateoids are not classed as a principal group of vertical migrators partly because of their relative rarity, but many species do have a broad vertical range. With more data, it may be possible to divide stromateoids into functional groups according to characteristics similar to those listed by Bone (1973) for myctophids.

ACKNOWLEDGMENTS

A number of people have allowed me to examine and in certain cases dissect specimens in their care. My thanks go to N. B. Marshall and Alwyne C. Wheeler, British Museum (Natural History); Richard L. Haedrich, Woods Hole Oceanographic Institution; Julian Badcock, Institute of Oceanographic Sciences, England; Elbert H. Ahlstrom and Elaine Sandknop, Southwest Fisheries Center, National Marine Fisheries Service, NOAA; Jørgen Nielsen, Zoological Museum, University of Copenhagen; Robert J. Lavenberg, Natural History Museum of Los Angeles County; and Richard H. Rosenblatt, Scripps Institution of Oceanography.

I sincerely appreciate the efforts of N. B. Marshall (now at Queen Mary College, University of London) who provided working space and facilities at the British Museum (Natural History), passed along a great deal of information on swim bladders, and read the manuscript. The reviewers gave valuable comments for improvement of the manuscript.

Paula K. McKenzie made the drawing of Figure 1.

Financial support for this study was provided in part by a NATO postdoctoral fellowship awarded through the National Science Foundation and held at the British Museum (Natural History) and in part by a Sigma Xi Grant-in-Aid of Research and by a Faculty Research Grant awarded by California State University, Fullerton.

LITERATURE CITED

- AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Wildl. Serv., Fish. Bull. 60:107-146.
1969. Mesopelagic and bathypelagic fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest. Rep. 13:39-44.
1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. Fish. Bull., U.S. 69:3-77.
1972. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. Fish. Bull., U.S. 70:1153-1242.
- ALEXANDER, R. MCN.
1966. Physical aspects of swimbladder function. Biol. Rev. (Camb.) 41:141-176.
- BONE, Q.
1973. A note on the buoyancy of some lantern-fishes (Mycetophidae). J. Mar. Biol. Assoc. U.K. 53:619-633.
- BONE, Q., AND C. E. R. BROOK.
1973. On *Schedophilus medusophagus* (Pisces: Stromateoidei). J. Mar. Biol. Assoc. U.K. 53:753-761.
- BUTLER, J. L., AND W. G. PEARCY.
1972. Swimbladder morphology and specific gravity of myctophids off Oregon. J. Fish. Res. Board Can. 29:1145-1150.
- CAPEN, R. L.
1967. Swimbladder morphology of some mesopelagic fishes in relation to sound scattering. U.S. Navy Electron. Lab., Res. Rep. 1447, 25 p.
- FÄNGE, R.
1953. The mechanisms of gas transport in the euphysoclit swimbladder. Acta Physiol. Scand. 30, Suppl. 110, 133 p.
1966. Physiology of the swimbladder. Physiol. Rev. 46:299-322.
- FOWLER, H. W.
1936. The marine fishes of West Africa, based on the collection of the American Museum Congo Expedition, 1909-1915, Part II. Bull. Am. Mus. Nat. Hist. 70:609-1493.
- GOODE, G. B., AND T. H. BEAN.
1895. Oceanic ichthyology. U.S. Natl. Mus., Spec. Bull. 2, 553 p.
- GOODING, R. M., AND J. J. MAGNUSON.
1967. Ecological significance of a drifting object to pelagic fishes. Pac. Sci. 21:486-497.
- GREY, M.
1955. The fishes of the genus *Tetragonurus* Risso. Dana Rep., Carlsberg Found. 41:1-75.
- HAEDRICH, R. L.
1967. The stromateoid fishes: systematics and a classification. Bull. Mus. Comp. Zool. 135:31-139.
1969. A new family of aberrant stromateoid fishes from the equatorial Indo-Pacific. Dana Rep., Carlsberg Found. 76:1-13.
- HAEDRICH, R. L., AND M. H. HORN.
1972. A key to the stromateoid fishes. 2nd ed. WHOI (Woods Hole Oceanogr. Inst.) Tech. Rep. 72-15, 46 p.
- HORN, M. H.
1970a. The swimbladder as a juvenile organ in stromateoid fishes. Breviora 359, 9 p.
1970b. Systematics and biology of the stromateoid fishes of the genus *Peprilus*. Bull. Mus. Comp. Zool. 140:165-261.
1972. Systematic status and aspects of the ecology of elongate ariommid fishes (suborder Stromateoidei) in the Atlantic. Bull. Mar. Sci. 22:537-558.
- HUNTER, J. R., AND C. T. MITCHELL.
1967. Association of fishes with flotsam in the offshore waters of Central America. U.S. Fish Wildl. Serv., Fish. Bull. 66:13-29.
1968. Field experiments on the attraction of pelagic fish to floating objects. J. Cons. 31:427-434.
- JORDAN, D. S., AND B. W. EVERMANN.
1896. The fishes of North and Middle America. Part I. U.S. Natl. Mus., Bull. 47, 1240 p.
- KLECKNER, R. C., AND R. H. GIBBS, JR.
1972. Swimbladder structure of Mediterranean midwater fishes and a method of comparing swimbladder data with acoustic profiles. Mediterr. Biol. Stud., Final Rep. 1:230-281. Smithsonian. Inst., Wash.
- LANE, C. E.
1960. The Portuguese man-of-war. Sci. Am. 202:158-168.
- LEE, R. F., C. F. PHLEGER, AND M. H. HORN.
In press. Composition of lipid stores in fish bones: possible function in neutral buoyancy. Comp. Biochem. Physiol.
- MACKAY, K. T.
1972. Further records of the stromateoid fish *Centrolophus niger* from the northwestern Atlantic, with comments on body proportions and behavior. Copeia 1972:185-187.
- MANSUETI, R.
1963. Symbiotic behavior between small fishes and jellyfishes, with new data on that between the stromateid, *Peprilus aepidodus*, and the scyphomedusa, *Chrysaora quinquecirrha*. Copeia 1963:40-80.
- MARSHALL, N. B.
1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Discovery Rep. 31:1-121.
1972. Swimbladder organization and depth ranges of deep-sea teleosts. Soc. Exp. Biol., Symp. 26:261-272.
- MAUL, G. E.
1964. Observations on young live *Mupus maculatus* (Günther) and *Mupus ovalis* (Valenciennes). Copeia 1964: 93-97.
- NEVENZEL, J. D., W. RODEGKER, J. S. ROBINSON, AND M. KAYAMA.
1969. The lipids of some lantern fishes (Family Myctophidae). Comp. Biochem. Physiol. 31:25-36.
- WOODLAND, W. N. F.
1911. On the structure and function of the gas glands and retia mirabilia associated with the gas bladder of some teleostean fishes, with notes on the teleost pancreas. Proc. Zool. Soc. Lond. 1911(1):183-248.
- ZAHL, P. A.
1952. Man-of-war fleet attacks Bimini. Natl. Geogr. Mag. 101:185-212.