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SOME OBSERVATIONS ON THE GILLS OF THE OCEANIC SUNFISH, *MOLA MOLA*

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(Figs. 1–8)

A description is given of the gross anatomy of the respiratory system with special reference to the gills and branchial circulation. A number of features of the gill anatomy are similar to those found in some other oceanic fishes, especially the strengthening of the gill system. The circulation shows an important difference from those of other large marine fish in that the afferent branchial arteries are double; but they are similar in that both afferent and efferent arteries are extended beyond their point of entry into the gill arch.

Measurements on the gills gave values for total filament length and surface area of the gills which were close to those which have been found in a wide range of marine fish showing intermediate levels of activity.

INTRODUCTION

The oceanic sunfish *Mola mola* is occasionally found close to our shores, its normal habitat being the oceans throughout the world. It is replaced by *Mola ramsayi* only in the South Pacific (Fraser-Brunner, 1951). Specimens which are caught around the British Isles normally come from the North Atlantic as a result of being washed inshore when the warm westerly winds are blowing during the summer.

Of the four species of sunfish (*Ranzania laevis*, *Masturus oxyuropterus*, *Masturus laceotabus*, and *Mola mola*) found in the northern hemisphere, *Mola mola* is the most common. During the summer of 1972 the opportunity arose to study two specimens because of their capture near Plymouth. This fish is of particular interest because of its great size; the maximum recorded being in excess of 10 ft in length and 1 ton body weight. A study of the gills of *M. mola* is especially valuable for comparison with other large marine fishes such as the tunas. In the literature there are many references to ocean sunfish but most are concerned with little more than recording its capture and gross measurements. A few anatomical studies have been made; one of the earliest being that of Goodsir (1840); Cleland (1862) made a detailed study of the anatomy and includes a brief mention of the gills. Van Roon & Pelkwijk (1939) and van Roon (1942) studied the anatomy of the head and body and its swimming muscles with special reference to swimming. Steenstrup & Lutken (1898) made an extensive study of the skeleton and body form of the Molidae; Gregory (1933) studied the skull and Gregory & Raven (1934) the anatomy with special reference to their affinities with other tetraodonts. Fraser-Brunner (1951) compared the anatomical relationships within the Molidae. Schmidt (1921*b*) described the young of *Ranzania* and *Mola*. The structure of the respiratory muscles and branchiostegal apparatus of *M. mola* were described by Willem (1949) who placed it in a special group of his classification of fish ventilatory mechanisms. Several papers refer to

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the gill parasites of this fish (McCann, 1961; Shiino, 1965; Hewitt, 1968) but little mention is made of the gill anatomy. Some early studies on the general structure of the gills were described by Bovien (1919).

The present paper is concerned with the structure of the gills at the gross and light microscopic levels. Measurements have been made on the gills of two of the specimens only. The particular interest of this fish is mainly because of it being a very large teleost having interesting life habits. The external features of the respiratory system attract attention because of the relatively small diameter of the mouth and the small external openings from the opercular cavities. The gills themselves also proved to be of great interest because of their gross form and degree of calcification. More detailed features of their anatomy were of interest in relation to studies made on other oceanic teleosts such as the tunas (Muir & Kendall, 1968; Muir & Hughes, 1969).

MATERIALS AND METHODS

Three specimens of *Mola mola* were obtained from different sources; the first and largest (97·5 kg) was scooped out of the sea by a Royal Naval helicopter. The second, a much smaller specimen (3·8 kg), was obtained from the Brixham aquarium. This specimen had been caught on a line and brought in alive, and maintained in good condition for some hours. The larger sunfish had been dead for 72 h before it arrived at the Plymouth Laboratory, whereas that from Brixham had only been dead for a few hours. A third specimen was obtained at Arcachon, south-west France, in the Autumn of 1973. This was also a relatively small specimen.

The gills were immediately fixed in sea-water Bouin solution and kept in fresh Bouin until they were used for measurements. The gill areas were estimated according to the methods described by Hughes & Morgan (1973). Microscopic investigations were made on paraffin wax sections cut at 10 and 20 μm and stained with haematoxylin/eosin.

RESULTS

Gross morphology of the gills

The gills of *Mola mola* are very large and lie in the region just posterior to the eyes and at an angle to the longitudinal axis of the body. They are oriented so that the ventral portion of the hemibranchs is more anterior than the dorsal part of the hemibranchs. Anatomically, the gills may be divided into three main regions; dorsal, middle and ventral. The upper 80 filaments constitute the dorsal region, the middle region is from about the 80th filament to the 150th filament, the remainder constitutes the ventral region. The precise number of filaments in each region varies according to the particular hemibranch and size of the fish. Larger fish will have more filaments than smaller fish and the first hemibranch has more filaments than the fourth hemibranch (Fig. 8). The filament numbers given above relate to the first hemibranch of a 3·8 kg fish. These regions may be defined more precisely in terms of the position of the gill arch skeleton. The dorsal region is that part of the hemibranch which is dorsal to the gill arch skeleton, the middle region that part occupied by the gill arch, and the ventral region is ventral to the gill arch.

Another feature of the gills is the reduction of the gill arch skeleton and the corresponding reduction of the internal gill slits. The middle region is the only area through which water can pass from the buccal cavity to the interbranchial region. The hemibranchs are joined at their bases by connective tissue thus preventing water entering the

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gill chamber except in the middle regions. The openings of the buccal cavity and the gill slits are in a direct line but the opercular opening, which is also restricted, is dorsal to the mouth and lies just anterior to the pectoral fin and behind the eye. The relative positions of the two openings means that the main stream of direct water flow is across the region of greatest filament length and area.

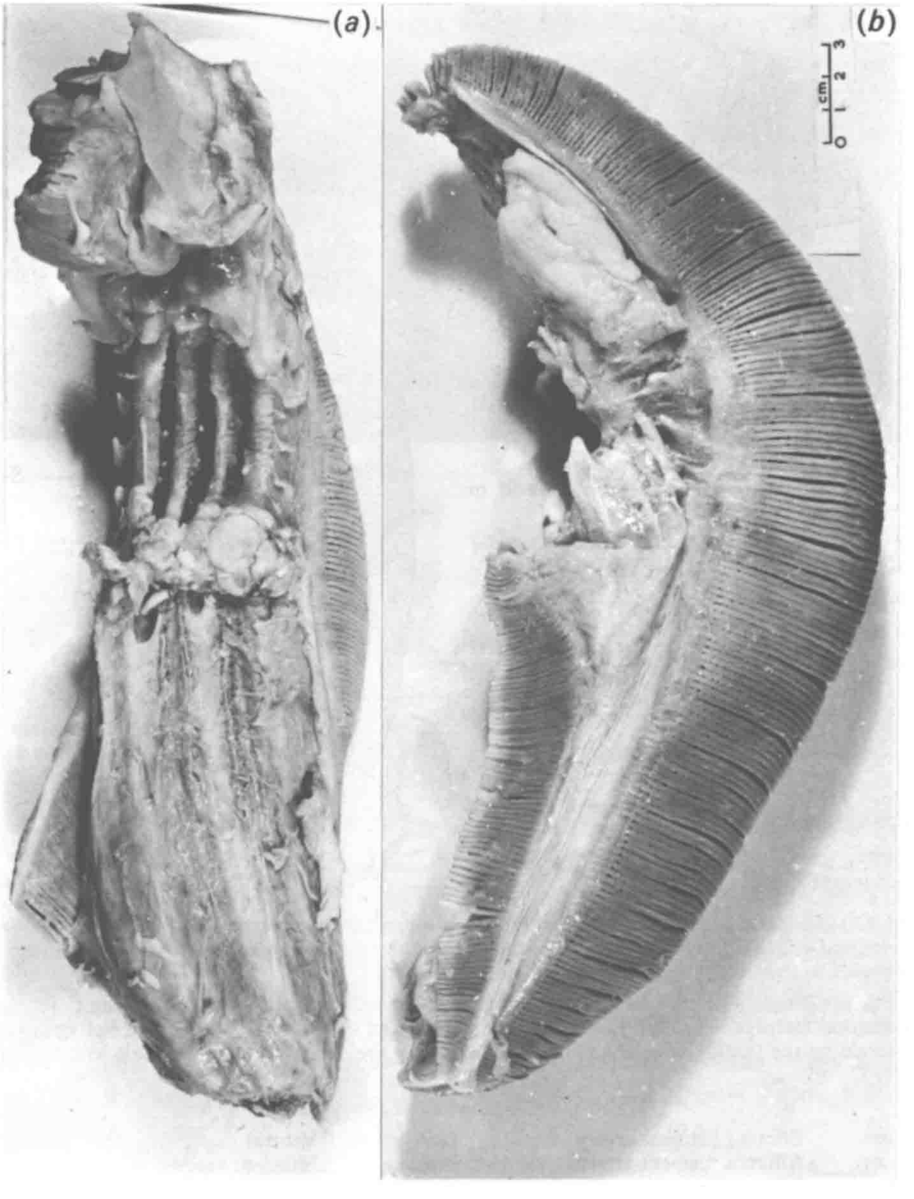

Fig. 1. Photographs of the gills from one side of the 97·5 kg specimen. (*a*) Anterior aspect showing gill rakers on the 4 gill arches and the restricted openings of the interbranchial region. (*b*) Lateral aspect of the gills of the left side. Note the reduction of the gill arch skeleton in the middle region of the hemibranchs.

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The restriction of the gill arch has necessitated a new support system for the gill filaments formed by the fusion of the bases of the gill rays which are enlarged antero-posteriorly and dorso-ventrally. The gill rays are fused to the adjacent filaments but not to filaments of the opposite hemibranch. However, the bases of the gill rays are connected to the opposite filaments by a thin layer of connective tissue and by the abductor filament muscles. This structure supports the hemibranch and replaces the gill arch. In the middle region where the gill arch is present there is no cartilaginous connexion between

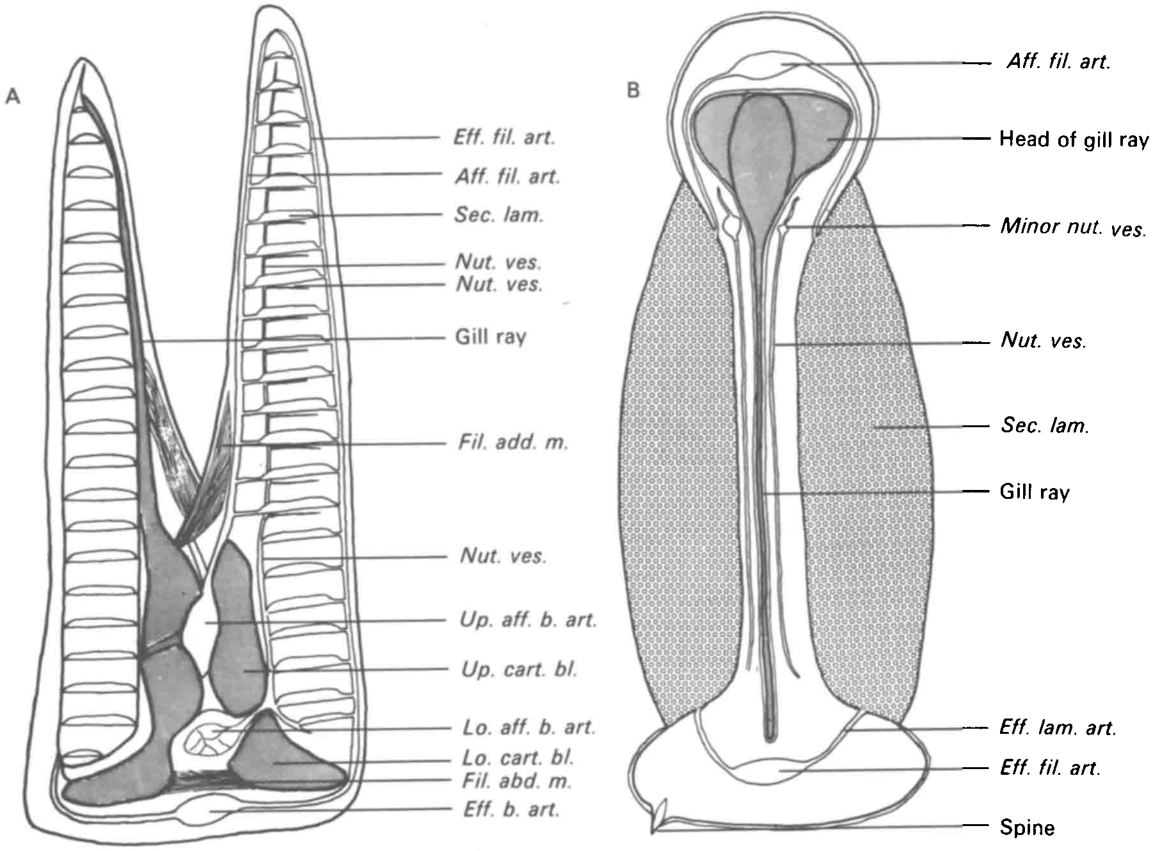

Fig. 2. (A) Diagram of a section across the two hemibranchs of a single gill arch to show main anatomical features. Note the absence of the gill arch skeleton in this section. The skeletal arch is restricted to the middle region of the gill arch (see text).

Fig. 2. (B) Diagram of a transverse section through the axis of a gill filament showing the main anatomical features of the gill filament in the middle and tip regions. The presence of spines is common on the leading edge of the filaments and they are present over their whole length.

Abbreviations

Eff. fil. art.	Efferent filament artery	*ven.*	Ventral
Aff. fil. art.	Afferent filament artery	*Nut. ves.*	Nutrient vessel
Eff. b. art.	Efferent branchial artery	*Sec. lam.*	Secondary lamella
Aff. b. art.	Afferent branchial artery	*Fil. abd. m.*	Filament abductor muscle
Lo. aff. b. art.	Lower afferent branchial artery	*Fil. add. m.*	Filament abductor muscle
Up. aff. b. art.	Upper afferent branchial artery	*Up. cart. bl.*	Upper cartilage block
dors.	Dorsal	*Lo. cart. bl.*	Lower cartilage block

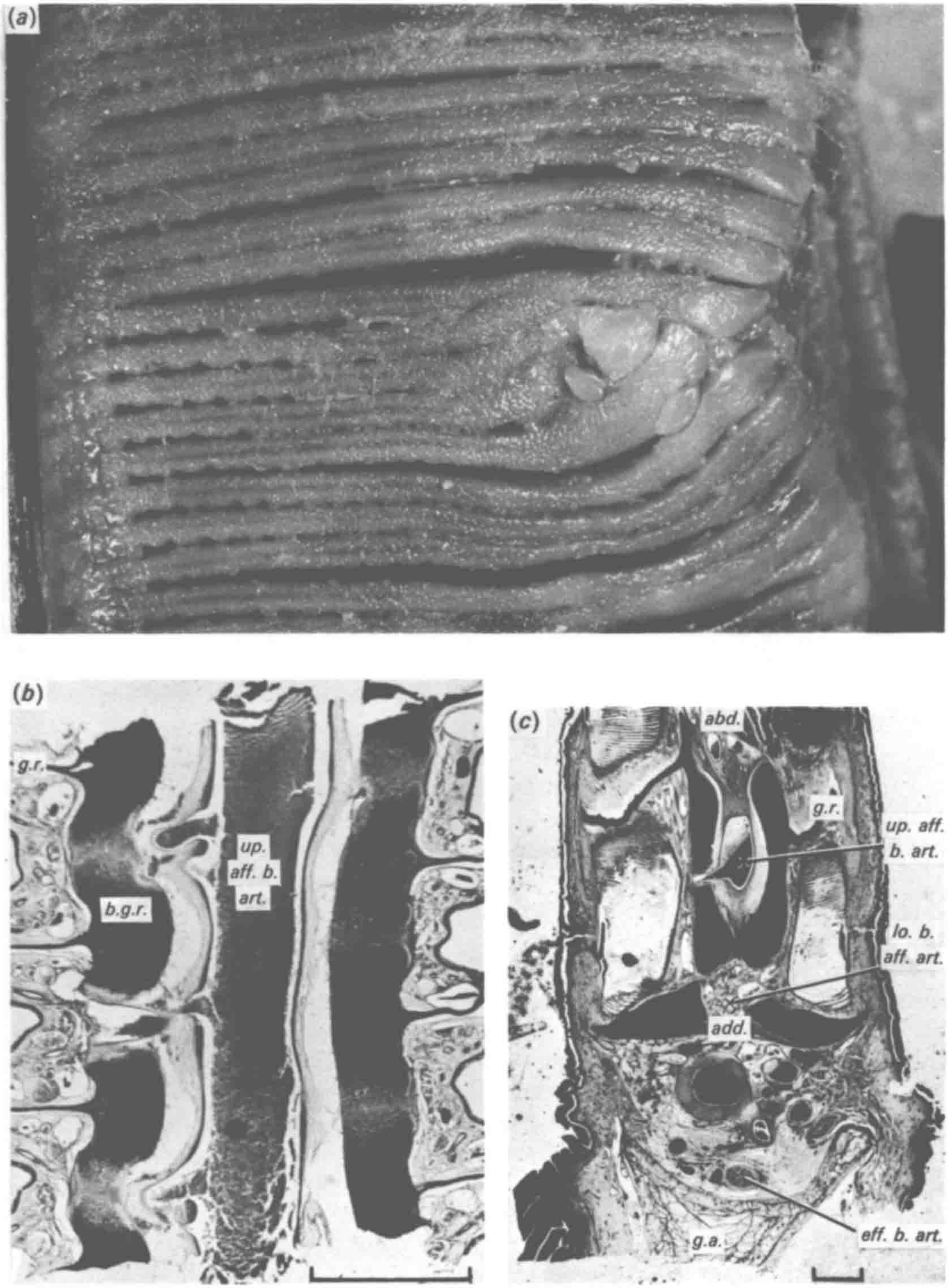

Fig. 3. (*a*) Tips of the gill filaments which have been damaged by the attachment of a parasite. Note clubbing and fusion at the tips of the filaments. The restriction of the openings between gill filaments is also visible in both damaged and undamaged filaments near their attachment to the gill arch. (*b*) Longitudinal section through a gill arch showing alternation in origin of filaments on the two sides (bar = 1·0 mm). (*c*) Transverse section through a gill arch showing filaments of the anterior and posterior hemibranchs with their secondary lamellae. The gill arch (g.a.), upper and lower afferent branchial and efferent branchial ateries, enlarged bases of gill rays (*b.g.r.*), abductor (*abd*) and adductor (*add.*) filament muscles are visible (bar = 1·0 mm).

the gill arch and the bases of the gill rays but they are only connected by connective tissue.

The gill filaments are large and dumbell-shaped in cross-section; the leading and trailing edges being covered by a dense layer of hard tissue. Embedded into this tissue are many spines which originate from the layer next to the outer layer (Fig. 2B). The tips of the filaments are bulbous and where parasitic damage occurs there is often fusion and enlargement of the filament tips (Fig. 3). Shiino (1965) has noted similar damage to the gills of *Mola mola* caused by the parasite *Cecrops exiguus*. Fig. 2A shows the position of the gill filament muscles. The adductor filament muscles originate on the trailing edge of the filaments and are attached to the top of the enlarged base of gill rays of the opposite filaments. This arrangement of the abductor muscles corresponds to the first type of Bijtel (1949). When the muscle contracts it works against the elasticity of the gill ray and the tips are drawn together. As has already been pointed out the abductor muscles are not found in the typical teleost position joining the gill ray to the gill arch, but joins two gill rays at their bases. Contraction of these muscles would cause separation of the tips of the gill filaments attached to a given arch.

Blood system

The branchial blood system of *M. mola* can be divided into two parts; the hemibranch system and the filament system. The former consists of the afferent and efferent hemibranch arteries, and the latter consists of the afferent and efferent filament arteries and the nutrient vessels. In Fig. 4 the afferent and efferent blood supply to a typical branchial arch of *M. mola* is compared with that of the trout. There are important differences in the basic plan of these two systems. The efferent artery gives off two branches, one dorsally and the other ventrally, and which extend respectively beyond the ventral and dorsal ends of the gill arch skeleton. The efferent arteries run close to the bases of the gill rays and the parent efferent artery enters the gill arch at the dorsal end of the gill arch skeleton. The afferent branchial artery branches in a similar fashion at the ventral end of the gill arches and it is double for most of its length. The lower of the two arteries runs at the base of the gill rays but above the abductor filament muscle and the efferent arteries. At the extremities of this artery it loses its discrete character and becomes a matrix of small vessels. The upper of the two afferent arteries runs between the two cartilaginous blocks at the base of the gill ray, and does not break down in the same way as the lower artery. The doubling of the afferent hemibranch artery found in *Mola* is unusual, whereas doubling of the efferent artery is quite common in several groups of fish. Doubling of the efferent arteries is also found among the sharks, sturgeons and some Actinopterygii (Sewertzoff, 1924), tunas (Muir, 1970) and in some air breathing fishes (Saxena, 1964). Mott (1950) has also observed it in the eel.

The arrangement of blood vessels in the gill filament of *M. mola* is summarized in Fig. 2. The lower afferent branchial artery gives off a pair of branches for each filament which run on either side of the gill ray. In the basal region they form the filament artery and in the middle and tip regions of the gill filament they form a pair of nutrient vessels which are of unequal size, the anterior one being larger than the posterior vessel. For each gill lamella they give off one branch which runs across the gill filament (Fig. 2B).

For each filament the upper afferent artery gives off one branch which forms the afferent filament artery in the middle and tip regions of the gill filament. The efferent artery runs below the base of the gill rays and it branches opposite each filament to form the efferent filament artery in the typical teleost pattern.

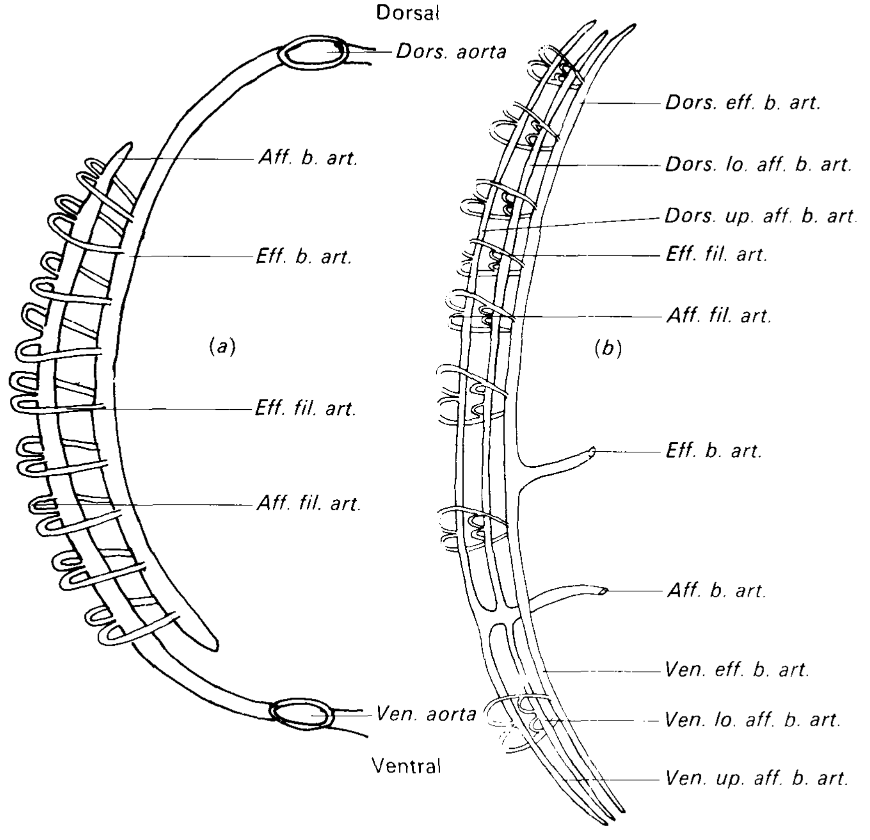

Fig. 4. Diagrammatic representation of the circulation through a single gill arch of (*a*) the trout (after Hughes & Morgan, 1973) and (*b*) the sunfish, *Mola mola*. In the sunfish there is a double afferent system whereas in the trout both afferent and efferent supplies are single. The filament arteries provide loops connecting branches of the afferent branchial artery to branches of the efferent branchial artery, but of course they are more numerous and longer than shown here.

Several investigators have reported the presence of internal blood spaces in the gill filaments (Steen & Kruysse, 1964; Vogel, Vogel & Kremers, 1973). From the observations made in this study there is no evidence that such blood spaces are present in *M. mola*. No dye injection experiments were conducted, however, and the gills were fixed after the fish had been dead for some hours. Consequently it is probable that spaces of this kind, if present, would not have been detected because of the methods used to fix the gills.

The secondary lamellae

The secondary lamellae of *M. mola* are simple, not large and their frequency is fairly low (Table 1). The number of secondary lamellae for each millimetre of filament being

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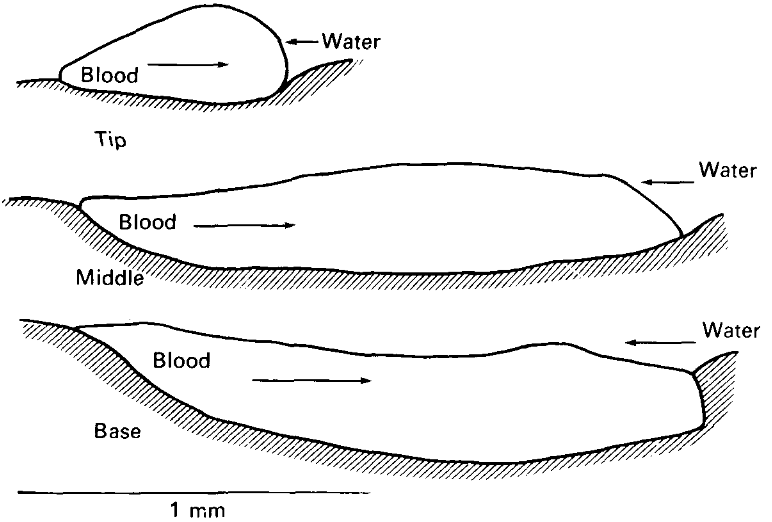

Fig. 5. Profiles of secondary lamellae isolated from the tip, middle and basal regions of a single gill filament. The seondary lamellae become more enclosed by the filament (shaded) in the more basal regions. The general directions of water and blood flow are indicated.

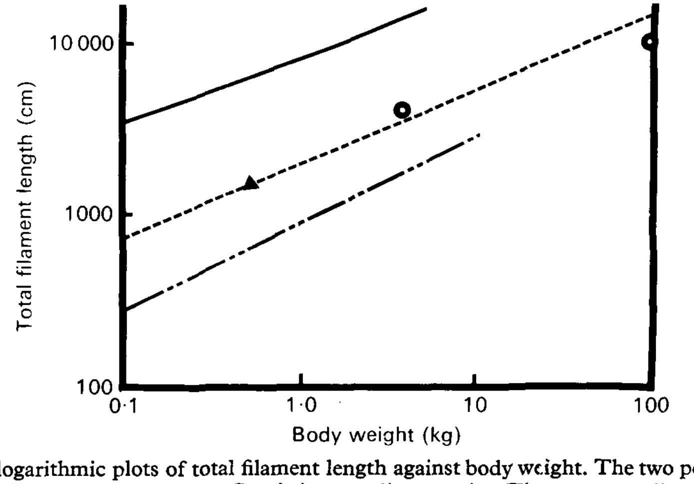

Fig. 6. Bilogarithmic plots of total filament length against body weight. The two points for *Mola* (○) fall close to the line given for Gray's intermediate species. The corresponding lines for tunas (——) and toadfish (— - - —) are also given. (▲) *Balistes*.

Table 1. *Summary of gill dimensions of* Mola mola

Body weight (g)	Total filament length (mm)	Number of filaments	Average filament length (mm)	Secondary lamellae/mm (one side)	Bilateral area of secondary lamella (mm^2)	Total area (cm^2)	weight specific area (cm^2/g)
97524	98624	2898	34·032	13·88	3·898	106719·5	1·094
3800	40921	2786	14·68	16·47	0·518	6982·3	1·837

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similar to that found in such sluggish fish as the toadfish and some rays (Hughes & Morgan, 1973). The profile of the secondary lamellae varies from the tip to the base of each gill filament, as in many other fish. Fig. 4 shows tracings of secondary lamellae taken from the tip, middle, and the base of the 100th gill filament of the second arch from the second specimen. The secondary lamellae at the filament tips are smaller than those found at their base and their profile changes from one in which the length and height are about the same to one in which the length is many times the height (Fig. 5). This

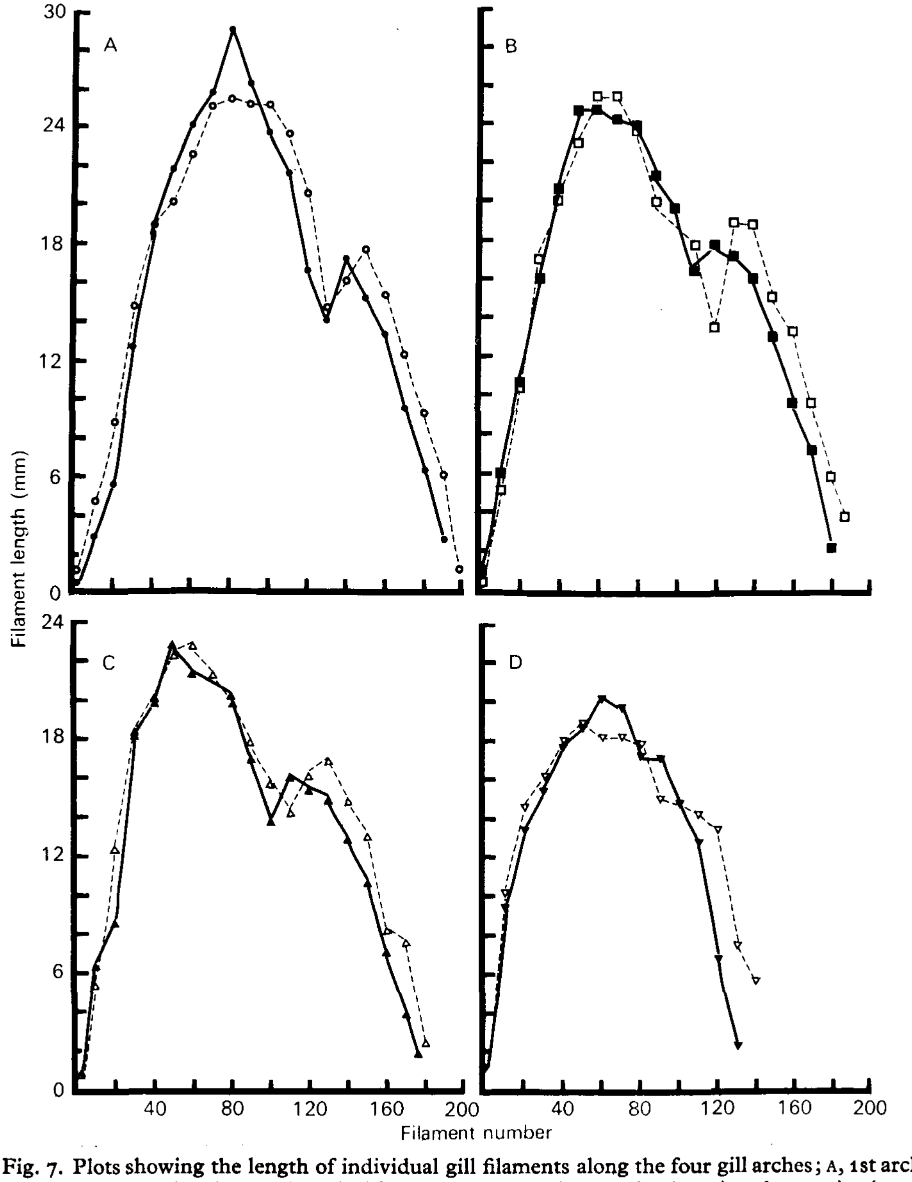

Fig. 7. Plots showing the length of individual gill filaments along the four gill arches; A, 1st arch; B, 2nd arch; C, 3rd arch; D, 4th arch. Measurements for the anterior (——) and posterior (– – –) hemibranchs are plotted separately.

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change of profile is similar to that found in the toadfish (Hughes & Gray, 1972). Another feature of the secondary lamellae is their increasing enclosure by the gill filament. The secondary lamellae at the tip stand free from the filament but those at the base are almost totally enclosed by the gill filament. This enclosure is due to an enlargement of the leading and trailing edges of the filaments.

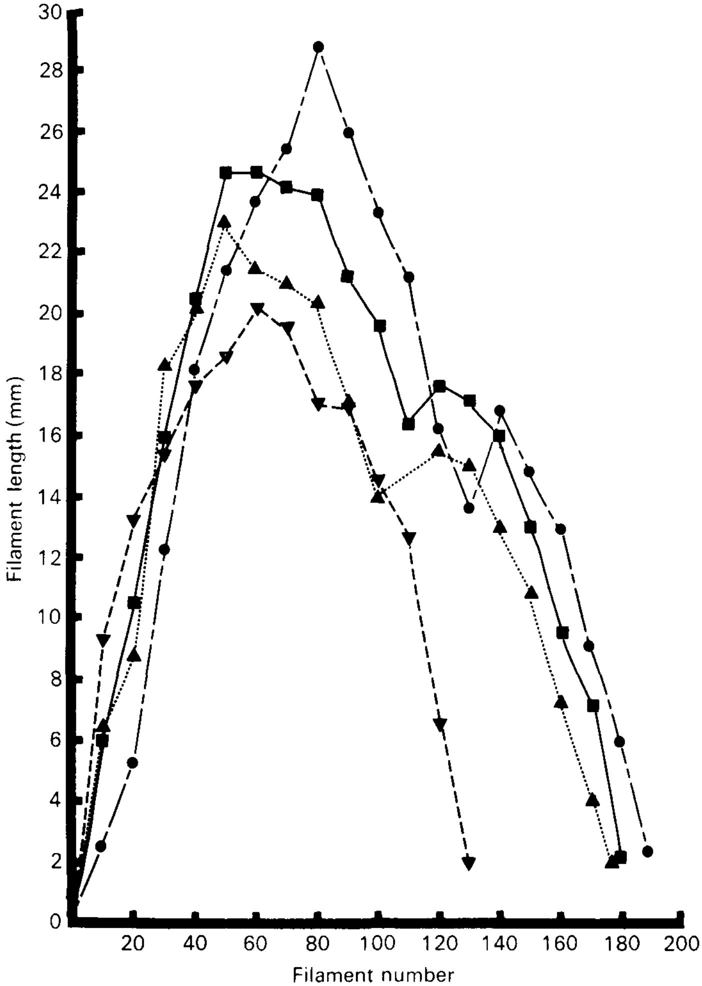

Fig. 8. Lengths of filaments from the anterior hemibranch of all four arches are plotted together on the same coordinates (●, 1st arch; ■, 2nd arch; ▲, 3rd arch; ▼, 4th arch).

Gill area measurements

Table 1 summarizes the gill parameters of the two specimens on which these measurements were made. When expressed per gram body weight the two gill areas fall within the range of 'Grays' intermediate fish' (see list in Hughes *et al.* 1974).

Values for the total filament length fell either side of the regression line for this intermediate group of fishes (Fig. 6). *Balistes capriscus*, the only other tetraodontid fish for

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which the gill area data is available, also falls within this group of fishes (Hughes, 1967). The moderately large gill area is in contrast to the low number of secondary lamellae per millimetre and the low average area of the individual secondary lamellae of the two specimens. These two values are closer to those found for more sluggish fish such as the toadfish (Hughes & Gray, 1972).

The number of filaments and the total filament length, however, are relatively high, and account for a higher total gill area than would be expected from the dimensions of the secondary lamellae and their frequency along the length of the filaments.

Figs. 7 and 8 shows the variation of the filament length in different regions of the hemibranchs. The anterior and posterior filaments are very similar in length but those of the posterior hemibranch tend to be slightly longer than the corresponding anterior filaments. A slight reduction in the length of the filaments occurs in the middle region of the hemibranch. This reduction in filament length coincides with the opening of the buccal cavity to the interbranchial region, i.e. the region of the gill arch skeleton.

DISCUSSION

The general conclusions from this study agree with those based on other anatomical studies on this species in underlining its specialization. The anatomy of the branchial blood system is quite different in a number of respects from that of trout, which might be considered to have a more typical teleost system. The branchial blood system of *M. mola* has undergone a number of adaptations, the main ones being; the presence of posterior and anterior afferent and efferent vessels; a pairing of the afferent branchial artery; and a blood supply to the bases of the filaments which is different from that to the middle and tip regions of the filaments.

Similar differences have been observed in other species. In *Mola* they are associated with the reduced skeletal gill arch and enlargement of the gill rays. The changes that have occurred in the anatomy of the structural support for the gill filaments have led to the afferent and efferent branchial arteries being displaced. This formation of anterior and posterior branches of the afferent and efferent branchial arteries has arisen because these arteries enter the hemibranchs in the middle of the arch. Extensions of the afferent and efferent filament arteries have been described for the tunas (Muir, 1970) and some air-breathing fish (Saxena, 1964). However, Mott (1950) also described a ventral branching of the efferent branchial artery which she considered to be a primitive feature. Its presence in many specialized teleosts would indicate that this feature may be secondarily developed in the tunas, *Mola* and some of the air-breathing fishes. The presence of a double afferent artery found in this study is very unusual. Paired efferent vessels have been described for several species of teleost (Saxena, 1964; Muir, 1970) but not paired afferent branchial arteries.

The reduction of the gill arch has necessitated a change in position of the abductor muscles. Typically these muscles run from the gill rays to the gill arch (Bijtel, 1949; Munshi & Singh, 1968) but in *M. mola* the abductor muscle has been found to join the two gill rays. The function of this muscle, however, is the same as for the muscles in the more typical position; on contraction the tips of a pair of filaments are drawn apart.

The external appearance of the gills of *Mola* is different from the more typical 'soft' gills of many fish in being robust, covered with spines and are generally stiffer. The leading and trailing edges of the filaments have been enlarged and the gill ray is stiffened. Secondary strengthening of the gills has also been described for other large oceanic fish, notably the tunas (Bovien, 1919; Muir & Kendall, 1968) and also for *Xiphias* sp. by Bovien (1919). The secondary strengthening observed in the tunas and *Xiphias* sp. is more pronounced than in *Mola* in that there is fusion between the different filaments (Bovien, 1919; Muir & Kendall, 1968); this is not found in *Mola* except when there is damage to the filament. The tendency for the gills of large teleosts to be secondarily strengthened may be related to the reduced septum whereas in the elasmobranchs the septum is well developed and this tendency for the gills to be secondarily strengthened is absent.

The gill area of *Mola* falls within the range of Gray's (1954) intermediate activity group of fishes and this correlates reasonably well with its known habits. Sunfish live mainly in the surface waters but it has been suggested by Wheeler (1969) that they may descend to moderate depths. They feed mainly on the larger members of the plankton and Fraser-Brunner (1951) gives a long list of organisms which have been found in the stomachs of these fish. The species found include: medusae, salps and ctenophores which form the main food of *Mola*, but Crustacea, ophiuroids and fish have also been recorded. Schmidt (1921 *a*) reports that they feed heavily on the leptocephalid larvae and Fraser-Brunner has found a *Molva macrophthalma* in the stomach of one of the specimens in the collection at the British Museum of Natural History. The stomach contents of the three specimens used in this study were not investigated. The wide ranging items in the diet would indicate that the oceanic sunfish is not too inactive. Caution must be exercised in the interpretation of the data presented in this paper in the absence of more definite data on the physiology and ecology of this species and consequently no firm correlations can be made between the gill area and its mode of life.

This study prompts many interesting physiological questions concerning the respiratory mechanisms of *M. mola*. In part, some of the answers may be inferred from the study of other tetraodontids such as *Balistes*, but for a complete understanding of the respiratory physiology of this fish, experiments would need to be performed on the live animal.

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