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Gill Structure of the Yellowtail and Frogfish

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Abstract The structure of the gills of yellowtail (*Seriola quinqueradiata*) and frogfish (*Phrynelox tridens*) have been investigated using transmission and scanning electron microscopy. It is shown that these two species of widely differing habits both have a basic structure which, although related to their activity, is very similar to that found for fishes in other marine habitats. Yellowtail have an extensive gill system in which the water comes into closer contact (4 μm) with the blood than in the more sluggish frogfish (6 μm). The water/blood barrier in both cases consists of epithelial, basement membrane and pillar cell flange layers. The outer surface of the epithelium has microridges which have a convoluted form in the yellowtail. Chloride cells are extensively developed in frogfish and in some cases extend to regions near the marginal channels. The frogfish gill forms a less dense network which will provide less resistance to water flow. The gill filaments are not so well developed and are absent from the posterior hemibranch of the fourth arch. There are about 28 secondary lamellae/mm on one side of each filament in yellowtail but only 14～15/mm in *Phrynelox*. Morphometric diffusing capacity is about 2.5 times greater in yellowtail than frogfish gills.

Many studies have now shown that there are good relationships between the structure of fish gills and their function (Gray, 1954; Hughes and Gray, 1972; Hughes and Morgan, 1973; Vogel et al., 1973; Laurent and Dunel, 1976; Hughes, 1966, 1980). These correlations range from adaptations at a gross morphological level including the number of arches and their organization, to structure of the gill filaments, development of the gill rakers (Iwai, 1964) and the presence of secondary connections within the system (Muir and Kendall, 1968). Measurements at the morphological level reveal differences in the number and total length of gill filaments, frequency and dimensions of the secondary lamellae along the gill filaments and consequently total gill area. From a respiratory point of view the actual surface area and its nature together with the distance that the respiratory gases must traverse between water and haemoglobin are the most important functional aspects. In general the more active fishes have relatively larger gill surfaces (A) with shorter diffusion distance (t) and consequently a greater diffusing capacity ($D_M=(A/t)\cdot K$; where K is the Krogh permeation coefficient for oxygen) than those of less active species. Correspondingly the more sluggish fish have gill sieves which have larger pores offering lower resistance to the water flow but as a consequence there will be greater distances for diffusion of oxygen from the water to the red blood cells (Hughes, 1966). This latter feature is important as several studies (Hills and Hughes, 1970; Scheid and Piiper, 1976) have shown that a significant portion of the resistance to oxygen transfer in fish gills resides in the water itself and not in the water/blood tissue barrier.

Among fish from Japanese waters relatively few studies have been made from this point of view and the present paper provides a comparison between the gill morphology of an active carangid fish and a much more sluggish, but also smaller species of frogfish. Comparison has confirmed some of the generalizations made above and has provided useful information about these fishes as they are frequently used in more physiological studies of fish respiratory biology (Kobayashi and Yamamoto, 1977; Umezawa and Hughes, 1983).

Materials and methods

Specimens of yellowtail (*Seriola quinqueradiata*) weighing about 1 kg were obtained from local fishermen and kept in the aquarium at the Usa Marine Biological Station. Frogfish (*Phrynelox tridens*) were also obtained by local fishing and were much smaller in size (63 g). Specimens were stunned by a blow on the head and small portions of gill filament were removed immediately and placed in fixative. For trans-

mission electron microscopy the gills were fixed in 5% glutaraldehyde in 0.1 M collidine buffer in sea water and post-fixed in 1% OsO_4. For scanning electron microscopy 2.5% glutaraldehyde in 0.2 M cacodylate buffer was used to which was added 25% sucrose, and some gill filaments were fixed in 25% glutaraldehyde alone. Other gills were fixed in Bouins fluid made up in sea water and this material was used for gross morphological and morphometric studies. Material was sectioned for TEM in an ultramicrotome and photographs taken in a Phillips 200 microscope at the Anatomical Institute, Berne, Switzerland and following critical-point drying the SEM material was viewed in a Cambridge S4 scanning microscope at Bristol.

Results

Fig. 1a shows the basic organization of the first and third gill arches of a yellowtail weighing about 1 kg. It can be seen that the bony arches comprise a relatively small portion of the whole gill and that the first arch has especially long gill rakers. Measurements of the gill area of these fish gave values of about 500 mm^2/g body weight which are not as great as those found in some rapidly swimming oceanic fishes such as *Coryphaena* and tunas. Frogfish have much smaller gills (Fig. 1b) and the gill arch skeletons comprise a much greater proportion of each gill. The filaments are not so closely apposed to one another and the whole structure gives an impression of providing less close contact between the water and the respiratory epithelium.

Scanning electron microscopy. Scanning electron micrographs confirm these general impressions as shown in Fig. 1c, d. The secondary lamellae appear coarsely arranged in the frogfish and their thickness is much greater relative to the interlamellar space which is narrower in absolute dimensions as there are fewer secondary lamellae/mm in the frogfish (14～15) than in the yellowtail (27～30). Another feature of frogfish gills is that the filaments of the two hemibranchs attached to a given arch are very separate from one another as there is scarcely any connection between them at the base (Figs. 1b, 2a) and it is this feature which tends to increase the impression of a less closely-organized system. In comparison with the frogfish secondary lamellae, those of yellowtail are thinner, and although the interlamellar spaces of yellowtail are wider relative to the thickness of the secondary lamellae in absolute dimensions they are narrower than those of frogfish (22 and 45 μm, respectively). The form of the secondary lamellae in the yellowtail changes along the length of the filament from almost triangular at the tip to a more rectangular shape although even towards the base of the filament it is perhaps best described as triangular with the leading edge much shorter than that of the trailing edge which goes back towards the inner surface of the filament.

In both species the surface epithelia of the filaments and secondary lamellae are covered with microridges of varying lengths. In some cases these can have quite complex convolutions and in most instances cell boundaries were well-defined (Fig. 2b, c, d, e). The whorled type of organization of the epithelial surfaces is well shown on both the filaments and secondary lamellae and perhaps in the latter the length of the individual ridges is less and in some areas this gives the impression of a more microvillous type of surface architecture (Fig. 2c). In all the materials there was often a closely-adhering mucous layer which makes it difficult to assess the true form of the ridging. Openings of mucous cells were visible along the surface of the gill filaments and a number of other cell types were evident (Fig. 2c, d). At higher magnification in areas where the ridges were especially clear (Fig. 2f) it was possible to see small pores on the epithelial cell surface between the ridges.

Transmission electron microscopy. The basic structure of the secondary lamellae is similar to that which has been found in other species, consisting of two outer epithelial layers, an intermediate basement membrane layer internal to which are the pillar cells and their flanges which line the blood channels (Fig. 3a, b, c). Running round the outer free edge of each secondary lamella is a marginal channel and this blood channel is lined on its outer border by endothelial cells whose flattened nuclei are clearly visible and the cells contained typical membrane-bound osmiophilic granules (Fig. 4a). As observed from the scanning and gross morphological studies the frogfish secondary lamellae are relatively thick (25 μm) and these extended to the actual water blood barrier (5.7 μm). Nevertheless, in certain regions these were found to be

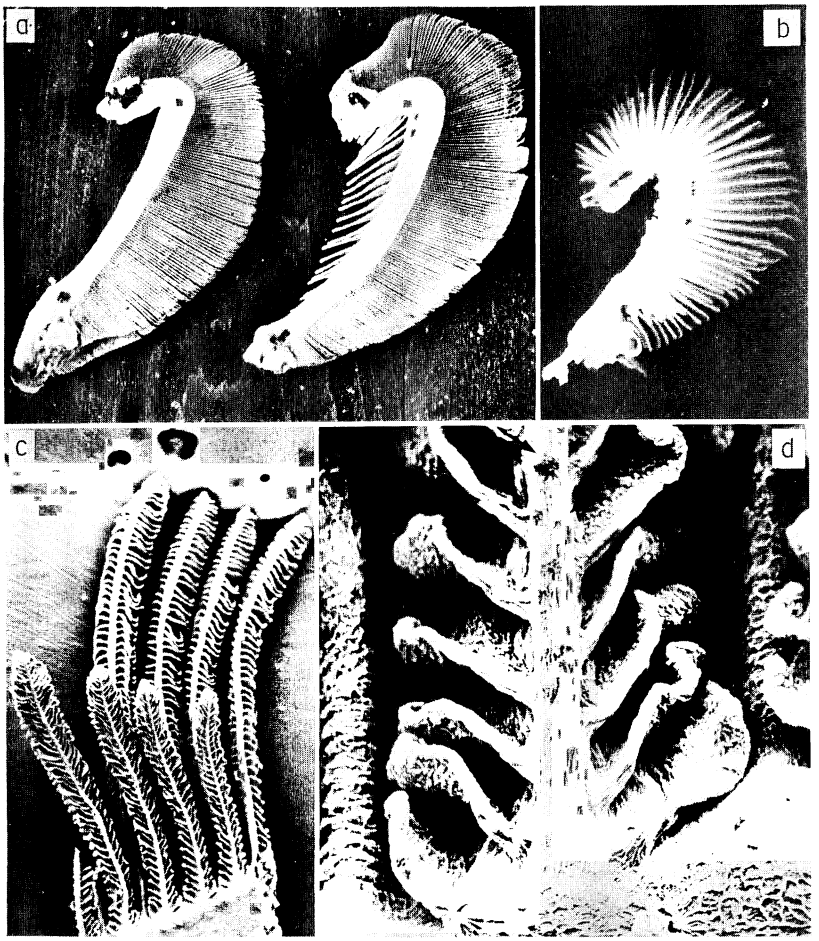

Fig. 1. (a) Photograph of the 3rd (left) and 1st (right) gill arches from the right side of a yellowtail (1,040 g). Note the well developed gill rakers on the first arch and the relatively narrow bony arches (×0.7). (b) 2nd gill arch from right side of a frogfish (63 g) (×1.57). (c) Scanning electron micrograph of part of a gill arch of a frogfish. There is a difference in length of the filaments from the two hemibranchs; the gill arch skeleton has approximately the same thickness as the length of the shorter filaments (×25). (d) Scanning electron micrograph of the origin of filaments from the gill arch of a frogfish. Filaments with secondary lamellae on one filament are clearly visible but also the axis and trailing edge of one of the alternating filaments from the other hemibranch attached to this arch. Again notice the absence of any close connection between adjacent filaments. Cell boundaries on both the filament and secondary lamellae are clearly visible. The shape of red blood cells in the efferent branchial vessel of the central filament can be identified (arrows) (×207).

fairly thin (Fig. 4b). In other places the water/blood barrier was increased in thickness because of the well developed intralamellar lymphoid spaces which often contain white blood cells and there seem to be a greater abundance of mitochondria-rich or chloride cells in the frogfish gills (Fig. 4a). The chloride cells were frequently found in the regions opposite the pillar cells and were overlain by a single epithelial layer, they often seemed to open at the surface between adjacent epithelial cells (Fig. 4a, c).

The basement membrane in frogfish is relatively thin (0.1 μm) and comprises both clear and fine fibrous layers. In yellowtail the basement membrane was thicker (0.17 μm) but once again there were a number of chloride cells especially in the crypt regions of the filaments (Fig. 3c), but absent in the more distal regions of the sec-

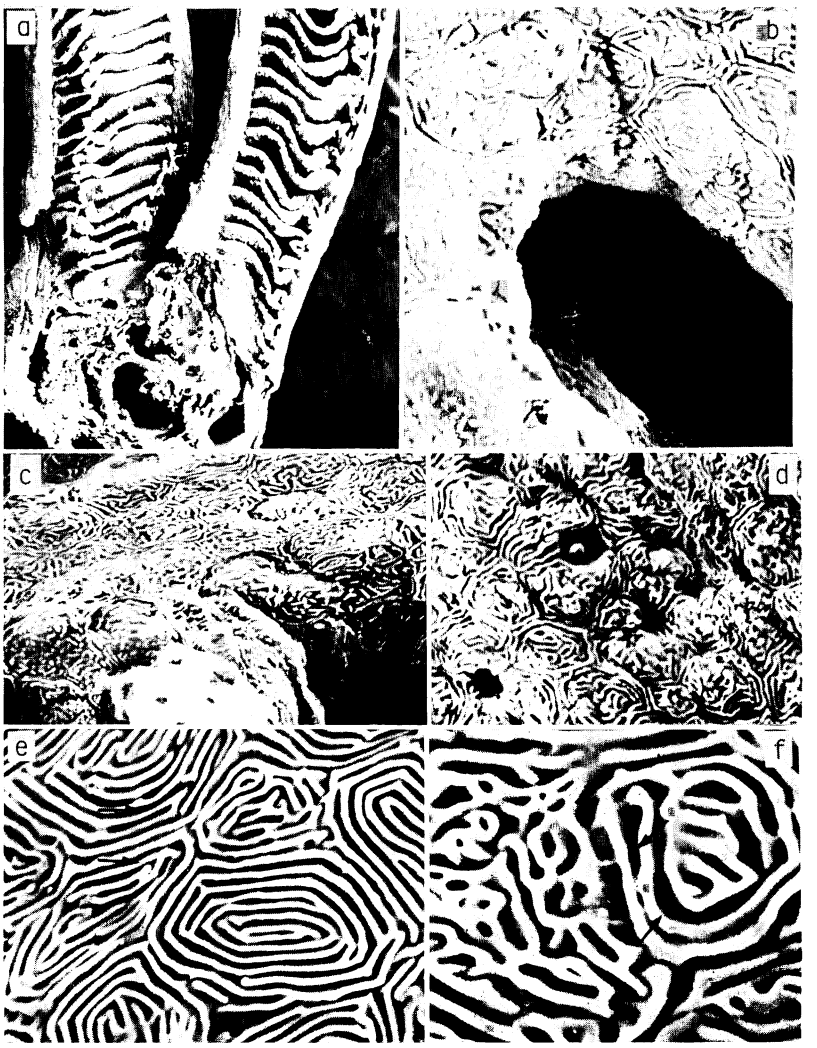

Fig. 2. (a) Frogfish. Scanning electron micrograph at the base of 2 filaments from hemibranchs showing their origin from the gill arch. The single afferent branchial and two efferent branchial arteries are shown in transverse section; note particularly the absence of any close connection between the 2 filaments at their base (×53). (b) Yellowtail. Scanning electron micrograph showing origin of secondary lamellae from a gill filament. Notice the whorled arrangement of the microridges in some cases often with quite complex patterns. The cell boundaries are clearly defined and their extension into the secondary lamella is also visible (×2,450). (c) Similar to Fig. 2 (b) but in this case note the presence of other cell types some of which are covered by microvilli and other forms of surface architecture. There are also some spaces between adjacent cells which are probably occupied by openings from mucous or chloride cells (×1,785). (d) Scanning electron micrograph of the surface epithelium from a gill filament of yellowtail showing many whorl-like microridged epithelial cells with numerous spaces probably occupied by mucous cells (×2,450). (e) High power scanning electron micrograph showing pattern of microridges on epithelial cells of a secondary lamella (×4,760). (f) High power SEM of surface architecture of epithelial cell of gill filament. The patterning is more complex and small pores are also visible between the ridges (arrows) (×10,850).

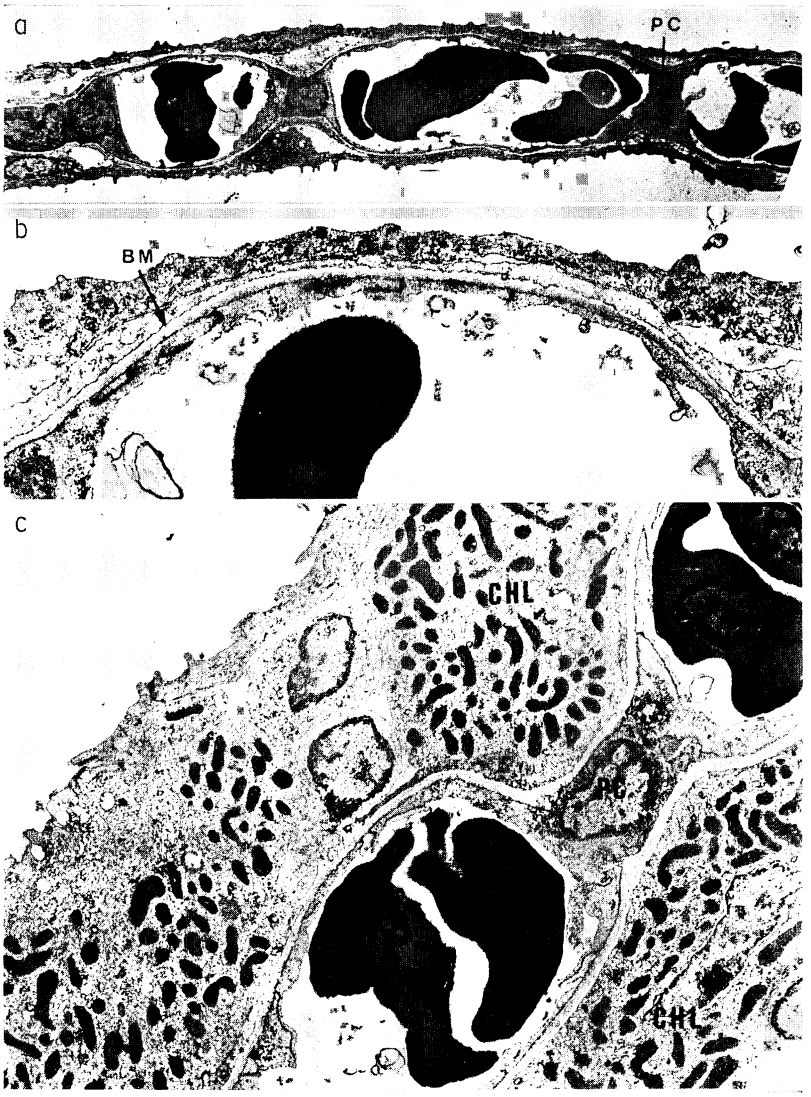

Fig. 3. (a) Yellowtail. Electron micrograph of a single secondary lamella. Notice the main layers of the water/blood barrier and pillar cells (PC) separating blood channels (×1,600). (b) High power micrograph through the water/blood barrier of a yellowtail secondary lamella showing the two epithelial layers, basement membrane (BM) and inner pillar cell flange layer (×10,600). (c) Transmission electron micrograph through the basal region of a yellowtail secondary lamella showing well developed chloride (CHL) cells in this region (×5,000).

ondary lamellae. Although present the collagenous columns within the pillar cells of both species were not especially well developed and seem to be correlated with the relatively thin basement membrane in these species. The outer surface of the epithelial layer was clearly formed of ridges especially in the case of the yellowtail, confirming the observations made with the scanning electron microscope.

Discussion

This study of the gills of two species having widely different habits has confirmed generalizations made for teleost fishes from other parts of the world. It is demonstrated that active species tend to have much better organized gill systems

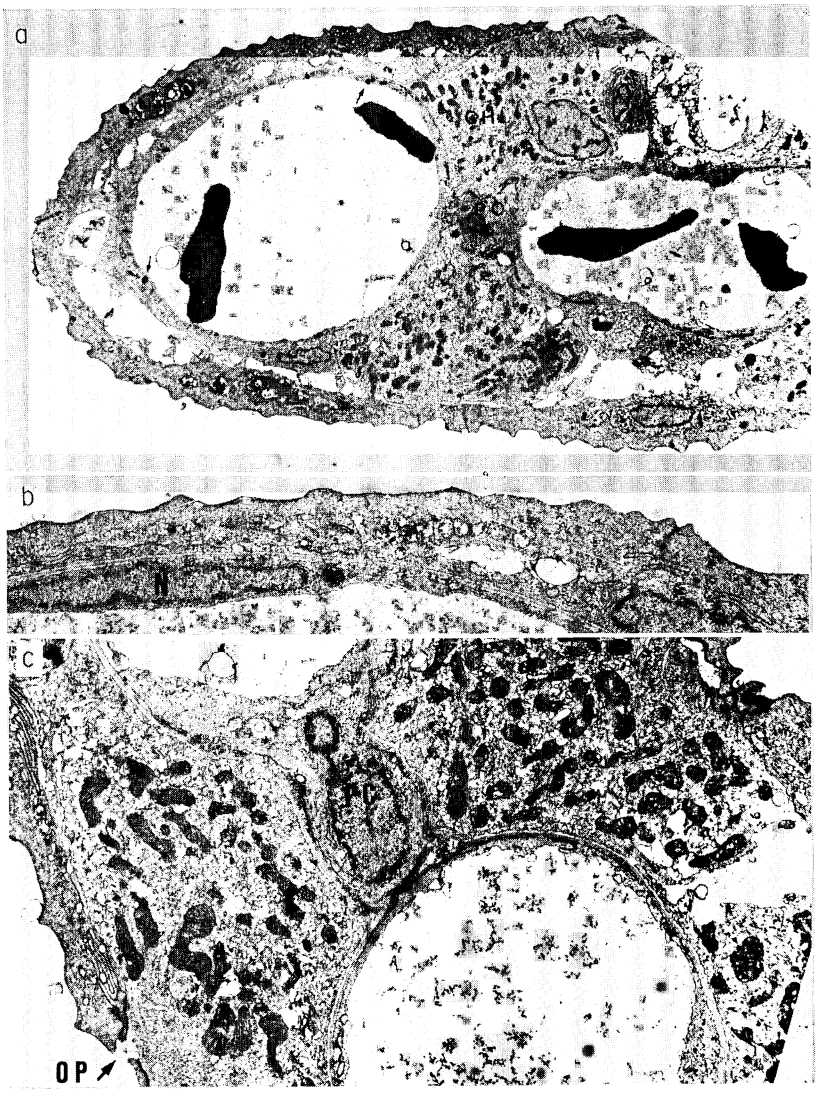

Fig. 4. (a) Frogfish, section through the marginal channel of a secondary lamella. Note Palade/Weibel bodies (arrows) in endothelium (×1,750). (b) High power micrograph through the water/blood barrier in thinner region of the marginal channel of a frogfish secondary lamella. Notice the flattened nucleus (N) of the endothelial layer lining this channel (×4,900). (c) Frogfish. Micrograph of a secondary lamella showing a pillar cell and well developed chloride cells with opening (OP) through the surface epithelium (×5,000).

with a larger area of contact between the water and gas exchange surfaces. The nature of these surfaces does not differ so widely as the secondary lamellae in both yellowtail and frogfish have many microridges. In the case of yellowtail the secondary lamellae are larger and the filaments have a greater total length and are closer together thus constituting a much tighter sieve through which the water passes. The frogfish has parts of the arches not bearing filaments and the filaments shorter in length and the arch itself occupying a much greater portion of each gill. Nevertheless the organization of the gill filaments in *Phrynelox* are of the so-called perciform type (Dornescu and Miscalencu, 1968; Hughes, 1980) in which the inter-filamenter

septum is very short and does not interfere with ventilation of most of the secondary lamellae. This type of gill is also found among carangid fishes as the mackerel and yellowtail.

It would appear that these structural modifications are well adapted to the completely different modes of life of these two species and fits in with physiological measurements which have shown that the resting oxygen consumption of yellowtail (80 ml O_2/kg/h) is greater than that of frogfish (50 ml O_2/kg/h), although it is difficult to compare specimens having such a large difference in body weight. More important, however, is the greater surface area and diffusing capacity of the yellowtail gill which provides the possibility for increased scope of activity whilst maintaining a mainly aerobic respiration. Although experiments have not been carried out, one would expect that frogfish would not be able to maintain aerobic respiration at low oxygen tensions for long periods, and that anaerobic mechanisms would soon be involved.

Coupled with differences in the 'tightness' of the sieve it can be estimated that the energy required for ventilation would be greater in fish like the yellowtail and constitute a significant part of the resting metabolism. The closer contact between water and blood not only helps provide an effective gas exchange surface but also a surface for the exchange of ions. In both species the secondary lamellae are well provided with chloride cells which play an important role in osmotic and ionic balance of teleosts (Sardet et al., 1980) whereas it seems that such cells are more densely distributed in gills of frogfish. Both fish are known to live under estuarine conditions and perhaps the frogfish are able to adapt better to a wider range of salinities?

To summarize, some of the major differences between the two types of gill are shown in Table 1 which, although based upon specimens of widely different body size, does give a true indication of the main differences between these fish of widely different types. In particular the morphometric diffusing capacity of the yellowtail is nearly three times greater than that of the frogfish. The value obtained for the yellowtail is similar to values obtained for rainbow trout whereas that of the frogfish is slightly less than that for the toadfish (Hughes, 1981).

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Table 1. Comparison of some features of the gills of yellowtail and frogfish.

	Yellowtail (1,020 g)	Frogfish (63 g)
Gill area	367 mm^2/g	192 mm^2/g
Number of arches	4	4
Number of hemibranchs	8	7
Number of filaments	3,808	637
Sec. lamellae/mm, one side of filament	28.0/mm	14.0～15.0/mm
Distance between sec. lamellae	21.4～23.5 μm	44.4～46 μm
Thickness of sec. lamella	12.2～14.3 μm	22.2～25 μm
Thickness of water/blood tissue barrier (arith. mean and range)	4.0 μm (0.91～8.33)	5.7 μm (2.98～10.42)
Morphometric diffusing capacity (D_M)	0.138 ml O_2/mm^2/μm/kg	0.051 ml O_2/mm^2/μm/kg

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ハマチ及びイザリウオの鰓構造

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ハマチ及びイザリウオの鰓の構造について透過及び走査電子顕微鏡を用いて調べた．これらの2種は習性が著しく異なっているが，両者とも他の海産魚類にみられる構造と非常に似通う基本的構造をもっている．ハマチは不活発なイザリウオ (6 μm) にくらべて呼吸水が血液とより密接 (4 μm) するような大きい鰓組織をもっている．これら両者にみられる水/血液の間の障壁は上皮層と基底膜及び柱状細胞層からできていて，ハマチでは上皮の表面に螺旋状の微小隆起がみられる．イザリウオでは塩類細胞がよく発達し，又，鰓は水流に対する抵抗が少なくなるような多少あらい網目構造をしている．更に鰓弁はそれほど発達していなく，第4鰓弓では後部 hemibranch が欠けている．各鰓弁の片面における1 mm当りの二次鰓弁の数はハマチは 28 であり，イザリウオではわずかに 14～15 である．体型測定的な拡散容積はハマチがイザリウオのおよそ 2.5 倍も大きいことになる．

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