THE RESPIRATORY AREA OF THE GILLS OF SOME TELEOST FISHES IN RELATION TO THEIR MODE OF LIFE

by

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ABSTRACT

From computations (by means of graphic interpolation and graphic integration) of the respiratory area, and transposition of these values to a respiratory area of a standard fish of 200 g (A_{200} value), it could be made plausible that the relation between respiratory area and mode of life of the fishes mentioned in this paper (Cod, Plaice, Conger, Flounder, Dab and Pike) fits in with the general pattern found in an earlier paper, although intraspecific differences were sometimes considerable.

In comparison with A_{200} values of other species, the Cod has a respiratory area that fits in with his mode of life and that of other typical sprinters. The Flounder has a considerably larger respiratory area than Plaice and Dab. Flounder feeds mainly on small fishes, while Plaice and Dab feed on molluscs and worms. Conger has to be considered a crawler. The Pike, as a typical sprinter, shows nevertheless large differences in its A_{200} values.

It was known already that freshwater biotopes do not allow fishes to develop into typical stayers. Thus, large differences between freshwater sprinters and crawlers can hardly be expected.

The relation between respiratory area and body surface cannot be used in a comparison between fishes of different species.

INTRODUCTION

The present study was undertaken to investigate the relation of respiratory area and mode of life in some teleost fishes. Meanwhile, the respiratory areas of the standardized fishes can be compared with those computed in an earlier paper (De Jager & Dekkers, 1975).

This paper deals with six species, viz. five marine species (Cod, Flounder, Conger, Plaice and Dab) and one freshwater species (Pike). Some of our measurements could be compared with data obtained by using different methods (Byczkowska-Smyk, 1957, 1959; Gray, 1954; Hughes, 1966, 1970, 1972).

MATERIALS AND METHODS

The work has been concerned with the following species: Cod, *Gadus morhua* Linnaeus, 1758 (4 specimens examined), Conger, *Conger conger* (Linnaeus, 1758) (1 specimen examined), Plaice, *Pleuronectes platessa* Linnaeus, 1758 (3 specimens examined), Flounder, *Platichthys flesus* (Linnaeus, 1758) (4 specimens examined), Dab, *Limanda limanda* (Linnaeus, 1758) (3 specimens examined), and Pike, *Esox lucius* Linnaeus, 1758 (3 specimens examined) of different weight and length (see table I).

The Cod was captured in September in the northern part of the North Sea, the Flounder, Plaice and Dab were obtained in spring in the Wadden Zee, the Conger was captured in September in the Irish Sea, while we got the Pike from the IJsselmeer.

The fishes were anesthetized by means of MS222 (Sandoz). The blood was changed via the heart against Ringer solution with heparine as anticoagulans. Ringer perfusion was followed by a Ringer plus indian ink (1 : 1) mixture, in order to make blood vessels better visible. After fixation in 10% formalin solution, the gills were stored in methyl benzoate, in which the tissue became clear except the indian ink filled blood vessels.

Calculation of the respiratory area of the gills from the sum of the total area of the secondary lamellae of the gill filaments seems an immense task. The number and area of a secondary lamella varies along each one of the gill filaments. In the same way, the length of a filament varies over the length of a gill arch, and over each of the gill arches these variations must be determined separately. So it is necessary to

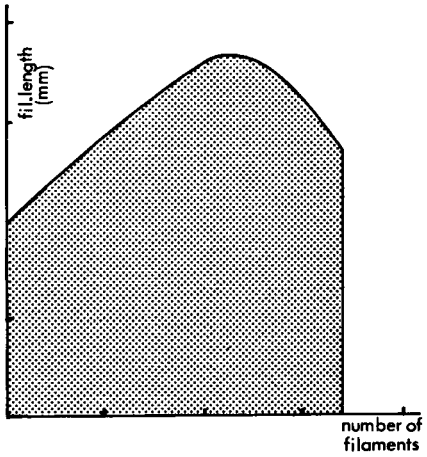

Fig. 1. Calculation of the total filament length of the gills by graphic interpolation (for explanation see text).

devise a sampling method that takes these variables as much as possible into account in the final calculation of the respiratory area.

To get to this final calculation of the respiratory area, the following data are necessary: (1) number of gill arches, (2) number of filaments, (3) total length of the filaments, (4) number of secondary lamellae per mm filament, and (5) area of the secondary lamellae.

1. The number of gill arches is 2 x four arches, as normal in teleosts.

2. The number of filaments is determined by direct counting. (Based on several measurements, the assumption was made that anterior and posterior filaments differ little or not in length).

3. The total length of the filaments can be calculated by graphic interpolation. For this purpose, four anterior filaments are taken from every gill arch on one side of the fish at $1/8n$, $3/8n$, $5/8n$, and $7/8n$ (n = total number of filaments of the gill arch). It is now possible to define the total length of the filaments of one gill arch by graphic interpolation. To this end, the total number of filaments is plotted along the x-axis, the length (mm) along the y-axis. After plotting the values of the sample filaments, the length of the other filaments can be defined by interpolation (the surface under the curve is compared with a standard surface representing a known length). The sum of the total filament length is doubled to take into account the arches of the other side of the fish (for Flounder, Plaice and Dab, both left and right gill arches were treated).

For example, the total filament length of gill arch 4 of the 661 g Pike is calculated by cutting out the dotted area (fig. 1) weighing 0.4770 g and comparing this area with a standard surface, representing 250 mm length, weighing 0.0974 g. Total anterior filament length is:

$$\frac{0.4770}{0.0974} \times 250\,\text{mm} = 1216.63\,\text{mm}.$$

So the total anterior and posterior filament length of gill arch 4 amounts to 2 x 1216.63 mm = 2433.26 mm. In the same way, the total filament length of gill arch 1, 2, and 3 of one side of the fish are determined at 4135.01, 3738.45, and 4008.21 mm, respectively. This would make the total filament length of the 661 g Pike : 14314.93 x 2 = 28629.9 mm.

4. The total number of secondary lamellae per mm filament was defined by counting the number of lamellae of the sample filament under the microscope and to divide this number by the measured sample filament length.

5. The area of the secondary lamellae is calculated by preparing out of 1 sample filament 10 lamellae of known place, regularly distributed over the filament (fig. 2A). The area of each sample lamella was measured by tracing the image of the lamella projected by a Reichert projection microscope and determining the surface by comparing the weight of the projection

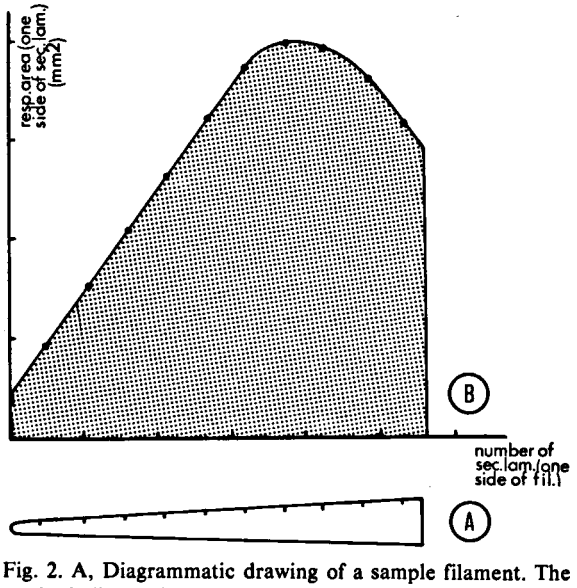

Fig. 2. A, Diagrammatic drawing of a sample filament. The marks indicate the places from where the sample lamellae were taken.
B, Calculation of the respiratory area of one side of one sample filament by graphic interpolation (for explanation see text).

on the trace paper with a standard area. By means of graphic interpolation, the respiratory surface on one side of the lamella, on one side of the filament, was measured. Because of the fact that the two sides of the secondary lamella take part into the respiration and the fact that both sides of the filament have secondary lamellae, the value found has to be quadrupled.

For example, plotting the respiratory areas on one side of 10 sample lamellae of sample filament 3 of gill arch 4 of the 661 g Pike, the dotted area under the curve (fig. 2B) corresponds to a respiratory area on one side of the lamella on one side of the filament of 7.7785 mm² (weight of the surface 0.6061 g, weight of the standard surface representing 2.5 mm² 0.1948 g). Total respiratory area of this sample filament equals 4 x 7.7785 mm² = 31.11 mm².

In this way it is possible to calculate the total respiratory area of the four sample filaments. With these four values it is possible to calculate the total respiratory area at one side of the fish by graphic integration. Along the x-axis the total number of filaments of one gill arch is plotted, along the y-axis the respiratory areas of the sample filaments. The area under the curve represents the respiratory area of the gill arch (this value is compared with that of a standard surface).

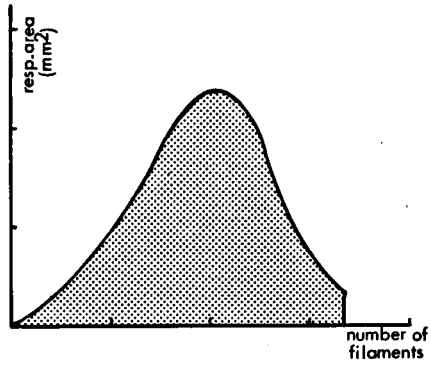

Fig. 3. Calculation of the respiratory area of one gill arch by graphic integration (for explanation see text).

For example, after plotting the four values of the respiratory area of the four sample filaments, the remaining values of the other anterior fila-

Table I. Results of the various calculations concerning the respiratory area of the gills in the 18 specimens examined.

species	weight (g)	length (cm)	body surface (cm²)	number of filaments	total fil. length (cm)	number of sec. lam./mm	average surface sec. lam. one side (mm²)	total resp. area (mm²)	resp. area (mm²) per g body weight	resp. area (mm²) per cm² surface	A_{200} in mm²/g
Gadus morhua	500	35.5	466.6	1512	10213.8	15.6	0.11	71869.5	143.6	154.0	169.5
(Cod)	580	37.0	539.0	1558	12744.8	14.8	0.14	104572.4	180.3	194.0	218.4
	580	39.0	563.6	1520	10790.4	15.8	0.12	83794.2	144.5	148.7	175.0
	640	40.0	559.0	1664	10505.4	14.4	0.16	98764.1	154.3	176.7	190.3
Platichthys	127	25.0	304.0	814	4516.0	14.0	0.11	27010.0	212.7	88.8	196.0
flesus	131	24.0	301.0	836	4046.0	15.0	0.10	25334.0	193.4	84.2	179.2
(Flounder)	156	25.0	340.0	892	4024.0	16.0	0.11	29054.0	186.2	85.5	178.1
	178	27.0	379.0	952	6020.0	16.0	0.12	47046.0	264.3	124.1	258.8
Conger conger (Conger)	1920	88.0	1877.5	2664	20825.0	15.5	0.18	232811.9	121.3	124.0	182.2
Pleuronectes	115	24.0	320.0	960	3830.0	17.0	0.05	12746.0	110.8	39.8	100.3
platessa	120	24.5	300.0	952	3668.0	17.0	0.07	17666.0	147.2	58.9	134.3
(Plaice)	182	24.5	360.0	920	3867.0	17.0	0.07	18460.0	101.4	51.3	99.7
Limanda	145	23.5	312.0	782	3148.0	17.0	0.08	16484.0	113.7	52.8	107.3
limanda (Dab)	151	23.0	310.0	854	3350.0	17.0	0.06	14176.0	93.9	45.7	89.3
	258	28.0	442.0	874	4496.0	14.0	0.12	30450.0	118.0	68.9	123.6
Esox lucius	661	49.0	678.7	3660	28629.9	18.4	0.06	118052.4	178.6	173.9	221.4
(Pike)	991	48.0	814.3	3540	29247.5	17.0	0.07	142079.0	143.3	174.5	191.2
	1397.5	59.0	1331.8	3724	34150.8	18.8	0.05	132365.4	94.7	99.4	134.4

A_{200} = standard gill area one would expect in a fish of 200 g; fil. = filament; lam. = lamellae; resp. = respiratory; sec. = secondary.

ments were obtained by graphic integration. So, for the 661 g Pike the dotted area (fig. 3) corresponds to the half of the respiratory area of gill arch 4 which amounts to 5704.47 mm² (the dotted area represents a weight of 0.4621 g; weight of the standard surface representing 100 filaments of 20 mm² respiratory area, 0.1620 g). Total respiratory area of gill arch 4 is 2 × 5704.47 mm².

By repeating this procedure for all four arches on one side of the fish the respiratory area on one side is determined. Doubling this value gives the total respiratory area.

In De Jager & Dekkers (1975) an A_{200} value is introduced, in order to make it possible to compare fishes of different size. This A_{200} value is determined by means of the allometric formula $A = c.W^b$ in which A is the total respiratory area (mm²), c is a constant, W is the weight of the fish (g) and b is the regression coëfficient. This formula is transformed in:

$$\log A = \log c + b \log W$$

Using computations of data given by several authors, De Jager & Dekkers made it admissible that for b a value of 0.82 is applicable. So in the present paper $b = 0.82$ is used for converting the total respiratory area to that of a standard fish of 200 g. This standard gill area (A_{200}(mm²/g)) can be defined as the gill area one would expect in a fish of 200 g.

RESULTS

The results of the various calculations are placed together in table I.

Gadus morhua: Of the four fishes examined, a specimen weighing 580 g and having a length of 37 cm appears to have the largest respiratory area. The reason is to be found in the extent of the total filament length, coupled with a slightly larger lamellar area on one side. So the A_{200} value, as well as the gill area/cm² body surface of this specimen are higher than the corresponding values of the other three specimens.

Platichthys flesus: Here we examined three fishes of the same age, while the fourth (27 cm) was a year older. In the older specimen the total number of lamellae has much increased as a result of an increase of the number of filaments whereby the total respiratory area increases c. 35%.

Conger conger: The unilateral area of the secondary lamellae is larger than that of the other fishes studied.

Pleuronectes platessa: The three fishes of the same age show a strong resemblance in secondary lamellae/mm, total filament length and total number of filaments. Only the 24 cm long Plaice has smaller secondary lamellae, through which also the difference in total respiratory area can be accounted for.

Limanda limanda: In the 28 cm long Dab the respiratory area has almost doubled. It is true, the implantation of the lamellae on the filaments is less dense, viz. 14 instead of 17, but the increase of the total filament length is great, while the surface of the secondary lamellae has also doubled.

Esox lucius: Just like Dab and Plaice, this freshwater fish has small secondary lamellae. The low value of A_{200}, gill area/g body weight and gill area/cm² body surface can to a certain extent be related to the small average area of the secondary lamellae.

DISCUSSION

The results show that there can be large interspecific differences. The A_{200} value, used by De Jager & Dekkers (1975) makes comparison possible with other species of a known A_{200} value. In fig. 4 and table I it is shown that the A_{200} values of Cod, Flounder and Conger can be clearly distinguished from those of Plaice and Dab, while the Pike, as the only freshwater species, takes an intermediate position and can better be considered separately.

The differences in A_{200} values in the various species originate mainly in the differences in the area of the secondary lamellae. In Flounder, Dab and Pike the surfaces of the secondary lamellae are obviously smaller than those in the three first mentioned species.

The Cod is a fish, which at the age of 3 to 4 years (as studied by us) feeds mainly on fishes present in large quantities. Blaxter & Dickson (1959) found by swimming speed determinations that the Cod is a slow swimmer which is quickly exhausted, when maximum swimming speed was kept going on. Boddeke (1971) reckons the Cod among the sprinters. Beamish (1966) gives values leading to the same conclusion. Comparison of the average A_{200} value of the Cod (188.29 mm²/g)

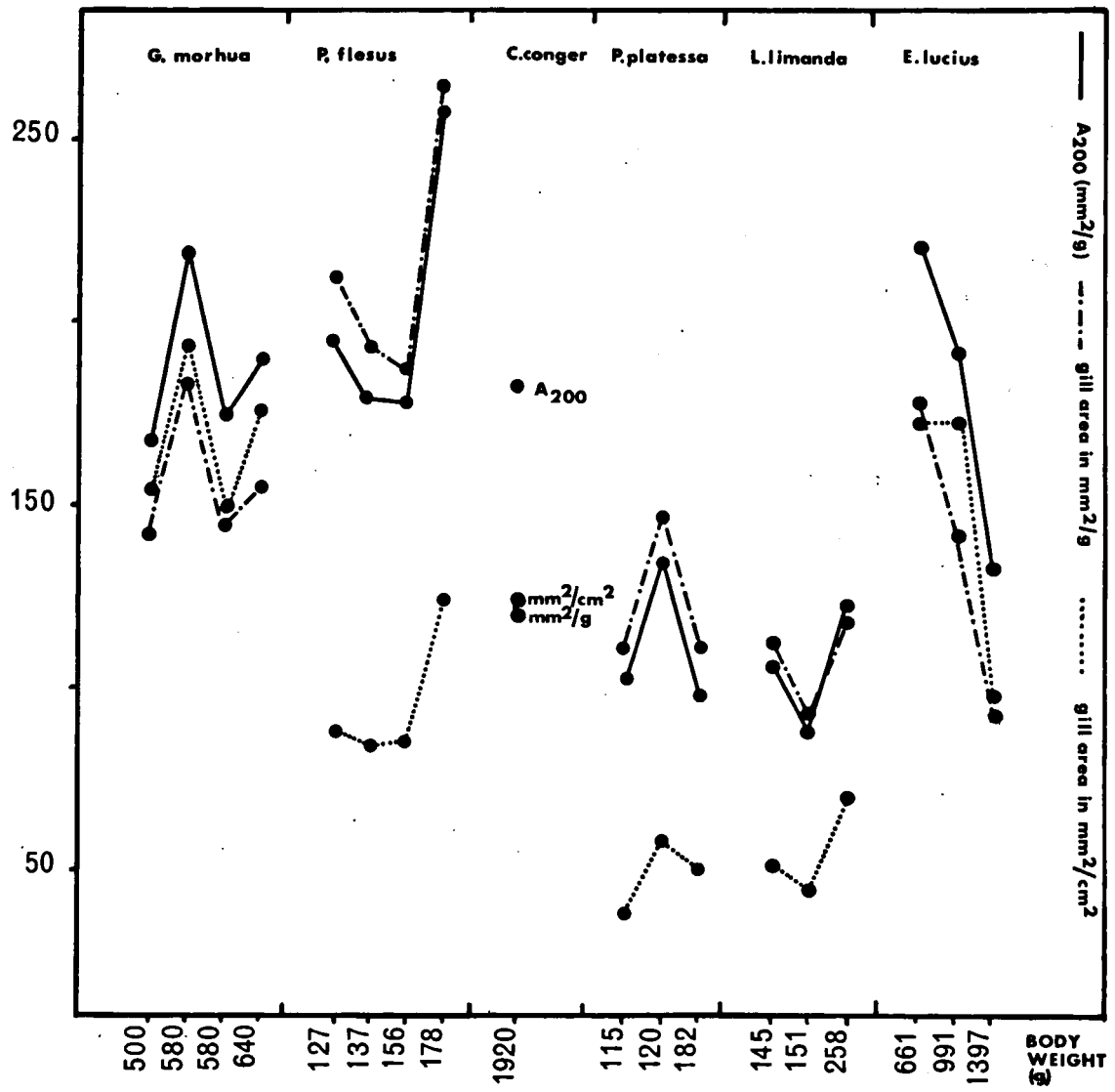

Fig. 4. A_{200} values, gill area in mm²/g body weight and gill area in mm²/cm² body surface of the 18 specimens (of 6 species) studied.

with A_{200} values calculated from literature data for a large number of species (De Jager & Dekkers, 1975) shows that the A_{200} value of the Cod lies in between those of the Toadfish, *Opsanus tau* (Linnaeus, 1766) (A_{200} = 184 mm²/g body weight) and the Dory, *Zeus faber* Linnaeus, 1758 (A_{200} = 190 mm²/g body weight). *Opsanus tau* has sluggish habits (Steen, 1971) and feeds on small crustaceans and small fish (Ladiges, 1970). *Zeus faber* has a diet consisting of Herring and young gadoids (Poll, 1947), on which he is hunting, while he has also long lasting periods of rest. Thus *Zeus faber* is a typical sprinter as well.

The three flatfish species, Flounder, Plaice and Dab show differences in their respective A_{200} values, which can be related to differences in their way of life and environment. *Pleuronectes* and *Limanda* migrate to deeper water when growing older, while *Platichthys* prefers shallow waters where there are muddy grounds. *Platichthys* feeds on crustaceans and small fishes, e.g. Sprat, and therefore has to be more active than *Pleuronectes* which when becoming adult changes his diet from small crustaceans to mainly molluscs (Boddeke, 1971). *Limanda* is as a hunter by vision designated to clear water and feeds on

crustaceans and worms (Münzing, 1970). Yet, the differences between *Platichthys* on the one hand and *Pleuronectes* and *Limanda* on the other hand are probably mainly related to the place where they are usually found: *Platichthys* on and in muddy grounds under intertidal conditions (the smaller animals often bury themselves during low tide) (Münzing, 1970), *Pleuronectes* and *Limanda* in clear water. In the muddy substrate, contamination of the gills takes place faster. The "overcapacity" of the respiratory area can serve as a compensation of the contaminated gill area. This "overcapacity" in *Platichthys* can also be one of the explanations of the phenomenon that Flounder stays longer alive than Plaice and Dab on board of fishing boats.

The A_{200} values found in *Pleuronectes* deviate strongly from the (converted) values found by Byczkowska-Smyk (1957) in *Pleuronectes*. Byczkowska-Smyk's data have to be rejected because of errors in the estimation of the area of the individual secondary lamellae (footnote in Hughes, 1966: 177). Hughes' (1966) value, calculated in one specimen, also shows a deviation. Hughes used a specimen weighing 86 g, of which the area of the secondary lamellae was larger than that of the fishes used in the present paper, while there were also more secondary lamellae/mm.

Conger conger frequents only hard bottoms. His food varies and includes many fish species, particularly bottom dwelling forms. He also feeds on a large number of crustaceans and cephalopods (Wheeler, 1969). *Conger* can be called a crawler. In comparison with the converted A_{200} value (A_{200} = 214 mm²/g) from data of Gray (1954), the difference appears to be hardly larger than the value found here (182.2 mm²/g).

Esox lucius shows great differences in values found, however, the A_{200} values decrease while the fishes increase in dimension. As the differences in oxygen consumption in freshwater fishes are rather little (De Jager & Dekkers, 1975), great differences in respiratory area are not to be expected. This is confirmed by comparing our data with other already calculated A_{200} values of different species. The Tench, *Tinca tinca* (Linnaeus, 1758), a typical crawler, has an A_{200} value of 198 mm²/g, calculated from data of Hughes (1970, 1972). Byczkowska-Smyk's (1959) values have to be rejected for the same reason as in *Pleuronectes*.

From the results of the relation between respiratory area and body surface of the different species it is clearly shown that this relation is strongly dependent on the shape of the fish. However, this relation is not appropriate in comparisons between different species, in contrast to what Pütter (1909) states in his paper on a number of fishes, particularly *Scorpaena*. He felt that the respiratory surface was proportional to body surface.

In fig. 4 it is clearly shown that flatfishes take a special place between the more "normally" shaped fishes in their relation respiratory area/cm² body surface.

ACKNOWLEDGEMENTS

We would express our gratitude to Dr. A. van der Stelt for critically reading the manuscript and suggesting many improvements and to mrs. F. Peeters-Pieters for her advices when making the manuscript ready for printing.

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Received: 1 June 1976