

USE OF THE FIRST GILL SLITS FOR WATER INTAKE IN A SHARK

By GORDON C. GRIGG*

Zoology Building, University of Sydney, Sydney, 2006, Australia

(Received 19 January 1970)

INTRODUCTION

Irrigation of the gills in elasmobranch fish is effected by two pumps which, coupled with interactions between the different parts of the respiratory system and its intrinsic elasticity, co-operate to provide a flow of water across the gills (Hughes, 1960; Hughes & Ballintijn, 1965). Hughes described in detail the operation of these respiratory pumps in both the dogfish, *Scyliorhinus canicula*, and the thornback ray, *Raia clavata*. Movements of the orobranchial cavity provide for the operation of the force pump while those of the parabranchial cavities constitute the suction pump. By analysing the difference in pressure between the orobranchial cavity and parabranchial cavities Hughes concluded that the flow of water across the gills is continuous except in the dogfish when the pressure gradient is reversed briefly during each cycle. In shark-like elasmobranchs water enters the orobranchial cavity mainly through the mouth, though some, such as *Scyliorhinus canicula*, have well-developed spiracles which also admit water. In the skates and rays, however, the spiracles are the major inspiratory openings. They are large, dorsally situated openings with active flap valves which prevent backflow. Hughes reported that water also enters through the mouth, particularly when rays are actively swimming, but when partly buried it is most likely that the spiracles alone function for water intake. The dependence of the skate on enlarged spiracles is clearly related to its dorso-ventral flattening, its bottom living habits and its mode of feeding.

Port Jackson sharks (*Heterodontus portusjacksoni*) are similar to dogfish in general body form. They are sluggish and live on the bottom where they feed on molluscs, crustaceans and echinoderms. The spiracles are much reduced. Normally, the respiratory water enters through the mouth and is exhaled through all five pairs of gill slits. G. C. Grigg (in the Press) has described the functional significance of septal canals along the back of the gill filaments. These canals serve as ducts carrying water to the parabranchial cavities after its passage between the secondary lamellae; in this way a counter-current flow between water and blood is provided at the respiratory surface. In deducing this pattern of water flow, the pressure profile between orobranchial and parabranchial cavities was studied, and it seems that the respiratory flow is unidirectional though pulsatile at the respiratory surface.

Under certain circumstances a hitherto undescribed pattern of respiration occurs in Port Jackson sharks. In this pattern, water intake occurs through the first gill slits, and in the present paper this mode of respiration is characterized, its physiological effectiveness evaluated and its functional significance discussed.

* Queen Elizabeth II Fellow.

MATERIAL AND METHODS

Five adult Port Jackson sharks varying in size from 5–16 kg. were used in these experiments. Sharks were captured by SCUBA diving in and near the entrance of Sydney Harbour. After capture specimens were maintained at 'Marineland', Manly, until required. In the laboratory, sharks were placed in a large stainless steel experimental tank through which filtered and aerated sea water circulated at 20° C. Port Jackson sharks conveniently have cartilaginous brow ridges and also strong spines in front of each of two dorsal fins. These 'handles' allow specimens to be clamped firmly in the experimental tank. The sharks are docile, and rarely struggled.

Direction of water flow was determined by releasing a small amount of nigrosin dye at appropriate places and observing its passage. Similar information was obtained by releasing slugs of chilled sea water and recording their appearance at a gill slit using a thermistor probe actuating a Grass polygraph. For this purpose the flap of the gill slit, usually the third, was cannulated by drawing a heat-flared polyethylene tube through a small hole in the flap until the flared end was snug against the inside of the flap. The thermistor probe was then threaded down the tube until its sensitive tip protruded about a millimetre into the stream of excurrent water.

A cannula was introduced into the dorsal aorta, after severing the upper lobe of the tail, and threaded up as far as the level of the first dorsal fin, opening near the junction of the fourth epibranchial arteries. The partial pressure of oxygen in blood removed through this cannula, and of water in the experimental tank, was measured with a Radiometer blood-gas analysis system held at the same temperature as the water in the experimental tank.

This changed pattern of respiration was invoked by lowering the oxygen tension of the water or by tying a plastic bag around the mouth so as to block the mouth completely without obstructing the eyes, spiracles or gills.

RESULTS

(a) Patterns of respiration

The mouth of Port Jackson sharks is situated ventrally but well forward on the rounded snout. The jaws are armed with dental plates suitable for crushing, and no valves are present on mandibular or maxillary margins to prevent backflow of water through the mouth. Spiracles are present but very reduced. There are five pairs of gill slits, notable in that their lengths decrease markedly from front to rear so that the first pair may be four to six times the length of the fifth pair.

Intake of water normally occurs through the mouth. Dye released into the water in front of the mouth soon appears spurting from all five pairs of gill slits. Under these conditions dye released into the water beside or under the flap of either first gill slit is not drawn in but flushed away by water expelled from the slit. If the oxygen tension of the water is lowered to about 30 mm. Hg (variable in different animals and depending on previous respiratory stress), the first gill flaps are seen to flare open. They still beat weakly in synchrony with the others, all of which continue the normal pattern. If dye is now released into the water near the first gill slit on either side, it is drawn into the orobranchial cavity through the slit and soon appears spurting from

the remaining gill slits on that side. Dye released in front of the mouth spurts from all gill slits except the first pair. As a response to hypoxia, therefore, the first gill slits can serve as an accessory to the mouth for intake of respiratory water.

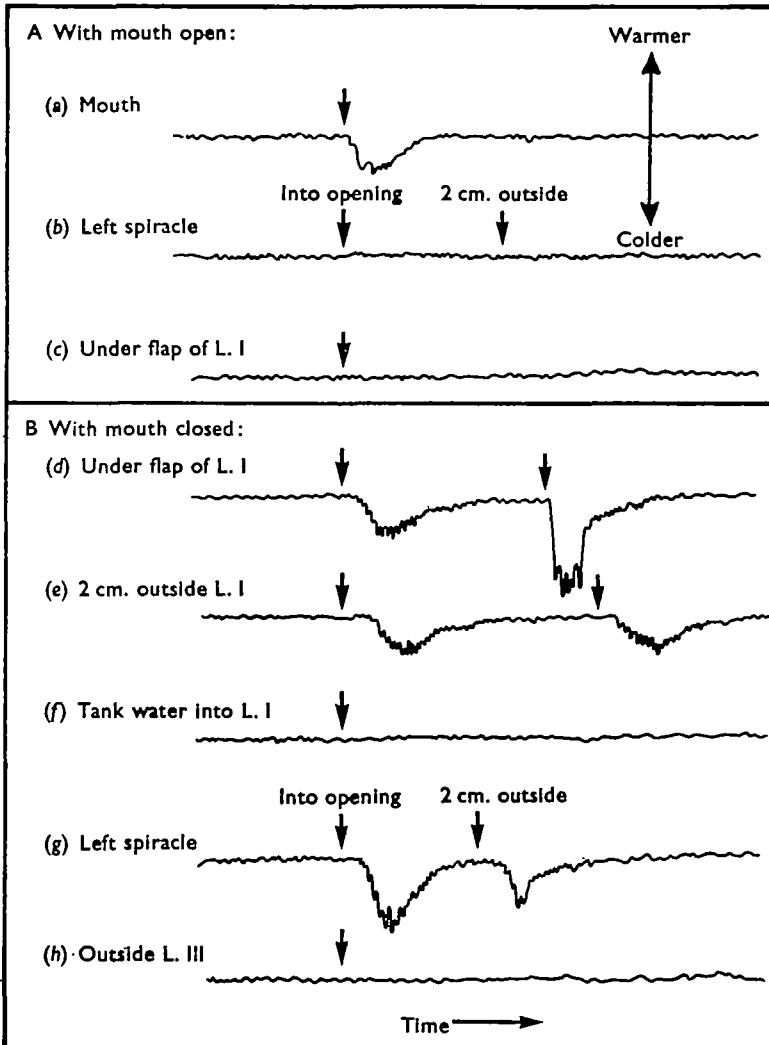


Fig. 1. Polygraph records from the thermistor placed in the third gill slit. Sites at which slugs of cold sea water were released identify each trace, and arrows mark the time of release.

Further evidence for the use of the first gill slits for water intake was obtained using the thermistor probe passed through the gill flap of the third gill slit on the left side (gill L. III). Results are shown in Fig. 1. In traces *a, b, c* the shark is respiring normally in well oxygenated water. A slug of cold water injected in front of the mouth is 'seen' by the thermistor at L. III (trace *a*). Cold water slugs released at the opening of the left spiracle (trace *b*) or under the flap of gill L. I (trace *c*) are not registered by the thermistor. Under these conditions, therefore, water flows in through the mouth

and out through the spiracles and all five pairs of gill slits. The mouth was then sealed completely with a plastic bag. Presumably the mouth is similarly blocked in coping with large pieces of food. Cold water injected either under the flap or outside L. I. (trace *d*, *e*) is drawn in and passed out over the other gills on that side, as is cold water injected into or outside the spiracle (trace *g*). Dye was used again to confirm these observations. Under these conditions water is drawn in both through the spiracles and through the first pair of gill slits. Because of the small size of the spiracles water intake through them can have little or no respiratory significance. Traces *f* and *h* are controls indicating that tank water is not 'seen' by the thermistor, and that the thermistor in L. III 'sees' only water which comes from the orobranchial cavity.

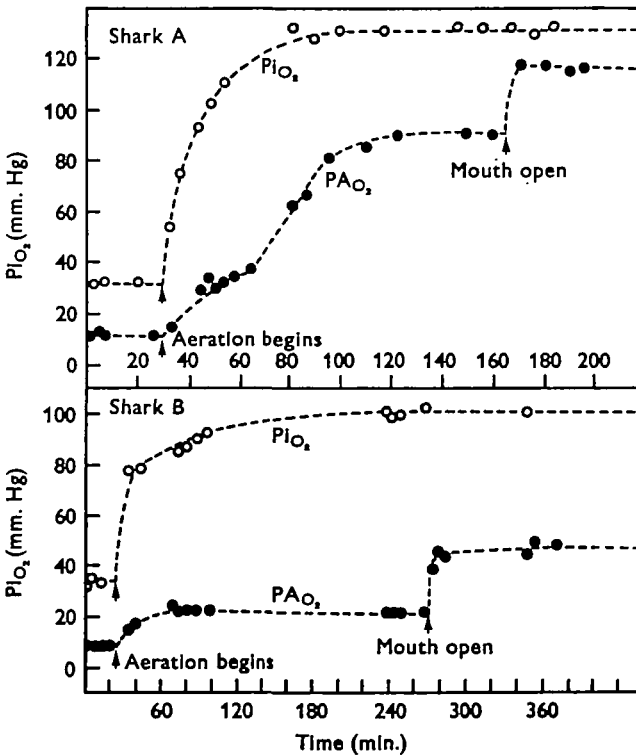


Fig. 2. Two experiments to evaluate the effectiveness of water intake through the first gill slits compared with intake through the mouth.

(b) *How effective is water intake via the first gill slits alone?*

Two experiments were performed to evaluate the respiratory effectiveness of water intake through the first gill slits alone. Sharks were held in deoxygenated water (which they survive very well) with the mouth sealed as before. The oxygen tension of ambient water (PiO_2) and of blood leaving the gills (PAO_2) were monitored as air was bubbled into the tank. The value which PAO_2 reached when PiO_2 reached its maximum is an indication of the effectiveness of ventilation via the first gill slits. After this value was established the seal was removed from the mouth and PAO_2 was monitored. In both fish it rose to a higher level as water was taken in through the mouth. Results

are shown in Fig. 2. Shark A (Fig. 2A) was a 5.63 kg. male. With the mouth sealed it elevated PA_{O_2} to about 90 mm. Hg ($Pi_{O_2} = 130$). From the oxygen equilibrium curve at 20° C. (unpublished data), this represents 94% saturation, so this shark was able to oxygenate its blood very effectively under those conditions. When the mouth seal was removed, PA_{O_2} rose to 118 mm. Hg (= 96% S). Shark B (Fig. 2B) was a 16.5 kg. female. With the mouth sealed PA_{O_2} rose to 22 mm. Hg ($Pi_{O_2} = 100$) representing an oxygen saturation of 57%. When the seal on the mouth was removed, PA_{O_2} rose to 55 mm. Hg ($Pi_{O_2} = 100$), which is equivalent to 89% S. The performance of the second shark was less spectacular than that of the first, and the difference between the two suggests these comments. Firstly, in work so far unpublished I have noticed a tremendous variability in PA_{O_2} in the same shark, and in different sharks under the same conditions. It seems that there is no 'normal' value for PA_{O_2} . Data reported by Piiper & Schumann (1967) and Baumgarten-Schumann & Piiper (1968) show a similar variation for *Scyliorhinus stellaris*. Secondly, I have noticed that in general large females have lower values for PA_{O_2} than do small males, and this will be commented on elsewhere. Thirdly, in the experiment with shark B aeration of the water did not result in as high a value for Pi_{O_2} as for shark A, so the values are not directly comparable. In each case, however, with oxygen saturation values of 94% and 57% respectively, the intake of water through the first gill slits provided an effective oxygenation of the blood.

DISCUSSION

It is interesting to note that the first pair of gill slits is innervated from the IXth cranial nerves, whereas the remaining gill slits receive branches from the branchial division of the Xth (Pope, 1938). The anatomy of the nervous system therefore would seem to facilitate independent operation of the first pair of gill slits. The actual mechanism seems to involve a relaxation of the activity of the first pair of gill pouches and increased activity of the suction pumps of remaining gill pouches.

What is the functional significance of water intake through the first gill slits? Port Jackson sharks are unusual among fish in having crushing dentition well forward in the mouth. Most fish with apparatus for crushing and grinding food have suitable teeth located well back in the pharynx (e.g. Scaridae). Such fish can 'chew' their food without interfering with the flow of respiratory water. Most fish, however, have 'tearing' teeth around the jaw margins and swallow food rapidly and in big chunks. Among the elasmobranchs, the skates and rays provide an example of food preparation in the mouth. They eat molluscs, crustaceans and echinoderms which they crush with maxillary and mandibular dental plates. The flow of respiratory water is not interrupted at such times, however, because rays use the spiracles for water intake. Interestingly, Port Jackson sharks have essentially the same diet and feeding habits as skates and rays, and have very similar dentition. Perhaps their special use of first gill slits occurs during feeding and is functionally analogous to the use of the spiracles by skates and rays. Furthermore, Port Jackson sharks grub around among the sand and mud for food (R. McLaughlin, personal communication) and at such times an alternate route for intake of water could be advantageous. A further parallel exists with lampreys which live attached to their hosts by a modified mouth. Respiration in this circumstance occurs by tidal flow of water in and out of the gill pouches via their external openings (Hughes, 1963).

SUMMARY

1. The use of the first gill slits as an alternate or accessory route for the intake of respiratory water in the Port Jackson shark is described.
2. This pattern of ventilation is an effective means of oxygenating the blood, but not as effective as normal respiration using the mouth.
3. The use of the first gill slits for water intake is thought to allow respiration to continue during either the crushing of food or obstruction of the mouth while scavenging for food on the bottom. This therefore provides an interesting parallel with the use of the spiracles in skates and rays.

I would like to express thanks to Professor G. H. Satchell for providing facilities and for helpful discussions, and 'Marineland', Manly, for their help.

REFERENCES

- BAUMGARTEN-SCHUMANN, D. & PIIPER, J. (1968). Gas exchange in the gills of resting unanaesthetized dogfish (*Scyliorhinus stellaris*). *Resp. Physiol.* **5**, 317-25.
- HUGHES, G. M. (1960). The mechanism of gill ventilation in the dogfish and skate. *J. exp. Biol.* **37**, 11-27.
- HUGHES, G. M. (1963). *Comparative Physiology of Vertebrate Respiration*. London: Heinemann.
- HUGHES, G. M. & BALLINTIJN, C. M. (1965). The muscular basis of the respiratory pumps in the dogfish (*Scyliorhinus canicula*). *J. exp. Biol.* **43**, 363-83.
- PIIPER, J. & SCHUMANN, D. (1967). The efficiency of oxygen exchange in the gills of the dogfish *Scyliorhinus stellaris*. *Resp. Physiol.* **2**, 135-48.
- POPE, E. (1938). The anatomy of *Heterodontus portusjacksoni* (Meyer, 1793). Part I. The nervous system. *Proc. Linn. Soc. N.S.W.* **63**, 412-30.