J. Exp. Biol. (1970), 52, 565–568
With 3 *text-figures*
Printed in Great Britain

WATER FLOW THROUGH THE GILLS OF PORT JACKSON SHARKS

BY GORDON C. GRIGG*
Zoology Building, The University of Sydney, Sydney, N.S.W.

(*Received* 10 *December* 1969)

INTRODUCTION

In teleost fishes highly efficient exchange of respiratory gas results from the counter-current flow of water and blood at the surface of the secondary lamellae (Hughes, 1963). In elasmobranchs the presence of large interbranchial septa would seem to prevent the operation of a similar counter-current system. Nevertheless, highly efficient oxygen uptake has been observed in a dogfish, *Scyliorhinus stellaris* (Piiper & Schumann, 1967), and in the Port Jackson shark, *Heterodontus portusjacksoni* G. C. Grigg, unpublished). In discussing their results Piiper & Schumann reject the possibility of counter-current flow because of the elasmobranch anatomy. They say '...respiratory water cannot easily continue on its way but is obstructed by the interbranchial septum. Therefore the respiratory water may have to flow along the length of the gill filaments attached to the septal wall on the greater part of their length.' To explain their results they propose that the 'multicapillary' model of gas exchange (Zeuthen, 1942) is applicable to the morphology of elasmobranch gills, and conclude that in this way their efficiency is increased.

In this paper evidence is presented which suggests that the possibility that a counter-current operates in elasmobranch gills cannot be dismissed so easily. Clearly the crux of the matter is to determine the direction taken by the respiratory water as it passes the gills of elasmobranchs, particularly its pathway in relation to the secondary lamellae which are the actual respiratory surfaces.

Between adjacent gill filaments a canal runs along the interbranchial septum towards the parabranchial cavity (Fig. 1). This canal is formed by the septal wall, the bases of adjacent gill filaments, and the row of secondary lamellae arranged along each filament. Kempton (1969) describes this canal in *Squalus acanthias*, and with regard to its functional significance writes 'With the known route for the blood, to give a complete counter-current it would be necessary for the water to move into the space between the outer ends of the lamellae, and then pass inward between adjacent lamellae to the enlarged water channel.... It is possible that this is the route taken by the water, but without further evidence this must remain dubious.'

Evidence for this is now presented, and I propose that, in the Port Jackson shark at least, water does in fact follow this route and so provides a counter-current flow of blood and water at the respiratory surface.

* Queen Elizabeth II Fellow.

METHODS AND RESULTS

Port Jackson sharks were captured in the vicinity of Sydney Harbour and maintained at Marineland, Manly, until required. Adult specimens of both sexes from 4 to 10 kg. were used. In the laboratory, specimens were placed in a large stainless-steel tank of sea water and clamped firmly by the brow ridges and the strong spines on each of the two dorsal fins. Aerated water was circulated through the tank throughout the experiment.

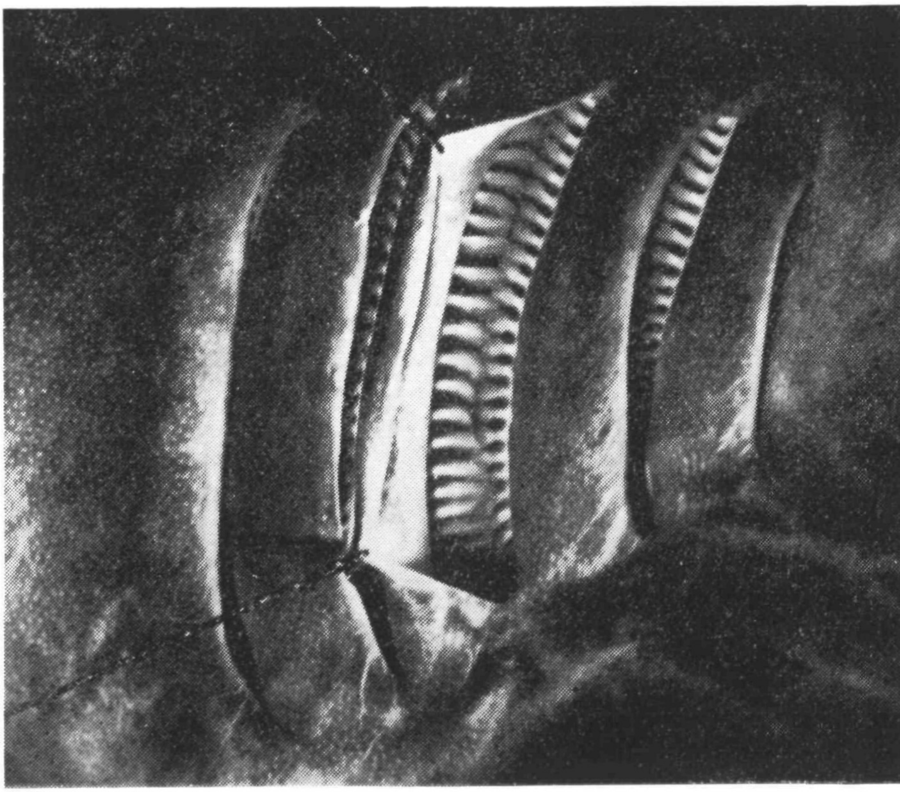

Fig. 1. View through gill slits of a Port Jackson shark showing distal ends of filaments and septal canals.

Dye observations

Nigrosin dye injected into the mouth of a Port Jackson shark, breathing normally and held on its side so as to facilitate observation, was seen to spurt from the septal canals into the parabranchial cavity. The tips of the filaments from each hemibranch of the gill pouch were held together during the expiratory phase (Fig. 1). They sometimes parted briefly in between the periodic expiration of water from the parabranchial cavities. Contraction of the gill pouches during expiration apparently pressed water (and dye) out between the secondary lamellae into the septal canals and so out to the parabranchial cavities. This was so even when the gill flap was drawn open with threads (Fig. 1), indicating an active mechanism closing the gap between hemibranchs on each side of the gill pouch.

Water pressure observations

A polyethylene cannula with heat-flared tip was passed through the interbranchial septum so that the cannula opened into the septal canal midway along its length without obstructing it. Similarly prepared cannulae were passed through the gill flap of the same pouch to record parabranchial pressure, and into the orobranchial cavity through either the spiracle or a gill slit. Cannulae were connected to Statham P23 BC transducers actuating a polygraph (Grass Instrument Co.). In addition, cannulae were con-

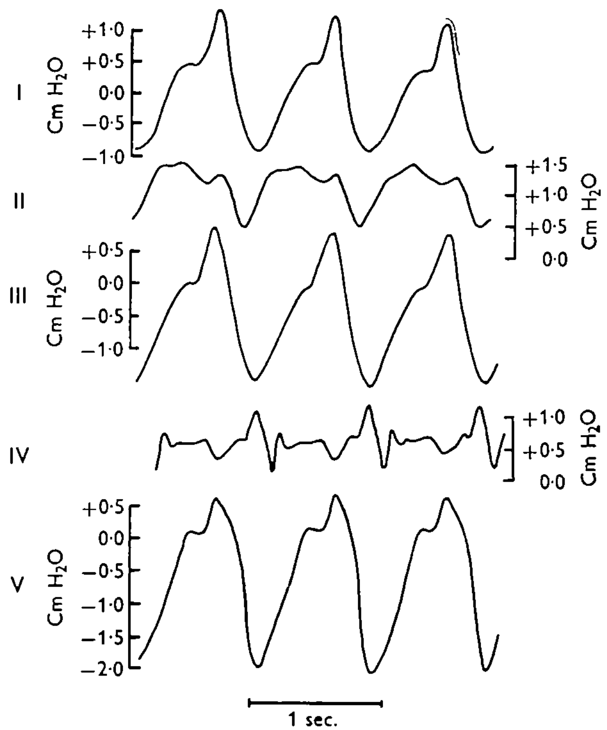

Fig. 2. Three respiratory cycles showing pressures in orobranchial cavity, I, septal canal, III, and parabranchial cavity, V. Trace II is the difference between I and III, and trace IV is the difference between III and V.

nected in pairs to a Sanborn differential transducer (268 B GH) to record pressure differences between orobranchial cavity and septal canal, and septal canal and parabranchial cavity. Accurate calibration ($\pm$ 1 mm. H_2O) of the transducers was achieved with a calibration manometer, the water surface in the experimental tank serving as zero level. Three representative cycles are shown in Fig. 2. The average pressure gradient between orobranchial cavity and septal canal (10 consecutive cycles) was 1·6 cm. H_2O, and that between septal canal and parabranchial cavity (10 consecutive cycles) was 0·57 cm. H_2O. These pressure gradients are consistently positive, indicating that no backflow occurs at any stage in the cycle, and so the observations support the hypothesis advanced in the introduction, and the importance of the septal canals as routes for water flow is indicated (Fig. 3).

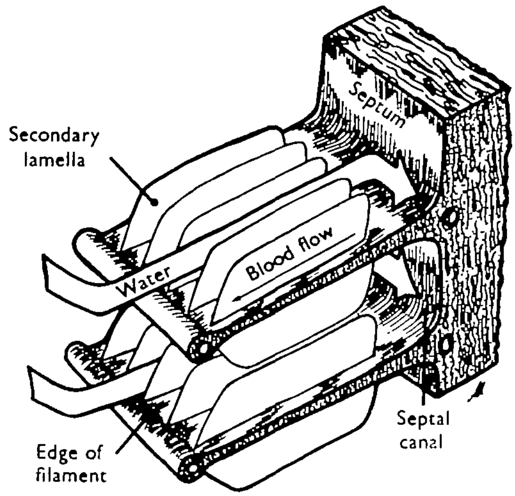

Fig. 3. Schematic diagram showing the direction of water flow between the secondary lamellae and into the septal canals.

DISCUSSION

With unidirectional flow of water into the septal canals the conditions for operation of a counter-current gas-exchange system are satisfied in the Port Jackson shark. Septal canals are present also in the large pelagic grey nurse shark, *Odontaspis arenarius*, the blue spotted ray, *Taeniura lymma*, the spiny dogfish, *Squalus acanthias*, and may be present in all elasmobranchs. Thus the possibility that gas exchange depends on a functional counter-current mechanism in elasmobranchs cannot be discounted on anatomical grounds.

SUMMARY

1. It has been said that the presence of interbranchial septa in elasmobranchs prevents counter-current flow of water and blood at the respiratory surface.

2. In contesting this opinion, attention is drawn to the importance of the septal canals as ducts carrying respiratory water in the Port Jackson shark.

3. Observations made on the passage of dye through the gills and on water pressures in the orobranchial cavity, septal canals and parabranchial cavity, indicate that water flows unidirectionally between the secondary lamellae and into the septal canals.

4. This provides a counter-current flow between water and blood at the respiratory surfaces.

I wish to thank Mrs Pattie Birch and Miss Merrilyn Packard for assistance, and Professor G. H. Satchell for generously providing laboratory facilities and for helpful discussions.

REFERENCES

HUGHES, G. M. (1963). *Comparative Physiology of Vertebrate Respiration.* London: Heinemann.

KEMPTON, R. J. (1969). Morphological features of functional significance in the gills of the spiny dogfish, *Squalus acanthias. Biol. Bull. mar. biol. Lab., Woods Hole* **136**, 226.

PIIPER, J. & SCHUMANN, D. (1967). Efficiency of O_2 exchange in the gills of the dogfish, *Scyliorhinus stellaris. Resp. Physiol.* **2**, 135.

ZEUTHEN, E. (1942). The ventilation of the respiratory tract in birds. *Kgl. Danske Videnskab. Selskab. Biol. Medd.* **17**, 1–50.