

VENTILATORY CURRENTS IN THE MANTLE OF CEPHALOPODS

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(Received 2 December 1981 - Accepted 1 March 1982)

SUMMARY

In *Octopus* and *Sepia* the inhalant water stream is sucked in to each side of the mantle cavity and passes into the centre of the corresponding gill. From here it runs counter-current to the blood vessels in the secondary gill lamellae and out into a common cavity created by expansion of the posterior part of the mantle. On exhalation the flow runs centrally, bypassing the gills and out through the funnel. This paper deals with the anatomy that ensures this pattern of flow, and with measurement of the P_{O_2} at various points in the mantle in normoxia and hypoxia. Utilization of oxygen from the respiratory stream is often better than 50% and the P_{O_2} of the exhalant water is regularly lower than the likely arterial P_{O_2} .

INTRODUCTION, AND SOME ANATOMICAL OBSERVATIONS

The gills of cephalopods are suspended in an expandable mantle cavity. At the open anterior end of the mantle cavity there is a funnel, attached dorsally and, in life, pressed ventrally against the inside lower margin of the mantle. The sides and siphon of the funnel form valves which collapse inwards when the mantle expands on inspiration. On expiration, the sides of the funnel flap outwards to jam against the sides of the mantle, so that the exhalant stream has to pass out through the siphon. The animals use the jet so created for locomotion, to blow away urine and faeces, and sometimes (as in *Octopus*) as a weapon to repel intruders. It also, of course, ensures that the exhaled water is prevented from mixing with the inhalant streams at the sides of the mantle.

Little attention has been paid to the way that the water flows within the mantle. Yonge (1947) correctly identified that the flow (in *Sepia*) must come in on the sides, through the gills and out along a central pathway between the gills. But he was plainly puzzled by the fact that this would apparently cause the respiratory stream to flow in the same direction as the blood. He refers to 'this important distinction between the Gastropods and the Cephalopods', and postulates a backflow to overcome the difficulty. As we shall see below, Yonge was depending upon an incomplete description of the gill folding and capillary arrangements. Other authors have chosen to believe that the flow in the mantle (of *Octopus*) is tidal, with the respiratory stream passing across the gills in both directions, and an attempt has even been made to

estimate the tidal deadspace that such an arrangement would imply (Johansen & Lenfant, 1966). Again, it will be shown that the flow is quite certainly not tidal.

In all living cephalopods except *Nautilus*, there is a branchial heart at the base of each gill. The beat of the branchial heart, superimposed upon a flow pulsed in by the lateral vena cava (Smith, 1982; M. J. Wells & J. Wells in prep.), drives the blood into the gill capillaries. Efferent vessels drain the gills into auricles that supply the single systematic heart. *Nautilus* lacks branchial hearts and the blood is pumped in by contraction of the branchial appendages and the lateral vena cavae alone (Bourne *et al.* 1978).

The pattern of the blood vessels in the gills has been described in the monographs of Isgrove (1908) for an octopod (*Eledone*) and Thompsett (1939) for a decapod (*Sepia*). Isgrove's is the more detailed account and Fig. 1, which outlines the situation in *Octopus vulgaris*, agrees in all respects with her description of *Eledone*. Each gill has a central cavity, with the primary lamellae alternating on the two sides of this. Each primary lamella is folded at right angles to its long axis, so that a series of secondary lamellae is formed, alternating on the two sides of the primary. It should be noted that this is *not* the same as in fish, where the secondary lamellae form a series of shelves, jutting out at right angles to the primaries. The main afferent vessel runs along the dorsal margin of the gill and down the inner surface of each primary

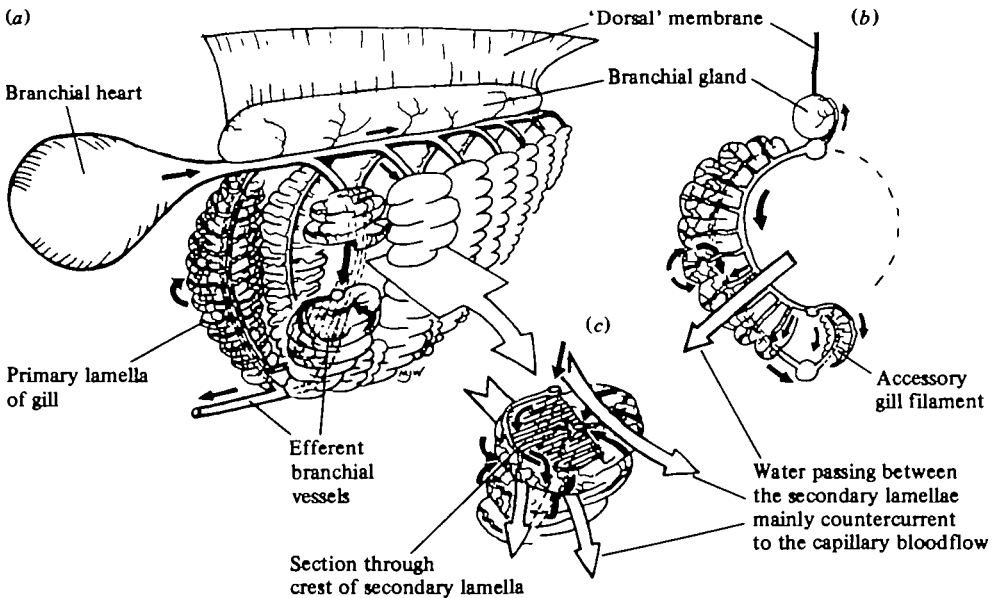


Fig. 1. Blood and water flows in a gill of *Octopus*. Black arrows show bloodflow, white show water flow. (a) LHS gill, seen from the midline of the animal; (b) transverse section of the gill, showing the pattern of blood flow in one of the primary lamellae. At this level blood appears to flow co-current with the water passing from the inside to the outside of the gill. In detail, however, the situation is reversed. As the water passes out between the secondary lamellae (insert c) it runs counter-current to the capillaries connecting the afferent blood vessels on the outside of the folds with the efferent vessels draining from the bases of the folds. (Semi-diagrammatic; the secondary lamellae are themselves considerably folded.)

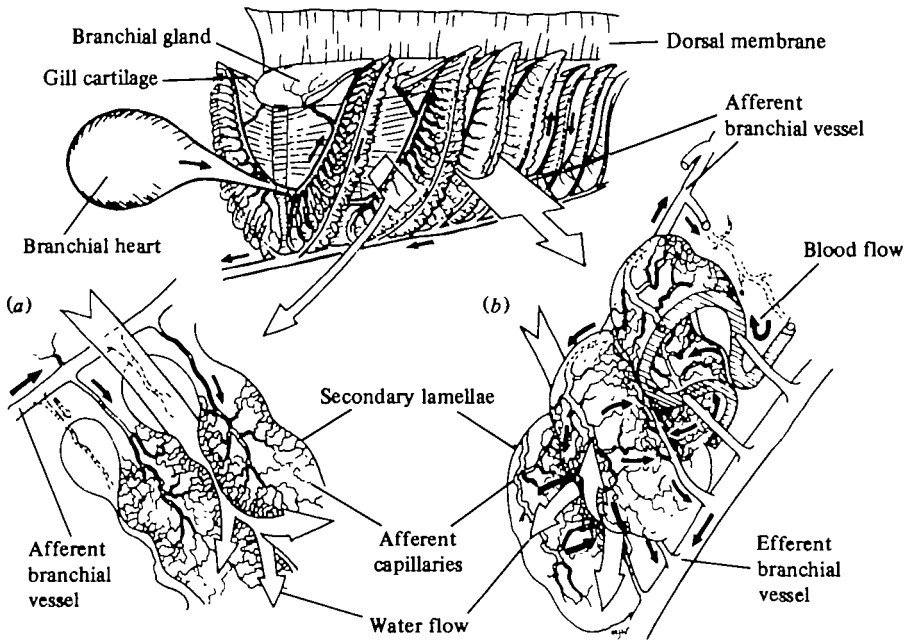


Fig. 2. Blood flow in a gill of *Sepia*. (Semi-diagrammatic; in life the primary lamellae are closely applied one to another.) Insert (a) shows the bases of two secondary lamellae with the wide opening between them; (b) shows how the secondary lamellae arise from folding of the primaries, so that the openings at their bases alternate on the two sides of the primary. Water escapes from the inside of the gill by passing along the insides of the secondary lamellae and out counter-current to the capillaries running inwards from the crest of each fold.

lamella. From here it branches outwards along the crests of the secondary lamellae, so that the afferent capillaries lie on the outer surface of each fold. The corresponding efferent vessels are more deeply buried at the bases of the secondary lamellae (Fig. 1). Thompsett's (1939) description of the gills of *Sepia* is less complete. The gill, unlike that of *Octopus*, is divided into a series of compartments by membranous partitions. One such runs vertically along the length of the gill, dividing it into two. At right angles to this a further membrane runs to each primary lamella. The lamellae alternate on the two sides. The dorsal extremity of each is supported by a cartilage; a series of these keeps the gill splayed out and open at the top (Fig. 2). In *Sepia* the afferent vessel from the branchial heart runs along the groove formed at the bottom of the gill. The corresponding efferent is external (Fig. 2). Thompsett did not describe the course of the blood vessels in the secondary lamellae, which are formed as in *Octopus* from folds in the primaries. If the primary lamellae are considered alone, one would deduce that the blood flow is co-current with the respiratory stream, as Yonge did in 1947. But the arrangement is in fact similar to that found in *Octopus*; the afferents branch and appear on the outside of the secondary lamellae; the corresponding efferents lie at the sides of each fold and will come in contact with the water first as it comes from the centre of the gill (Fig. 2b).

If the flow in and out of the mantle were tidal and the gills lay longitudinally, as they appear to do in dissections made in the traditional manner by splitting and folding back the mantle, the finer efferent blood vessels would never come in contact with the respiratory stream. Since it hardly seemed possible that the active cephalopods, of all molluscs, would have failed to evolve a blood flow countercurrent to the water flow across the gills, we have re-examined the anatomy of the mantle cavity, paying particular attention to the location of the gills *in vivo*, and measuring the oxygen tension of the respiratory stream at various places in the mantle to find out at what stage(s) the oxygen is extracted. The measurements show that the incoming stream must be directed into the cavity in the middle of the gill and out radially between the secondary lamellae counter-current to the blood flow. From the post-branchial compartment it is expelled along a central channel and out through the siphon without further contact with the gill capillaries.

METHODS

Octopus vulgaris of form 500 to 1500 g, and *Sepia officinalis* of 200–400 g were used. They were kept in aquaria with continuous circulation, tested at 20–22 °C and fed on crabs. Cannulae of Soft 'Portex' tubing, 3 or 4 mm O.D. were implanted under 2% (or for *Sepia* 1.5%) ethanol anaesthesia, as described under the several experiments discussed below. The animals were free to move about in their tanks (indeed experiments were interrupted on several occasions when the octopuses chose to climb out) and sand was provided for the cuttlefish in case they wished to bury themselves. Cannulae were led out of the aquaria through a system of taps to allow sequential sampling of water by an EIL model 7130 oxygen probe. This was equipped with a magnetic stirrer so that the flow rate and the volume of water extracted ($\approx 50 \text{ ml min}^{-1}$) could be kept low enough not to interfere with the bulk flow through the mantle cavity. In some experiments the EIL 7130 was also used to sample the tank water; in others this was sampled using an EIL 15A oxygen probe, the two electrodes being calibrated against one another (and against a saturated standard) before each experiment.

In the present series of experiments we did not attempt to monitor the P_{O_2} in the blood entering or leaving the gills. We have done this elsewhere for *Octopus vulgaris* (Houlihan *et al.* 1982) under conditions very similar to those of the present experiments. Measurement of the blood P_{O_2} here would have required further cannulae in the gills and/or in the dorsal aorta, and we wished to study oxygen extraction and respiratory flow under conditions where the mantle and gills could move as freely as possible.

The anatomy of the gills and mantle was investigated in freshly dead specimens, killed by ethanol anaesthesia and dissected under water, with the animal in the orientation that it would have had in life and with the mantle supported so far as possible in the position that it would have held when expanded. Details of the blood vessels in the gills were examined after injection with microfil (a latex emulsion) or indian ink.

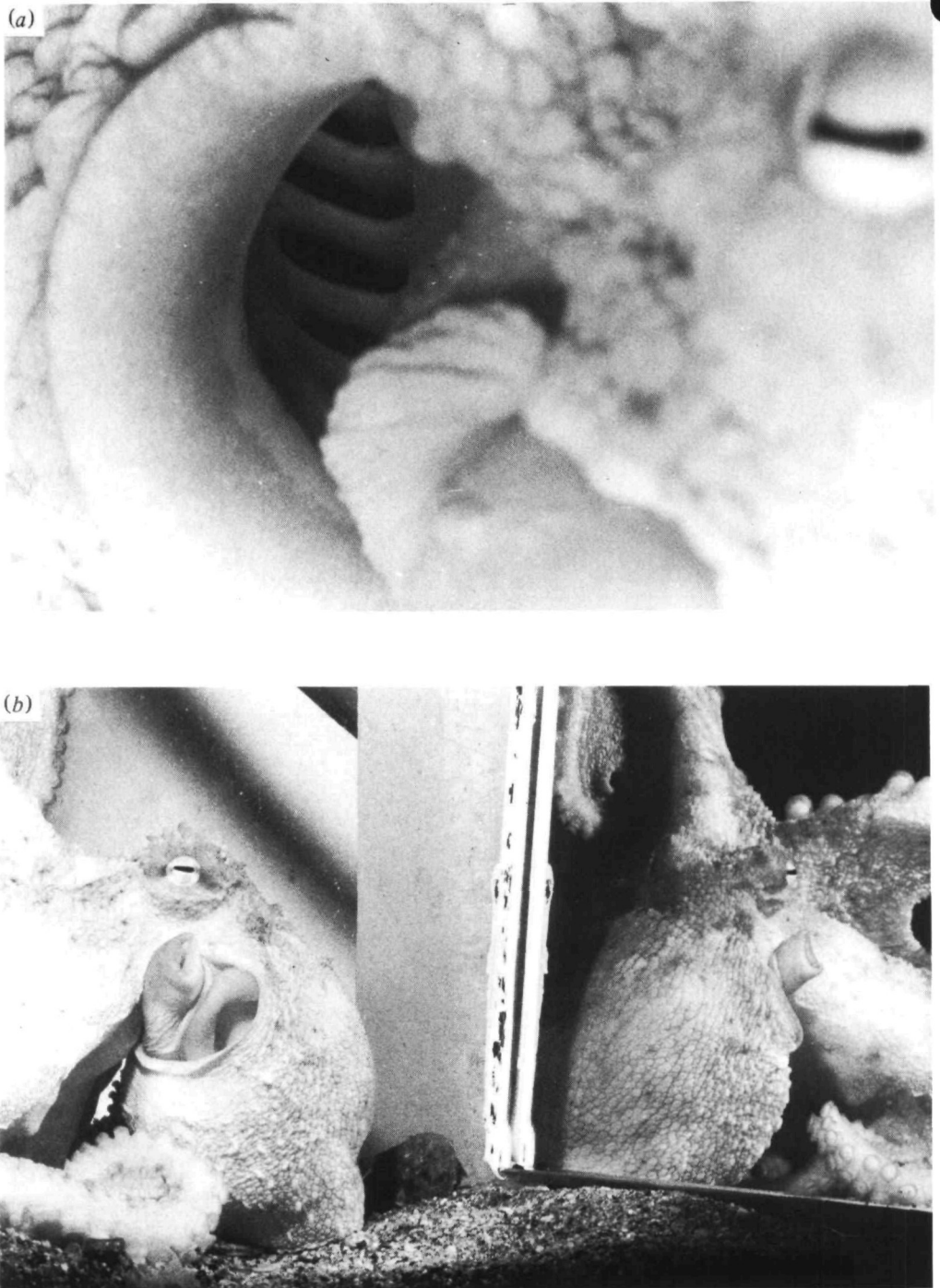


Fig. 3. (a) *Octopus vulgaris*. Looking down into the right-hand side of the expanding mantle, one can see past the bare parts of the primary lamellae into the hollow centre of the gill. (b) The mantle during inflation. The side of the funnel has collapsed inwards and the siphon is closing. At this stage the lateral pre-branchial-dorsal mantle space is inflated but the post-branchial chamber is not yet full. (Photographs by M. Lecomte and Roger Hanlon, Laboratoire Arago Banyuls.)

RESULTS

*Anatomy**Octopus vulgaris*

The octopod gill is asymmetric, with the primary gill lamellae on one side (described as 'central' by Isgrove, 1908) bare of leaflets for the first third of their length. In life, one can see the gills when the animal expands the mantle to draw in water. Each gill has the appearance shown in Fig. 3*a* (plate); the bare parts of the 'central' gill lamellae face dorsally, lying across the incoming water stream. The much-folded, respiratory exchange part of the gill can often be glimpsed through the bars. Dissection of a freshly killed specimen from above shows how the gill is held to give this appearance (Fig. 4*a*), while further extension of the opening downwards and laterally reveals the respiratory surfaces (Fig. 4*b*). In this lateral view, and in T.S. (Fig. 4*c*), the gill can be seen hanging down into the posterior part of the mantle cavity. The gill is bounded on one side by the membrane (usually described as 'dorsal') which attaches it to the side wall of the mantle, and on the other by the funnel retractor muscle. On inspiration, the siphon and the lateral walls of the funnel collapse and the central margin of the mantle is held tight against the funnel and the digestive gland lying above it. Water can only enter the posterior part of the mantle cavity by passing from above through the open section of the gill lamellae into the middle of each gill and then out across the respiratory surfaces. This route (shown by black arrows in Fig. 4) carries the incoming water counter-current to the capillary flow which runs from the afferents on the outside of the secondary gill lamellae to the efferents on the inside (Fig. 1).

On exhalation, the flaps at the side of the funnel expand to block any view of the gills. But any tendency for the water to flow back into the lateral chambers above and in front of the gills will be prevented by collapse of the gill folds which radiate from the primary lamellae, away from the hollow centre of each gill. The exhalant water is thus forced to bypass the gills and escape ventrally, along the midline of the animal and out through the funnel.

Sepia officinalis

Figure 5*a* shows the appearance of one gill in a dissection made from above and to the side. As with *Octopus*, the dorsal-facing surface of the gill is bare of respiratory surfaces; one can look down into the gill through a series of bars. The resemblance to *Octopus* is superficial, however, because the bars are not formed from parts of the gill lamellae devoid of respiratory folds. The decapod gill is not asymmetric, like that of octopods, and the bars are cartilagenous, holding the primary lamellae apart at the top on either side of a membrane which suspends the central axis of the gill from the roof of the mantle (Fig. 5*b*). One side of each gill is held against the funnel retractor muscle, and the other against the lateral wall of the mantle. As in *Octopus*, the respiratory stream can only reach the posterior part of the mantle by passing down between the bars, into the centre of the gill, and out radially across the gill lamellae (black arrows in Fig. 5 show the direction of flow). The secondary lamellae are open

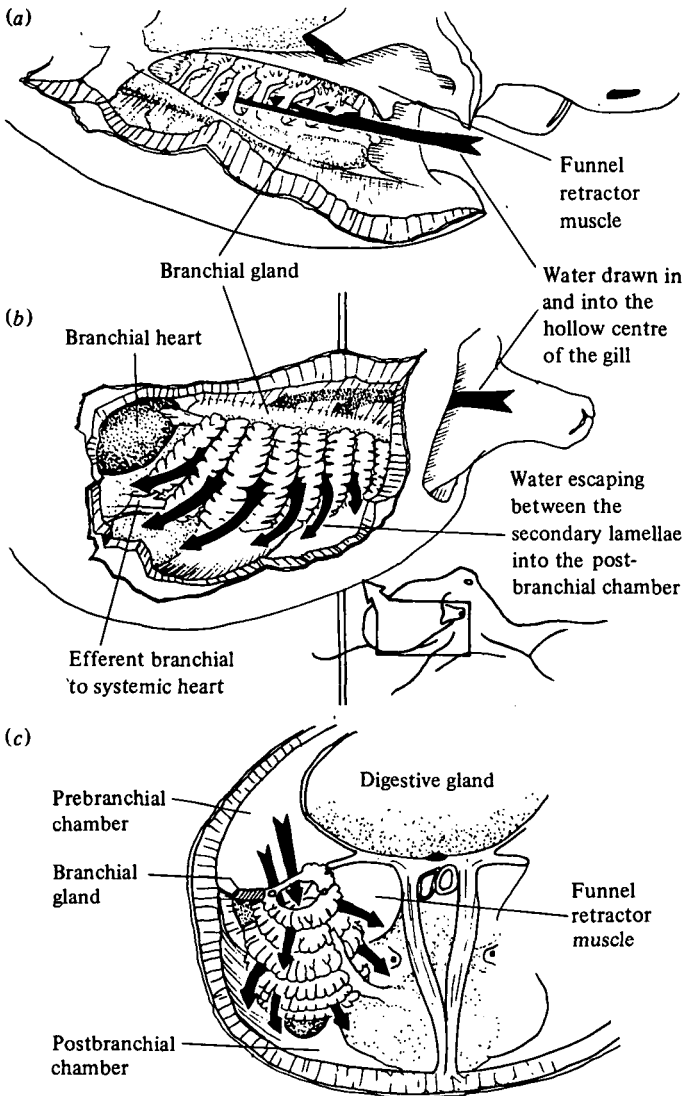


Fig. 4. The position of the gill of *Octopus* in a freshly killed specimen. (a) As seen from above and to the side (compare Fig. 3a). (b) A lateral view. (c) In section, looking towards the hind end of the mantle in a specimen cut through at the level indicated in drawing (b). Black arrows show the directions of water flow through the gill.

at the base, on the inside of the gill, so that the water will pass up between them and out, counter-current to the blood flow (Fig. 2b, c).

Once again, a return flow is prevented by the radial nature of the gill folds and the lack of large apertures to channel the water between these. On contraction of the mantle the exhalant stream is forced forward and centrally, out through the funnel.

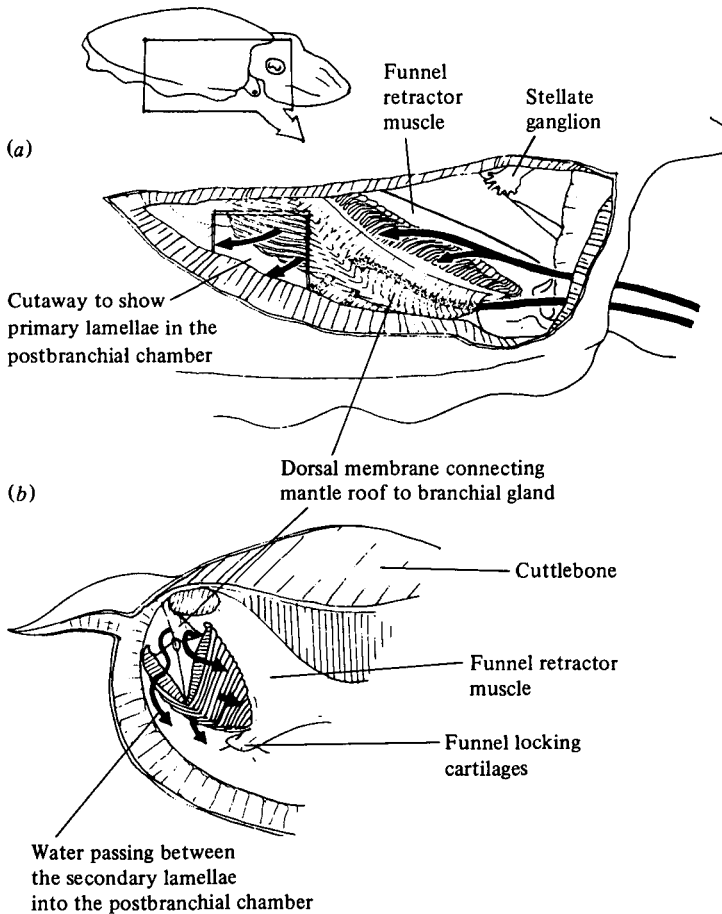


Fig. 5. The position of the gill of *Sepia* in a freshly killed specimen. (a) From above and to one side. (b) In an animal cut transversely, viewed from behind looking forwards. Black arrows show the direction of water flow through the gill.

Experimental results: Octopus

Series 1. P_{O₂} of the exhalant stream

The siphon of the funnel collapses on inspiration. A cannula placed here should thus be blocked when the animal breathes in, and so collect only exhalant water. Animals were fitted with a cannula inserted through the tip of the abdomen, just below the level where the viscera join the wall of the mantle. The cannula ran along just below the viscera, between the two gills. The open tip was sewn to the muscular roof of the funnel, projecting into the tube of the siphon. Fixed in this way, a cannula did not appear to interfere with the normal movements of the mantle or of the funnel; the siphon was free to move from side to side and could be used in the normal way to direct a jet at a hand placed near the octopus in its tank. External to the animal the cannula was carried out of the tank and down past the oxygen electrode. Flow was

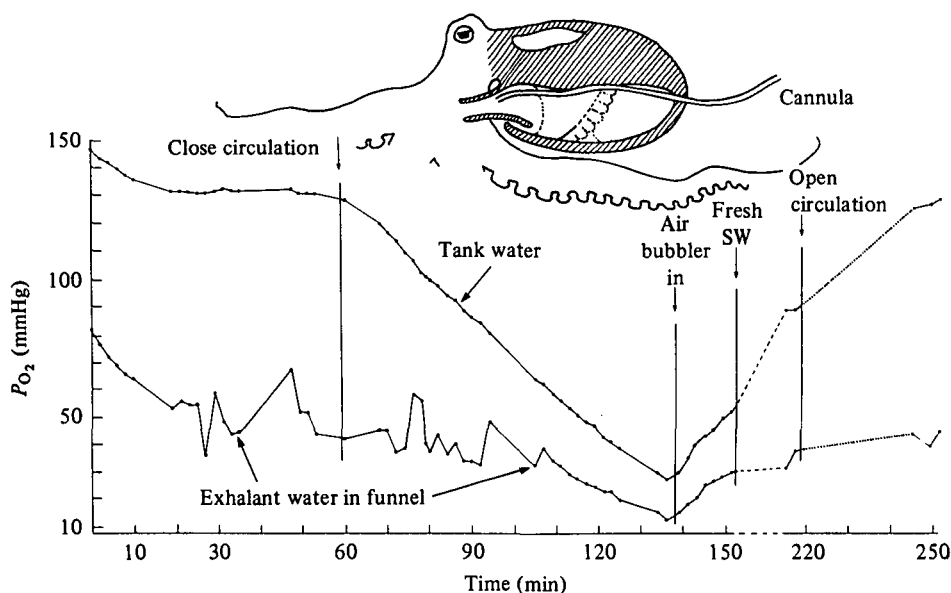


Fig. 6. Measurements of the inhalant (tank-water) P_{O_2} and the exhalant (siphonal) P_{O_2} in animal 09, first in open circulation, then subjected to acute hypoxia by closing the circulation, and finally in recovery after restoration of the circulation.

regulated by adjusting the level of the electrode relative to the surface of the water in the octopus tank.

Table 1 lists representative values for the P_{O_2} of the exhalant stream obtained in this manner from seven animals. Fig. 6 shows details of one of these experiments. The P_{O_2} of the exhalant water varied from minute to minute, depending on what the animal happened to be doing. If it was moving about or blowing away faeces, oxygen extraction fell. The lowest exhalant P_{O_2} values were obtained when animals were sitting quietly and apparently at rest. It is these resting values that are listed in Tables 1-3.

Houlihan *et al.* (1982) measured the P_{O_2} and oxygen content of the arterial blood in nine *Octopus vulgaris* under conditions very similar to those used here to examine the respiratory water stream. At an external, tank water, P_{O_2} of 145 mmHg, the P_{O_2} of the blood in the dorsal aorta was found always to lie close to 80 ± 2 (mean \pm 1 S.E.), declining (in six animals subjected to acute hypoxia) linearly to 25 ± 3 at an external P_{O_2} of 50. From their data one can predict the arterial P_{O_2} for any value of external (inhalant) P_{O_2} . When this was done for the tank-water values found in the present series of respiratory experiments, the predicted arterial P_{O_2} was often equal to or greater than the measured exhalant P_{O_2} (Table 1).

The fact that such values can occur at all, and particularly in a situation where any activity on the animal's part (movement, defaecation, blowing with the funnel and so on) would have tended to increase the exhalant P_{O_2} s, can only have one explanation. Gas exchange across the gill must involve a counter-current system.

Table 1. *Octopus vulgaris*. Experiments in series I

(Extraction of oxygen, measured by comparing tank P_{O_2} ($= P_{i, O_2}$ - inhalant water)* with P_{O_2} of the exhalant stream (P_{e, O_2}) sampled from inside the siphon. Most of the animals were first tested with the water flowing continuously, and then subjected to acute hypoxia by shutting off the flow and recirculating the water.)

Animal	P_{i, O_2}	P_{e, O_2}	Extraction (%)	Animal	P_{i, O_2}	P_{e, O_2}	Extraction (%)
05	136	102	25	09†	131	53‡	60
	134	98	27		131	36‡	76
	114	87	24		109	39‡	64
	79	47	41		84	33‡	61
06	134	98	27		47	25‡	47
	131	81	38		28	11‡	61
	118	76	36		026	145	95
	79	48	39	112		70	37
	47	25‡	47	78		43‡	45
	23	8‡	65	47		26‡	45
07	145	95	34	39		22‡	44
	141	85	40	027	145	48‡	67
08	144	75‡	48		109	45‡	59
	143	71‡	50		78	39‡	50
	115	61‡	47		48	23‡	52
	70	42‡	40	39	22‡	44	
	40	25	38				
	28	9‡	68				

* Table 2 and Fig. 7 show that P_{O_2} s measured in the aquaria alongside the animal were the same as those of the inhalant water measured inside the mantle in the pre-branchial cavity.

† Further details of the performance of 09 are given in Fig. 6.

‡ Values which are equal to or lower than the arterial P_{O_2} predictable at the P_{i, O_2} shown.

Series 2. Experiments in which the P_{O_2} of the respiratory stream was measured at more than one point in the animal

For these experiments, two cannulae were inserted into each animal, always from behind, as described above. In any one experiment, samples were drawn from two out of the four following places:

(a) The post-branchial space, below and behind the gills.

(b) The dorsal mantle space above the digestive gland; this is continuous with the lateral pre-branchial spaces in *Octopus*. The equivalent space does not exist in decapods.

(c) From a point lateral to the vertical muscular septum that divides the front part of the mantle into two in octopods.

(d) From the inside of the siphon, as before.

Four animals were used in these experiments. Representative results are given in Table 2, with further details of two of the experiments in Figs. 7 and 8. Samples were normally taken sequentially (see 'methods') and generally 2.5 min apart (this gave time for each sample flow completely to replace the previous sample flow from the piping and electrode compartment, and for the EIL 7130 electrode to equilibrate at

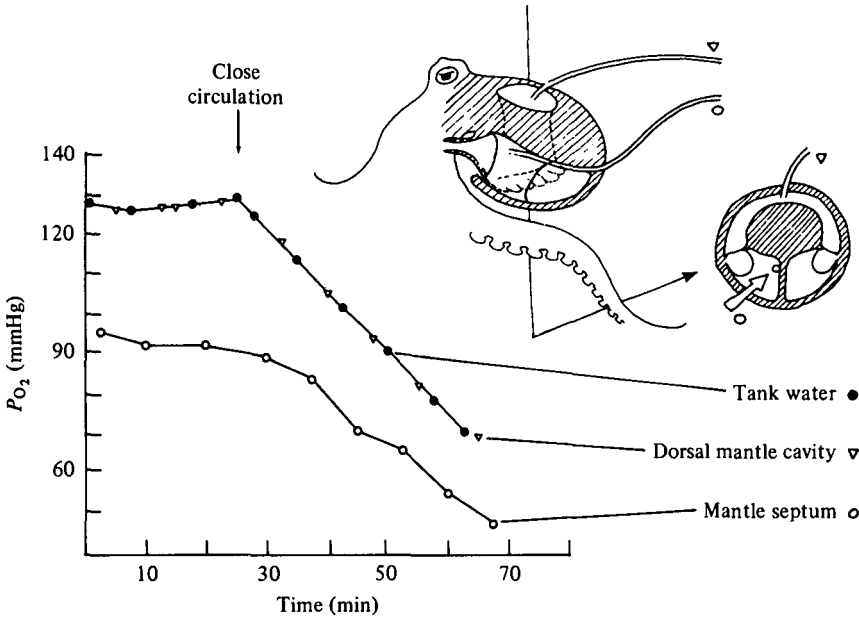


Fig. 7. Animal o32. Oxygen tensions in tank water, in the dorsal mantle space, and alongside the vertical mantle septum.

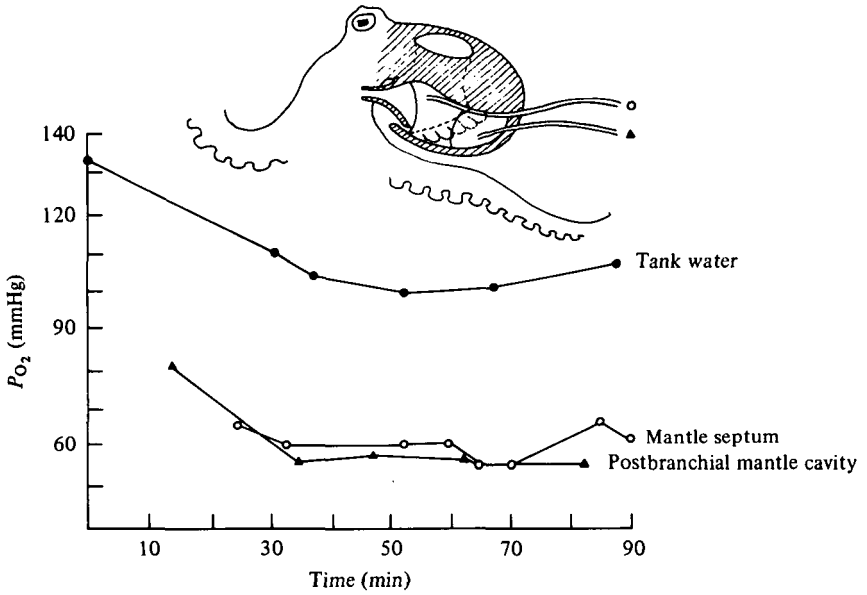


Fig. 8. Animal o30. Oxygen tensions in tank water, post-branchial space, and beside the vertical mantle septum.

Table 2. *Octopus vulgaris*. Experiments in series 2 in which the P_{O_2} was measured at more than one point in the ventilation stream*

Animal	Tank (P_{i, O_2})	Dorsal mantle	Funnel	Septum	Post-branchial
029	131	134			
	123	121			
	118	120			
	126				79
	109				67
	76				44
	65				39
	109			65	
	73			50	
	54			39	
030	121			75	75
	124			65	65
	143			78	
	118			68	
	90			53	
	104			61	57
	101			56	56
031	127			87	90
	135			87	93
	129			82	82
032	134	126		95	
	124	118		89	
	109	106		79	
	75			47	

Acute hypoxia
 ↓
 Following a further operation (3rd cannula installed)

Acute hypoxia
 ↓
 Next day

Acute hypoxia
 ↓

Table 2a. *Octopus vulgaris*. Glove finger experiment

028	124				67
	124				57
	109				62
	78				44

Acute hypoxia
 ↓

* The positions of the cannulae used to make these measurements are shown in diagrams attached to Figs. 6, 7 and 8.

each new value). Samples obtained in quick succession in this manner are listed along single lines in Tables 2 and 2a.

It is quite clear from these results that samples taken from various places in the mantle fall into two distinct populations. Samples from the dorsal mantle space are plainly pre-branchial and have the same P_{O_2} s as the external tank water. All the other points yield values similar to those obtained in the series 1 (exhalant water) experiments. There is no evidence for a further extraction of oxygen as the water passes from the post-branchial space, past the central septum and into the funnel. The values obtained at the levels of the septum and funnel are as low as those found in the post-branchial space, which further suggests that there is no mixing with unextracted water on the way out.

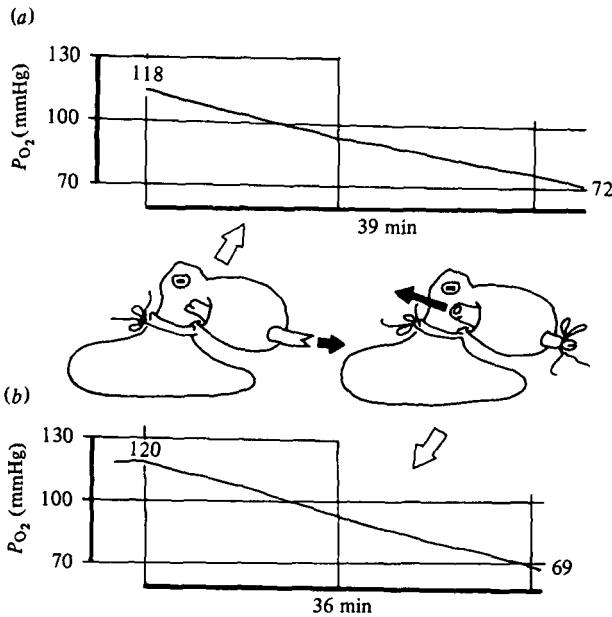


Fig. 9. Oxygen uptake in a closed system by *Octopus o28*, which had the finger of a rubber glove sewn into the hind end of the mantle (see text). In (a) the glove finger, slit at the end to form a duckbill valve, was open. In (b) it was closed. Oxygen uptake and the ability to extract oxygen under increasingly hypoxic conditions were not affected by the change in the path of the outgoing stream.

Series 3. Experiments with an alternative exhalant flow

If oxygen extraction is complete by the time the respiratory stream reaches the post-branchial space, oxygen uptake should be unimpaired if the water then fails to flow forward and out by the normal route through the funnel. Following this reasoning, an artificial funnel made from one finger of a thin surgical rubber glove was sewn into a 2 cm hole cut through the tip of the mantle, into the post-branchial space of one octopus. Slit at the tip, the glove finger formed a duck-billed valve with an action very similar to that of the normal funnel. Because the water could escape more readily through the glove finger when the mantle contracted, the real funnel remained collapsed on exhalation. The glove finger, moreover, could be tied off, so that it was possible to compare oxygen uptake when using the artificial funnel and a backwards exhalant stream, with oxygen uptake using the normal funnel and a forward flow. The results of this experiment are shown in Fig. 9; total oxygen uptake and the capacity to remove oxygen as the external P_{O_2} fell were not altered by the inability to exhale normally. Once again it seems that all the oxygen that is going to be removed has already been extracted by the time that it has passed once backwards through the gills. For this experiment the arms of the octopus were enclosed in a loose muslin bag since it was feared that it might otherwise pull out the stitches and remove the glove finger.

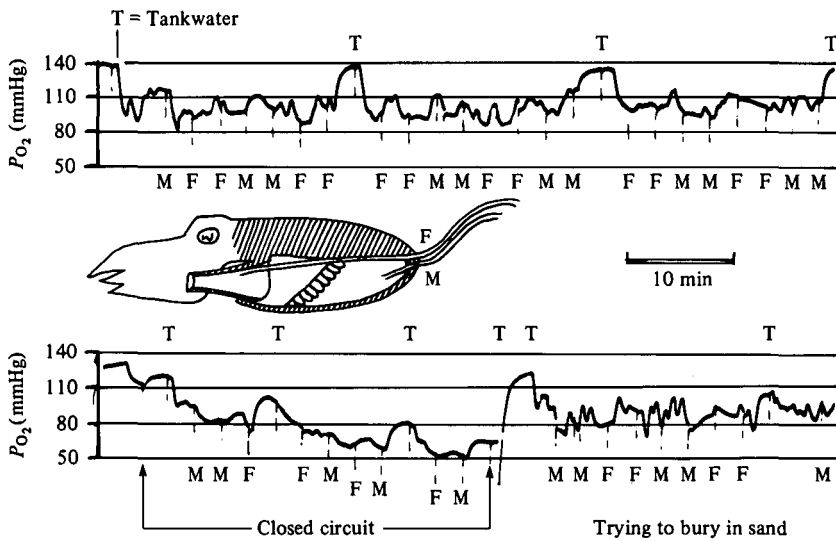


Fig. 10. Oxygen uptake by *Sepia*, animal S3. The animal had cannulae in the post-branchial space (records labelled M), and in the siphon (F). A further cannula sampled tank water (T). Tests were made successively at the three stations in the sequence indicated.

Experiments with Sepia officinalis

Experiments similar to those made with *Octopus* were carried out with three *Sepia*. Once again cannulae were led in at the posterior tip of the mantle cavity. Each animal had two, one terminating in the post-branchial space, the other further forward, in the roof of the funnel. Decapods have no dorsal mantle space and no vertical septum at the front end of the mantle.

As with *Octopus*, it was found that oxygen extraction varied considerably, depending on what the animal happened to be doing (Fig. 10). Sand was provided so that the animals could bury themselves, but none did so, although at least one tried; perhaps the cannulae protruding from the hind end of the animal made it difficult to dig in. This means that for *Sepia* we have no real 'resting' values. The animals were always hovering above the sand or swimming about, both activities that one might expect to reduce the efficiency of oxygen uptake, since the respiratory stream is also being used for locomotion.

Oxygen extraction was nevertheless regularly in excess of 40% (Table 3), with the P_{O_2} of the exhalant water ($P_{e.O_2}$) in the region of 90 mmHg. Figures for the arterial P_{O_2} ($P_{a.O_2}$) of *Sepia* are not yet available, but are likely to be higher than those for *Octopus*, since *Sepia* blood *in vitro* has a considerably lower oxygen affinity (Wolvekamp, 1938). At 90 mmHg, the $P_{e.O_2}$ is likely to be substantially less than the $P_{a.O_2}$ in normoxia.

Table 3 also shows that the P_{O_2} in the post-branchial chamber is regularly as low or lower than the $P_{e.O_2}$, measured in the exhalant siphon. As with *Octopus*, this can only mean that oxygen extraction is complete after a single inwards passage through

Table 3. *Sepia officinalis*. The P_{O_2} s of the inhalant (P_{i,O_2}), post-branchial and exhalant (P_{e,O_2}) respiratory streams*

Animal	P_{i,O_2}	Post-branchial	P_{e,O_2}	Extraction (%)		
				Post-branchial	P_{e,O_2}	
S1	138	40	44	71	68	
	134	51	67	62	50	↓ Acute hypoxia
	124	71	73	43	41	
	103	57	70	45	32	
	79	53	61	33	23	↓ Next day
	145	68	79	53	46	
S2	137	84	98	39	28	
	131	54	65	59	50	↓ Acute hypoxia
	131	59	84	55	36	
	101	68	65	33	36	
	68	56	61	18	10	↓ Next day
	140	99	102	29	27	
S3	138	78	93	43	33	
	131	89	92	32	30	↓ Acute hypoxia
	123	70	78	43	37	
	78	44	44	44	44	↓ Next day
	145	121	113	17	22	
	145	81	98	44	32	

* The positions of the cannulae are shown in a diagram forming part of Fig. 10.

the gills. The fact that the P_{O_2} in the funnel was often in excess of that found behind the gills is a little puzzling. It could be interpreted as indicating a tidal deadspace in the respiratory stream but is more probably a reflexion of imperfect technique. Cuttlefish muscle is softer and the whole animal is more fragile than *Octopus*, and although the cannulae were the same size, the animals were much smaller. The fact that the P_{e,O_2} can equal the post-branchial P_{O_2} for considerable periods (during the whole of the sequence recorded in Fig. 10 for example) suggests that the other results may arise from leakage where the cannulae have in some manner prevented the proper apposition of the soft tissues valving the system.

DISCUSSION

Oxygen extraction by *Octopus vulgaris* has been studied by Winterstein (1925), who tied a rubber glove finger over the funnel, and by Hazlehoff (1938), who collected samples from the exhalant stream in the region of the funnel, using a pipette. Oxygen uptake was found to vary from about 50 to over 80% (Hazlehoff's mean figure was 63%). In a more recent study Johansen & Lenfant (1966) working with *O. dofleini*, found much less efficient use of the respiratory stream, quoting an average figure of only 27%. They suggest that the difference from *O. vulgaris* might arise from the large size of *dofleini* (several kilograms) or from the low temperature (11 °C instead of 22 °C) at which this species lives. But it seems far more probable that the apparent inefficiency of *dofleini* arose from the presence of cannulae which were led in through the mantle opening to take blood samples, and from the condition of the siphon.

which was kept from closing by a plastic ring sewn into the funnel (Johansen, 1965). Any cannula coming in through the mantle aperture would inevitably interfere with the proper seating of the funnel valves. In our experience (with *O. vulgaris*) the animals are peculiarly sensitive in the region of the mantle edge, and the presence of cannulae here (let alone of a plastic ring sewn into the funnel) would have irritated the animals. Even a touch on the edge of the mantle generally causes contraction by the gills and hyperventilation. Johansen & Lenfant found P_{e, O_2} s in excess of P_{a, O_2} s and were obliged to postulate a tidal deadspace (in the region of the vertical septum) and/or a venous shunt in the gill to account for the discrepancy. Neither assumption is necessary to account for the results with *O. vulgaris* where the predicted P_{a, O_2} is often in excess of the measured P_{e, O_2} .

The situation in *Octopus vulgaris* may be summarized as follows. Water is drawn in by expansion of the mantle; what one sees on careful observation is that the sides and dorsal spaces expand first, closely followed by the post-branchial mantle space (Fig. 3). This draws the inhalant stream into the gills and out counter-current to the blood flow. Incoming water cannot bypass the gills, because these are attached to the mantle walls laterally, and lie tight against the funnel retractor muscles centrally. The siphon collapses, and the ventral part of the funnel is drawn upwards to press against the viscera along the midline. The mantle then contracts, in towards the midline and then at the rear. Unable to escape past the gill filaments, which act as a series of valves blocking the return flow, the exhalant stream is pressed forward along the midline. The vertical septal muscle presumably relaxes, so that there is a free flow out through the siphon. The lateral flaps of the funnel jam against the mantle edge. In principle, this could trap water in a pre-branchial space on either side, but in practice the close matching of post-branchial, siphonal and septal P_{O_2} s suggests that the volume left here at the end of inspiration is negligibly small.

The experiments with *Sepia* show that the system in this decapod is functionally very similar to that reported for *Octopus*. The gills differ in being bilaterally symmetrical, with the suspensory membrane running upwards to the roof of the mantle from a central axis. One side of the gill is thus bounded by the membrane and the funnel retractor muscle, the other by the membrane and the outer wall of the mantle. Incoming water passes between cartilaginous bars into the centre of the gill and then out, counter-current to the bloodflow in the secondary folds of the gill lamellae. On exhalation, the oxygen-depleted water in the post-branchial space is channelled forward and out through the siphon, just as it is in *Octopus*. Oxygen extraction from oxygen-rich water is comparable in the two species examined, and when the animals are inactive the P_{e, O_2} regularly exceeds the probable P_{a, O_2} . The few results listed in Table 3 suggests that *Sepia* may be less well adapted than *Octopus* to extract oxygen under hypoxic conditions, as one might expect from the ecology and habits of the two species.

The authors would like to thank the Director and Staff of the Laboratoire Arago, Banyuls, for their hospitality and the facilities that they provided. This work was done during a period when M.J.W. was supported by SRC grant GR/B 44132.

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