

THE VENTILATION CYCLE IN *OCTOPUS*

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SUMMARY

Pressure measurements made at various points inside the mantle show that the ventilatory stream of the resting animal is driven by very small (often less than 0.5 cmH₂O) pressure differences. Inspiration occupies less than one-third of the total cycle time, while flow across the gills is evidently continuous, since there is always a pressure differential between the prebranchial and postbranchial parts of the mantle cavity. The fact that branchial heartbeats do not correlate with ventilatory movements is further evidence that water flow through to the gills is both steady and continuous.

INTRODUCTION

A number of anatomical accounts have shown how the mantle sac of cephalopods can expand by contraction of radial muscles associated with a connective tissue lattice (Ward & Wainwright, 1972; Packard & Trueman, 1974; Gosline, Steeves, Harman & Demont, 1983). Zoologists have tended to assume that the incoming ventilatory stream is sucked in by expansion of the mantle, and blown out, through the funnel, by its contraction; in other words that the flow is tidal.

A recent examination of the mantle water oxygen content during normal ventilation, has shown that the flow passes only once across the gills, counter-current to the gill capillaries (Wells & Wells, 1982). It flows in at the sides of the mantle, through the gills and into a central post-branchial space before being expelled along the midline and out through the funnel.

The demonstration of a counter-current flow through the gills does not, however, settle the question of how the flow is propelled, or indicate for how much of the cycle water is actually passing through the gills. The account that follows is an attempt to answer these questions.

MATERIALS AND METHODS

Octopus vulgaris (Cuvier), of 400–600 g, and *Eledone moschata* (Lam.), of 200–300 g, were studied at the Laboratoire Arago, Banyuls-sur-Mer. Cannulae of soft

'Portex' tubing (3 or 4 mm outer diameter) were implanted in either the dorsal mantle space, one of the lateral prebranchial spaces, the postbranchial space or at the base of the funnel, as described by Wells & Wells (1982). To minimize any complication from a Bernoulli effect, the cannula in the funnel terminated as an L, with an opening on the upper side of the short arm, and was sewn to the mantle septum so that this faced the oncoming stream. The animals were free to move around in their tanks. Pressure records were made with Statham (P23V) and S.E. laboratories SE4-82 pressure transducers connected to a Washington 400 MD26 pen recorder.

The transducers were set to read zero with their cannulae in the tanks. Since the cannulae were open-ended, their position in the water column as the animal moved about did not affect zero. Calibration for pressures above and below zero was made, before and after each recorded run, with a cannula outside the tank, raised and lowered against a scale with zero at the water level.

RESULTS

Absolute pressures during the ventilation cycle

These measurements were made using *Octopus vulgaris*. Fig. 1A shows the pressure changes on either side of the gills during normal quiet ventilation. In these instances the cannulae were sited in the prebranchial space and in the rear of the postbranchial cavity. The upper trace, using the Statham transducer, is noisier than the lower (SE4), but the magnitude of the pulses is very similar, 1–2 cmH₂O. The following points are worth noting. (a) The maximum positive pressure is greater in the prebranchial cavity. (b) The maximum negative pressure is greater in the postbranchial chamber (indeed, the negative pressure is scarcely detectable prebranchially).

Visual observation of the ventilation cycle shows that the sharply rising phase of the pressure cycle corresponds with the closing of the mantle aperture at the end of inspiration. The abrupt fall precedes the opening of the aperture at the end of expiration as the sides of the mantle expand, just before the funnel opening collapses.

Fig. 1B compares the pressure pulses in the prebranchial space (this time the record is made with the SE4-82 transducer) with the pressure changes just inside the funnel at the front of the vertical septum (Statham). The septum divides the forward half of the mantle cavity below the digestive gland. The two pulses rise and fall as before, but the changes in the funnel are smaller in magnitude and the rising phase lags a little behind the rise in the prebranchial space. In this record the opening and closing of the

Fig. 1. (A) Pressures in the lateral prebranchial and central postbranchial parts of the mantle cavity during quiet ventilation (B) Pressures in a lateral prebranchial space and at the entrance to the funnel. The large solid and open arrows show, respectively, the points at which the funnel tip opening collapses inwards on inspiration and the mantle flaps occlude the opening of the mantle sac on exhalation. The small arrows mark the opening of the end of the funnel on exhalation. (C) Pressures in the dorsal mantle space, which joins the two lateral prebranchial chambers, and in the funnel, at the level of the septum. (D) Diagrams of the octopuses showing the positions of the cannulae used to make the recordings.

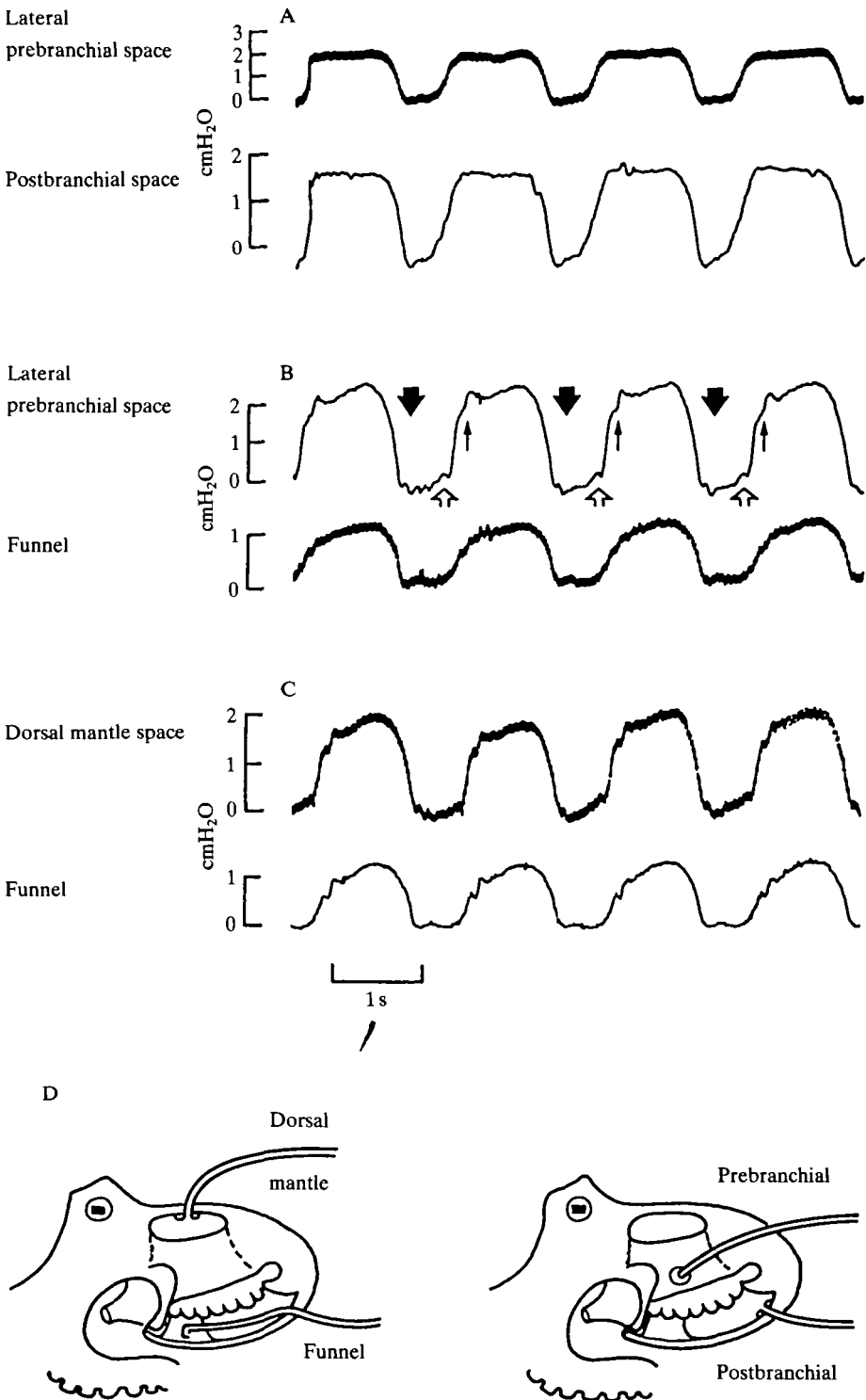


Fig. 1

funnel was marked by pressing a contact while watching the animal. The large downward-facing arrows (Fig. 1B) record the inward collapse of the end of the tube of the funnel. The mantle flaps (the collar folds forming the lateral margins of the cone of the funnel) open earlier as the prebranchial pressure drops towards zero. The closing of these valves in exhalation is shown with the open arrows, and the opening of the end of the funnel rapidly follows this (small arrows).

Oxygen tension records (Wells & Wells, 1982) from the lateral prebranchial and dorsal mantle spaces are the same during ventilation and it is evident that the dorsal mantle space and the two lateral prebranchial spaces function as a unit. Fig. 1C confirms this by showing pressure changes in the dorsal mantle, similar in magnitude to those found in the lateral prebranchial spaces in the experiments illustrated in Fig. 1A and 1B. Once again, the magnitude of pulse is greater prebranchially than postbranchially.

What these results indicate is that there is always a pressure differential across the gills, from pre- to postbranchial spaces. The implication is that flow across the gills is continuous, throughout the ventilation cycle.

Differential pressures in the pre- and postbranchial spaces

The pressure differences during the flow through the gills are small, often as little as 0.5 cmH₂O. Changes of this magnitude were close to the resolution of our pressure recording system.

It should be noted, however, that what matters in this situation is not so much the absolute values but the existence of a continuous down-hill pressure gradient across the gills. To check the existence of this, three very simple experiments were carried out by running cannulae that bypass the gills from the prebranchial to the postbranchial spaces.

In the first of these, using *Eledone* (with its arms in a netting bag closed by a drawstring just in front of the eyes), the cannula ran from the lateral space in front of one gill to the postbranchial space, looping between the positions of the cannula ends shown in Fig. 1D. A hypodermic needle was stuck into the pipe half-way along its length, and pulses of Methylene Blue were injected. These always flowed posteriorly, from the pre- to the postbranchial spaces. Flow was generally steady, at 2–3 cm s⁻¹, but occasionally pulsed, with the rearwards flow slightly slower during inspiration, as the foreward edges of the mantle expanded.

The bypass tube was then cut, and the rise and fall of the water-level in the two ends compared while holding them just above the level of the water. Both showed a distinct negative phase (about 0.5 cmH₂O) with the posterior distinctly larger in magnitude (confirming the results shown in Fig. 1A). The negative phase was followed by a much longer positive pressure phase (prebranchial pressure greater than postbranchial), as the mantle closed and water was expelled through the funnel.

In a second experiment (with *Octopus*), the bypass ran from the dorsal mantle space to the postbranchial mantle cavity. Flow was again always rearwards, with the flow fastest in expiration.

The third experiment (*Eledone*) compared pressures in the lateral prebranchial space with those at the entrance to the funnel, at the level of the septum (as in Fig. 1D). Flow was towards the funnel throughout the ventilation cycle, with little or no flow on inspiration. As in the first experiment, above, the bypass was then cut and the rise and fall of the meniscus in the tubes compared. The pressure pulse in the prebranchial tube was considerably greater (at approximately 2 cm) than in the funnel, where it was in the region of 1 cm. The prebranchial pressure rose before that in the funnel, and the two fell together.

The steady rearwards flow between the chambers during normal ventilation can be examined further by calculating the differential pressure across the gill from pressures recorded simultaneously in the pre- and postbranchial chambers. In normal quiet ventilation (Fig. 2A) the mean differential is positive ($0.38 \text{ cmH}_2\text{O}$ in this instance) and at no point is the pressure higher in the postbranchial chamber. The lowest pressure gradient between the two chambers occurs at the end of inspiration but in general the variation throughout the cycle is remarkably small (s.d. $\pm 0.15 \text{ cmH}_2\text{O}$). This is in contrast to the situation when the octopus is disturbed, blowing a jet of water at an intruder, defaecating, or for any other reason making strong ventilation movements (Fig. 2B). On these occasions the differential shows a higher mean pressure gradient and a much greater range (here $0.63 \pm 0.86 \text{ cmH}_2\text{O}$). There is also a clear reverse gradient across the gill during inspiration.

Oxygen extraction, which is often better than 50% in quiet ventilation, drops markedly as the movements become more vigorous (Wells & Wells, 1982).

DISCUSSION

We can summarize what we now believe to be the cycle of events in normal octopod ventilation. Fig. 3A and B show the beginning of inspiration. The dorso-lateral part of the mantle edge begins to thin out, opening the apertures into the lateral prebranchial spaces. At the beginning of this phase, water is still being expelled through the siphon, but this soon closes and the sides of the funnel collapse inwards. The bottom edge of the funnel is still applied to the ventral wall of the mantle, and it may be that the vertical septum contracts to ensure this, since the water entering the postbranchial space in normal quiet ventilation is always deoxygenated, indicating that it has passed through the gills at all stages in the cycle (Wells & Wells, 1982).

Contraction of the radial muscles (and/or elastic recoil by the connective tissue, see Gosline *et al.* 1983) in the rest of the mantle wall follows almost at once, so that as soon as water is sucked into the two lateral prebranchial spaces it is also drawn down through the gills into the common postbranchial cavity (Fig. 3A,B).

Inspiration is comparatively brief, occupying less than one-third of the total cycle time (see Figs 1, 2). The lateral mantle edges soon contract again, trapping a volume of water in the prebranchial/dorsal mantle spaces, jamming the sides of the funnel against the mantle walls and squeezing the water through the gills and into the posterior space (Fig. 3C,D). This is itself now contracting again, though always less

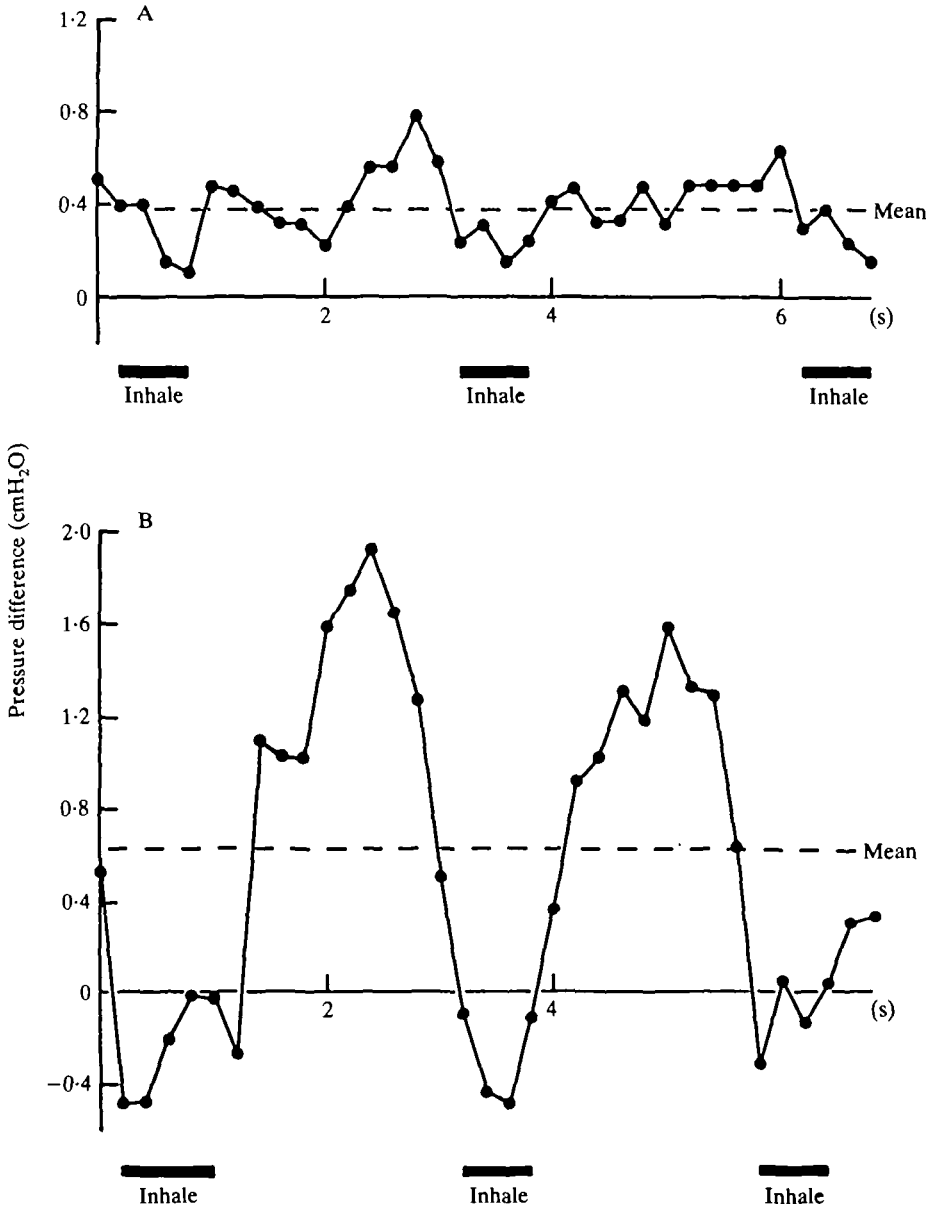


Fig. 2. (A) Pressure differential across the gills during normal quiet ventilation in *Octopus vulgaris*. The broken line is the mean differential. (B) As in (A) but during strong ventilatory movements.

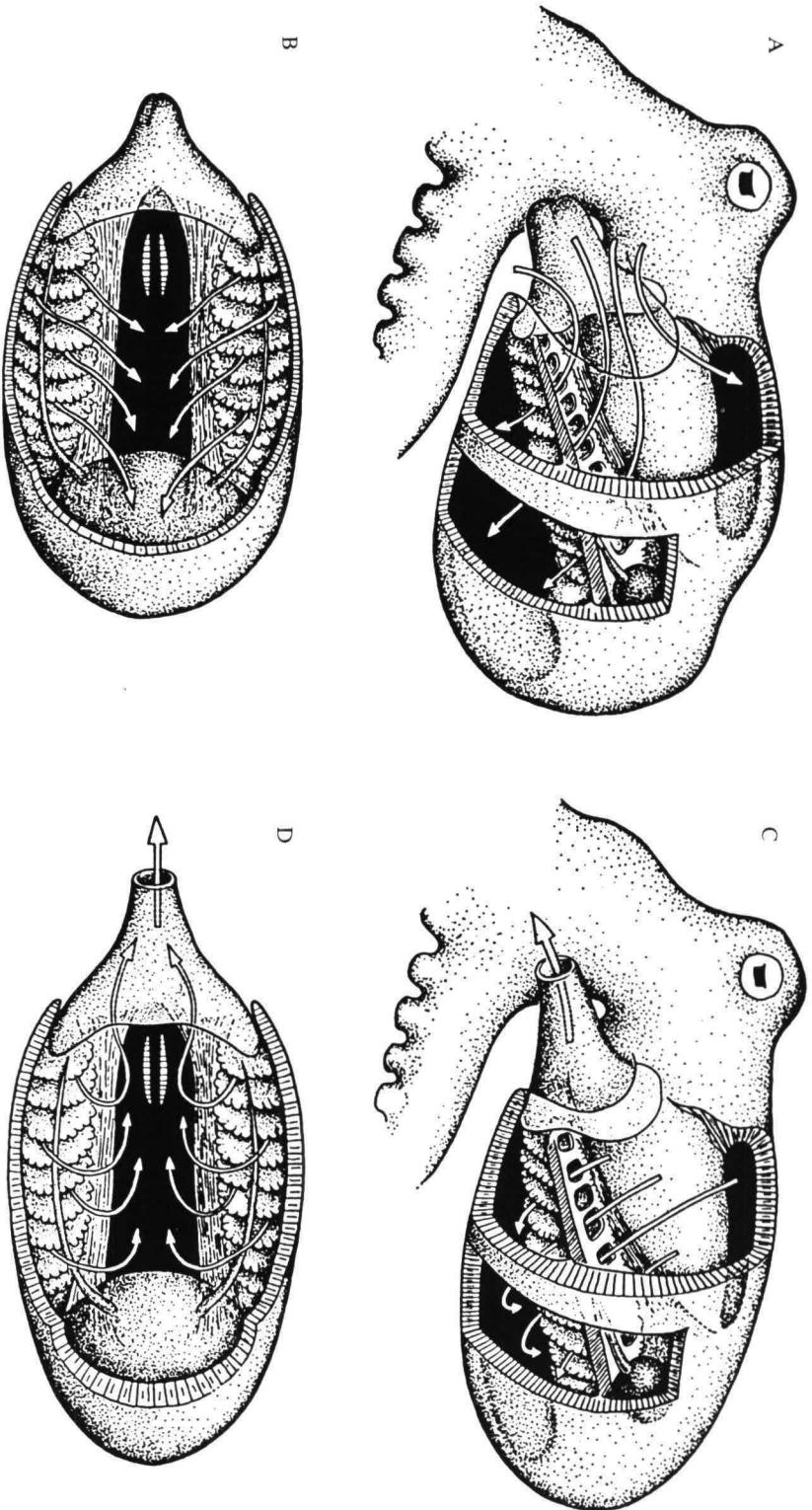


Fig. 3. Water flow during inhalation and exhalation. (A) and (B) show views from the side and from below during the longer, exhalant, part of the cycle. (C) and (D) show flows during the longer, exhalant, part of the cycle.

powerfully than the lateral anterior parts of the mantle. Water can only escape through the funnel, and a flow is set up which continues throughout most of the cycle; the anterior spaces are emptied and the cycle begins again, with expansion at the upper margins of the mantle.

These events correlate with what is known of the behaviour of the muscles in the mantle. Packard & Trueman (1974) used needle electrodes threaded longitudinally into the mantle muscle to record mantle movements throughout the respiratory cycle. Their records show that contractions of the circular muscles are more abrupt and vigorous in the anterior than in the posterior part of the mantle, as one would expect from our observations. In fact their records from the posterior part of the mantle (in *Sepia* and *Loligo*) showed no regular cycle and they concluded that the small pressure changes in the ventilatory stream were produced by contractions in only the anterior half of the mantle. This may be true of decapods, which we have not yet investigated. It cannot be true of octopods, however, where the pressure gradient is maintained even during inspiration, a state of affairs that could only arise from active expansion of the posterior part of the mantle cavity.

In teleost ventilation, Shelton (1970) has pointed out that the concept of the dual pump, the buccal and opercular (paralleled in octopus by the pre- and postbranchial chambers) rests on a gill curtain offering appreciable resistance to water flow. Certainly, the octopus gill will form an effective curtain but without knowing the resistance, the flow pattern and rate across the gill cannot be assessed from differential pressures alone. However, since the differential remains quite constant in normal quiet ventilation (Fig. 2A) flow probably continues throughout the ventilatory cycle.

An additional reason for supposing that flow is steady in quiet ventilation is the apparent lack of correlation between normal ventilatory and cardiac events. The gill hearts in *Octopus* and *Eledone* normally beat more frequently than the mantle contracts; there is no straightforward arithmetic relation between the two (Johansen & Martin, 1962; Smith, 1979; Wells, 1979). If water flow over the gills were other than continuous, heartbeat frequency might be expected to lock to the ventilation cycle, thus passing blood through the gills only when the water is flowing and the diffusion distance minimal. In practice, heart rate as slow as ventilation seems only to occur under hypoxic conditions, where the progressively slowed heart rate eventually reaches the same frequency as ventilation. Active regulation of oxygen uptake is already beginning to fail as this point is reached. During hypoxia, ventilation tends to remain almost constant in rate, while increasing progressively in stroke volume (Wells, 1979; Wells & Wells, 1983, 1985).

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