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VENTILATION AND OXYGEN UPTAKE BY *NAUTILUS*

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SUMMARY

The shell of *Nautilus* prevents the mantle from playing any part in creating the ventilatory stream. This is generated instead by movements of the collar and funnel folds which fuse to form flaps (the 'wings'), overlapping below and joined to the head above. The gills lie horizontally, dividing the space enclosed by the wings into three cavities, two lateral and prebranchial, on either side of the head, and a common ventral postbranchial space. Water is drawn in above, behind the eyes, and expelled forward through the siphon of the funnel, which is used both for ventilation and jet propulsion. The pressures driving the ventilatory stream are small (of the order of 0·1 kPa), but the complex movement of the wings, described below, is such that there is (very nearly) always a pressure differential and a water flow across the gills, despite a pulsed intake and outward jet. Oxygen extraction is low by the standards of other cephalopods, only 5–10 %, falling during jet propulsion and rising (exceptionally to 40 %) at rest after exercise. Ventilation frequency, 35 min^{-1} at 16 °C, rises with temperature. Ventilation stroke volumes ranged from 5 to 22 ml for an animal of 395 g. At 17 °C *Nautilus* can regulate its oxygen uptake down to a P_{O_2} of about 75 mmHg. Uptake at rest ranged from 0·22 to 0·46 ml kg^{-1} min^{-1} (exceptionally 0·75 ml kg^{-1} min^{-1} after feeding) for animals of 351–395 g. In terms of flesh weight, this yields an average of 0·50 ml kg^{-1} min^{-1}, half to one-third of the uptake one would expect from coleoids of similar weights and at similar temperatures.

INTRODUCTION

Because it is the only surviving cephalopod with an external shell, representing more than two thousand extinct genera of Nautiloids and Ammonoids, *Nautilus* has long been of peculiar interest to zoologists and palaeontologists. Anatomical descriptions have been available since Owen's (1832) monograph, but it is only comparatively recently that systematic observations have been made on the behaviour and physiology of the living animal.

Key words: *Nautilus*, ventilation, oxygen uptake.

In vivo studies of the animals' ventilatory system date from Bidder's (1962) observations in the aquarium at Noumea and at Rabaul; she described the role of the funnel in ventilation and swimming movements. This was followed by a trio of papers arising from the 1975 *Alpha Helix* expedition (Bourne, Redmond & Johansen, 1978; Redmond, Bourne & Johansen, 1978; Johansen, Redmond & Bourne, 1978) in which ventilation frequency and stroke volume, blood pressures and gas exchange were recorded. More recently Packard, Bone & Hignette (1980) have examined the musculature concerned and the pressures generated in quiet ventilation and jet propulsion.

The present account adds three further sorts of information. One is anatomical; the way the gills are held *in vivo* is important in relation to their function and has been ignored, or described incorrectly, in the past. The second is related to this and to the physiology of gas exchange. Notwithstanding a previous report (Redmond *et al.* 1978), it now emerges that *Nautilus* is quite capable of regulating its oxygen uptake over a wide range of ambient oxygen tensions. Comparison of the oxygen contents of the inhalant and exhalant streams from free-moving *Nautilus* have allowed us to observe extraction at rest and in movement and (where the oxygen uptake was also known) to estimate ventilation volumes. The present account also includes a description of observations indicating a continuous pressure differential across the gills so that the flow of the respiratory stream is in all probability continuous, as it is in coleoids (Wells & Wells, 1982; Wells & Smith, 1985).

MATERIAL AND METHODS

Nautilus pompilius L. was caught in wire-netting traps, baited with dead fish and set in 100–200 m off Horseshoe reef, near Port Morseby, Papua New Guinea. The animals, three males and three females, weighing 367–497 g, were taken to the Motupore Island Research Department of the University of Papua New Guinea. The first three (all males) died within hours, as we had at first no means of refrigerating the sea water, then circulating at 29 °C.

The subsequent three *Nautilus* were more carefully treated. They were placed in insulated boxes of sea water at about 17 °C as soon as captured, and rushed back to the laboratory, where we now had a small refrigeration plant operated by a generator. In the laboratory they were kept in refrigerated aquaria of 45 litres capacity, at temperatures between 14 and 20 °C.

For most of the experiments the animals were held at 15–17 °C. At this temperature they survived well, with spontaneous intermittent activity. Despite the attachment of pipes to collect samples from the ventilatory stream, and various surgical treatments to be described below, the animals were always ready to take food and at various times devoured dead fish, freshly-killed crabs, beefsteak and (on two occasions after feeding on more nourishing fare) lengths of plastic pipe from the aeration and sampling systems.

The animals were kept for 7–10 days and then killed by prolonged anaesthesia

in 2 % ethanol, a treatment that stopped ventilatory movements and any response to touch after 3 or 4 h.

Oxygen tensions were measured using an EIL 7130 probe. Inhalant and exhalant measurements were made from samples collected through 3 or 4 mm o.d. 'Portex' tubing. The inhalant cannula was glued to the shell, with the aperture just above the inhalant aperture on one side. The exhalant cannula was glued to the underside of the shell and curved round so that it entered between funnel and mantle, emerging between the lower margins of the funnel just below the gills (Fig. 3B). Looking down the funnel it could be seen in place, and did not appear to disturb the funnel-fold movements in any way. The animal was free to swim around as it wished. The two sample cannulae were connected as required to feed into a chamber just large enough to contain the oxygen electrode and a magnetic stirrer. Flow rates through the chamber were in the region of 20 ml min^{-1}. The electrode was, of course, outside the refrigerated tank and with an ambient temperature around 10 °C higher than the tank water, the sample inevitably heated up a little (usually by 3–4 °C) with a consequent increase in saturation by the time it was measured. Corrections have been made for this and the table and all figures show P_{O_2} values at tank temperature.

Pressures were measured using a Radiospares 303–343 pressure transducer, glued to the underside of the shell, with a catheter penetrating the shell and mantle into the central, ventral part of the mantle cavity. This transducer responds to changes in pressure relative to the ambient pressure (in this case immediately below the shell); so the animal was able to swim about and change its depth in the tank without affecting the baseline. We did not have a pen recorder so were unable to record rapid transient pressures. We could, however, observe these, using a rapid-response voltmeter with an LED bar display. The pressure transducer was calibrated manometrically.

Surgical techniques included the fenestration of the shell at various locations (specified in the details of experiments below). The mantle would normally bulge into the hole, making visible the mantle pressure cycle at the location concerned. Alternatively, it was possible to cut away a section of the mantle and replace the shell with a polythene window, glued to the shell. This allowed us to view the activities of the wings of the funnel, and of the gills.

RESULTS

Anatomical observations

Fig. 1 outlines the anatomy of the structures in and around the mantle cavity and shows the names that will be used in the description that follows; various names have been used in the past, these are translations of the terms adopted by Mangold, Bidder & Portmann (1986).

In the absence of any information about the embryology of *Nautilus*, the homologies of parts with apparently corresponding structures in coleoids can only be speculative. But it seems reasonable to adopt the same names for the funnel and

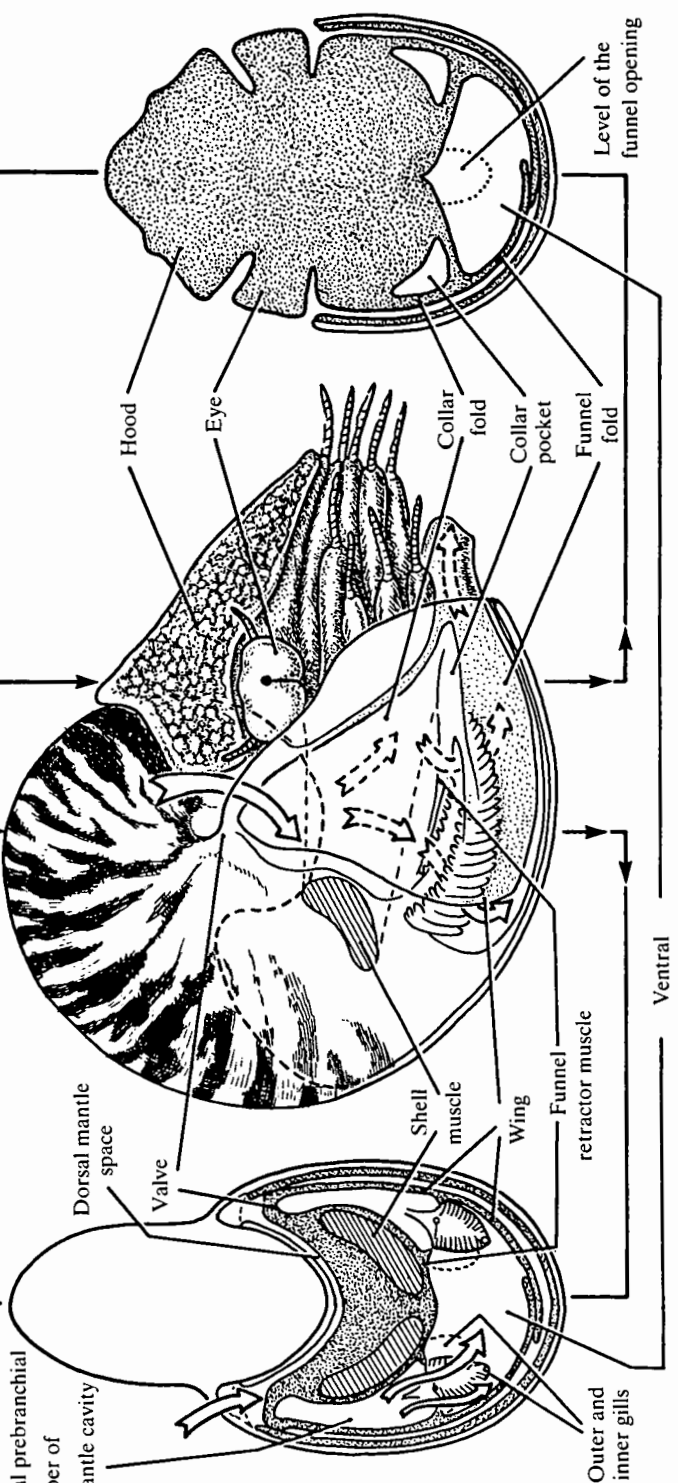

Fig. 1. Structures within the mantle cavity of *Nautilus*. Open arrows show the direction of water flow.

collar folds and to assume that the free edges forming the wings behind the funnel are formed by fusion of these folds. The collar pockets, above the funnel folds, are in a typical position, but the collar folds extend much further backwards than in coleoids, because the mantle aperture, determined by the shape of the shell, slopes backwards rather than at right angles to the body length. The nuchal region is below the hind end of the hood. Behind the eye on each side the margin of the collar fold turns in and thickens forming a valve that separates the dorsal mantle space, open above, from the mantle cavity within the shell (Fig. 1).

The position of the gills is critical to their respiratory function. The gills, mantle and wings all contract on fixation, so that little can be learned about the precise location of the gills from fixed material.

For the present series of observations, holes were drilled into the shells of freshly dead or deeply anaesthetized animals, and sections of the shell were broken away, creating windows through which the underlying structures could be seen. If an animal in its normal orientation is dissected from the side, breaking away the shell, but leaving the weight of the tissues supported by water, the mantle can be cut back and the wing pulled forward to reveal an outer gill in the position shown in Fig. 2B.

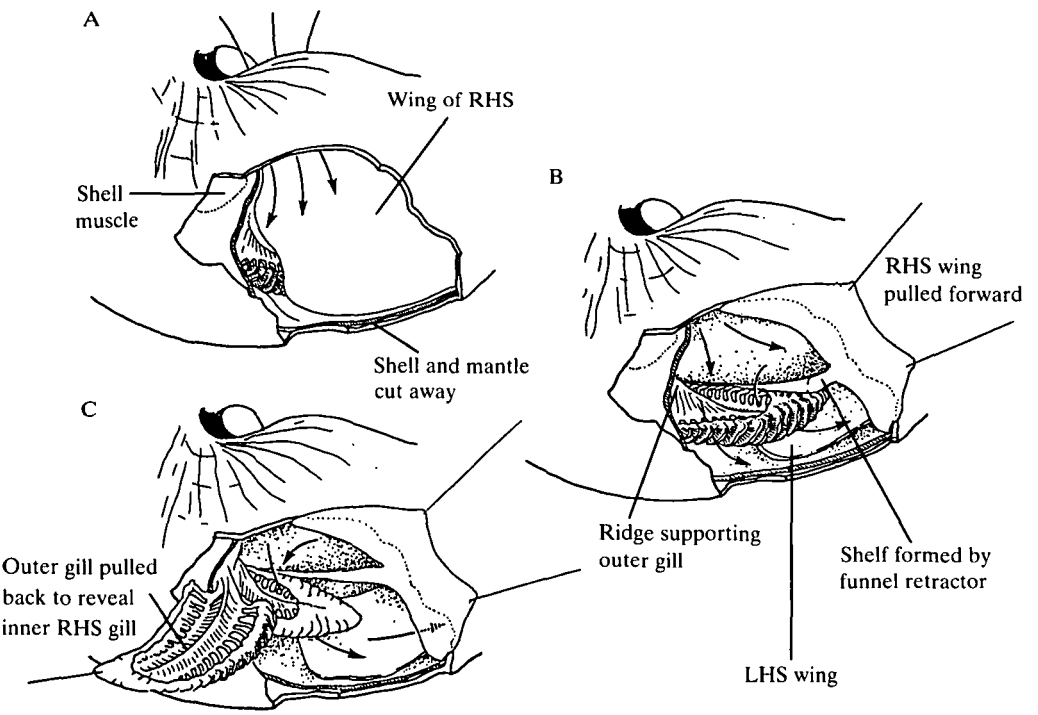

Fig. 2. Drawings made at three successive stages in the dissection of a *Nautilus*, to show the position of the gills in life. The animal was freshly dead (alcohol anaesthesia). Part of the mantle has been cut away to reveal the wing formed from the collar and funnel folds on the right hand side (RHS). LHS, left hand side.

The gill lies horizontally, tip forward, with a central dorsal rib bracketing it to the vertical wall formed by the viscera at the posterior extremity of the mantle cavity (Figs 1,2). From the central rib, a series of bars extends at right angles, supporting the gill lamellae, which hang down from the bars at right angles to the longitudinal rib (Joubin, 1890, includes a good description of the gross anatomy).

The coarse sieve formed by the bars of the outer gill accurately fills the anterior two-thirds of the space between the wing on the outside and a ridge of tissue, presumably homologous within the funnel retractor of coleoids, on the inside (Fig. 2B).

If the outer gill is folded aside, as in Fig. 2C, a second smaller gill, with a similar structure to the first, can be seen. Again, this lies mainly horizontally, bracketed to the hind wall of the mantle cavity. It fills a space between the posterior third of the outer gill and the angle between the central, anterior, part of the visceral mass and the hind wall of the mantle.

In life, with the intact animal in its normal position, the gills can be seen by looking horizontally down the funnel. What one sees are the lower filamentous undersides of the gills. The outer pair is more readily visible, sometimes hiding the smaller inner pair behind it. A central rib, carrying the efferent branchial vessel can be seen running along the lower margin of each gill.

The gills thus divide the mantle cavity on each side into two. An upper part, roofed by the collar fold, ends anteriorly in the collar pocket and posteriorly at the vertical wall formed by the viscera. The cavity is open to the dorsal mantle space and the outside world when the dorsal margin of the collar fold bends downwards in the course of ventilation. This upper part of the mantle cavity is floored by the gills on each side, which block direct access to the common ventral section. The gills will allow flow in one direction only; the soft respiratory lamellae hang down from the gill bars and would collapse against one another in the event of any tendency for the water to flow upwards from the ventral to the lateral parts of the mantle cavity.

Movement of the wings and funnel

In life, the wings move continuously. If a window is made in the side of the shell (see Methods section) the wing on that side can be seen to run through a cycle, extending backwards, margin pressed outwards against the mantle, and then bending in and moving forwards. The start of the forward movement coincides with the opening of the valve below the hind part of the hood.

If a window is made mid-ventrally, the overlapping folds forming the lower margin of the funnel can be seen. They too move rhythmically, expanding and contracting. The start of inward contraction slightly precedes the opening of the valves below the hood.

In quiet ventilation, the hood moves very little or not at all, so that the volume of the mantle cavity must remain constant. The mantle itself, lying against the shell, can play no part in creating the pressure changes that drive the ventilatory stream. The funnel and collar folds must do that alone.

To establish how these structures drive the ventilatory stream, we began by considering pressures in the pre- and postbranchial parts of the mantle cavity.

Pressures and pressure gradients

Packard *et al.* (1980) measured exhalant pressures in quiet ventilation by holding a catheter in the exhalant stream from the funnel. They noted a peak amplitude of less than 0·1 kPa (about 1 cmH_2O).

In the present series of experiments, a pressure transducer was glued to the underside of the shell, with a short ($\sim$1 cm) catheter penetrating the shell and mantle, to record pressures in the posterior ventral, postbranchial, part of the mantle cavity. The animals were free to swim about as before, trailing a wire from the transducer. Because pressure changes were small, and the baseline of the amplification system tended to drift a little, it was not possible to be certain of absolute values. We could, however, readily measure pulse amplitudes and these ranged from 0·5 to 1·0 kPa above baseline. Slightly higher (1·3 kPa) pressures were noted on two occasions when an animal had been disturbed by handling. We did not attempt to record pressures when the animals were jetting. Packard *et al.* (1980) did so and found pressures rising to 3–4 kPa. In quiet ventilation very clear brief reductions in pressure punctuated much longer positive pulses which began as the dorsal margins of the collar folds rose to close the inlet from the dorsal mantle space to the rest of the mantle cavity, and ended when these valves reopened.

Two series of experiments were made in attempts to identify the pressure gradients driving the ventilatory stream. For the first, holes were drilled in the shell laterally, above the gills, and centrally, below these. Punctures were made in the mantle and a loop of clear plastic tubing (4 mm o.d.) was cemented in, connecting the two apertures, bypassing the gills (Fig. 3A). Pulses of milk were injected into the middle of this loop by hypodermic syringe. The milk always moved slowly from the pre-to the postbranchial chambers; flow was generally pulsatile, but never backwards. When the loop was cut, milk injected into either end was expelled. The implications are (1) that pressures in both the pre- and postbranchial chambers are normally positive and (2) that there is a pressure differential between the two chambers throughout the greater part of the cycle and always from the upper lateral to the lower central part of the mantle cavity.

In a second series of experiments, holes were made in the same position as for the pressure cannulae and extended to make windows about 2 cm in diameter. These were always blocked by the mantle, which bulged out of the holes. By observing the convexity of the mantle bulges and any tendency to dimple inwards one could assess when pressure was positive or negative. It was nearly always positive at both sites with a brief dinting inwards as the inlet valves opened; this was most marked at the ventral postbranchial site. Maximum outward bulging closely followed the closing of the inlet valves and the start of a steady outflow through the funnel. If the animal was held and tilted, it made forceful jets; between these, negative pressures were quite marked. It is possible that a

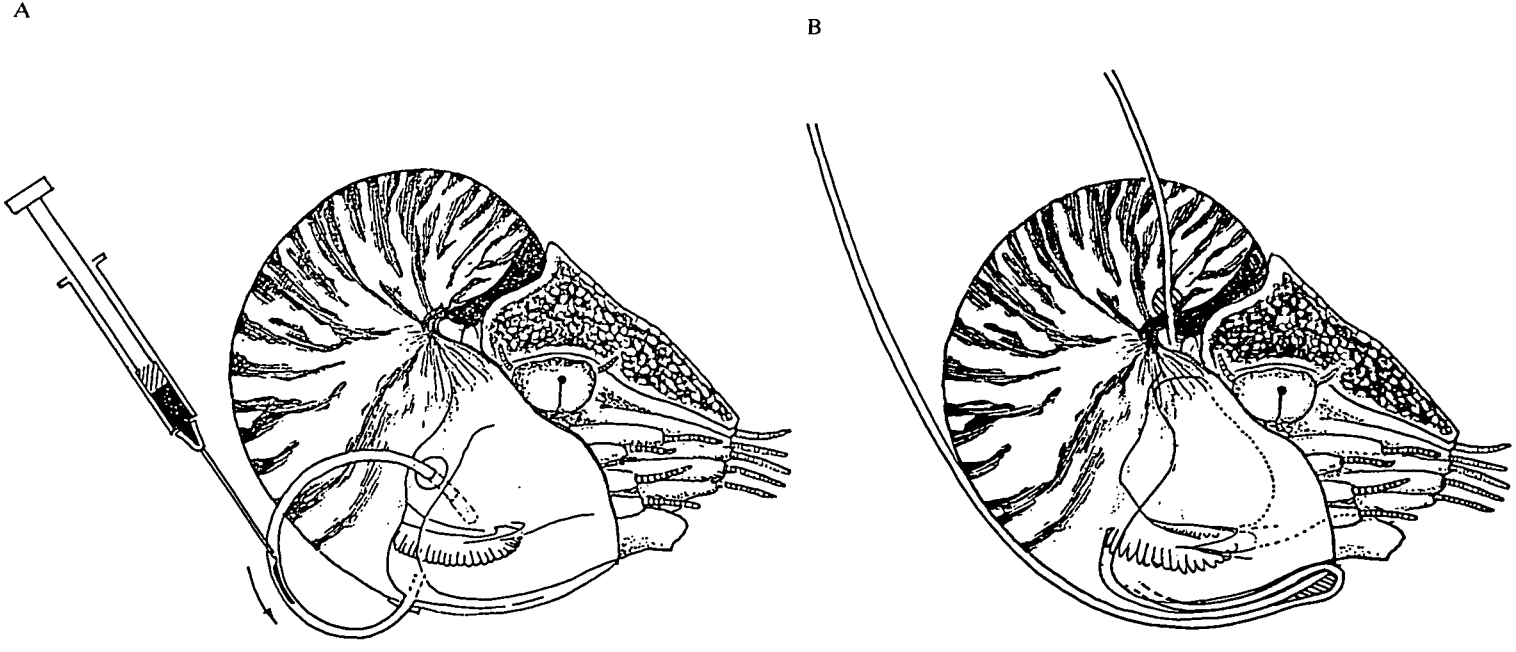

Fig. 3. (A) The position of a loop of clear plastic tubing, glued to the shell, and penetrating into the ventral part of mantle cavity, and above the gills on one side. The animal was unrestrained but tested only when at rest. Skimmed milk was injected as marker to reveal differences in pressure between the pre-and post-branchial parts of the mantle cavity. (B) The position of cannulae glued to the shell, used to sample the inhalant and exhalant streams in experiments of the type summarized in Figs 5 and 6. The exhalant sample cannula is bent in below the wings to emerge between them at the hind end of the mantle cavity, below the gills.

forward-facing flap valve in the roof of the funnel comes into play on these occasions, but we were unable to observe what was happening. We can confirm Bidder's (1962) observation that the funnel valve plays no part in normal quiet ventilation.

Ventilation frequency

Ventilation frequency can be observed at a number of sites; we generally observed the inlet valve on one side. As Fig. 4 shows, ventilation frequency is temperature dependent. It also depends on activity; an active animal (or one held, and struggling) can double the resting frequency as it produces jets from the siphon (Figs 4,6).

Oxygen uptake and the capacity to regulate as the P_{O_2} falls

Fig. 5A shows how the oxygen tension in a closed respirometer was reduced progressively in two typical runs. In these, oxygen uptake was almost constant, down to a P_{O_2} of 75 mmHg (< 50 % saturation). In one of four further experiments an animal continued to regulate successfully down to 50 mmHg. Oxygen

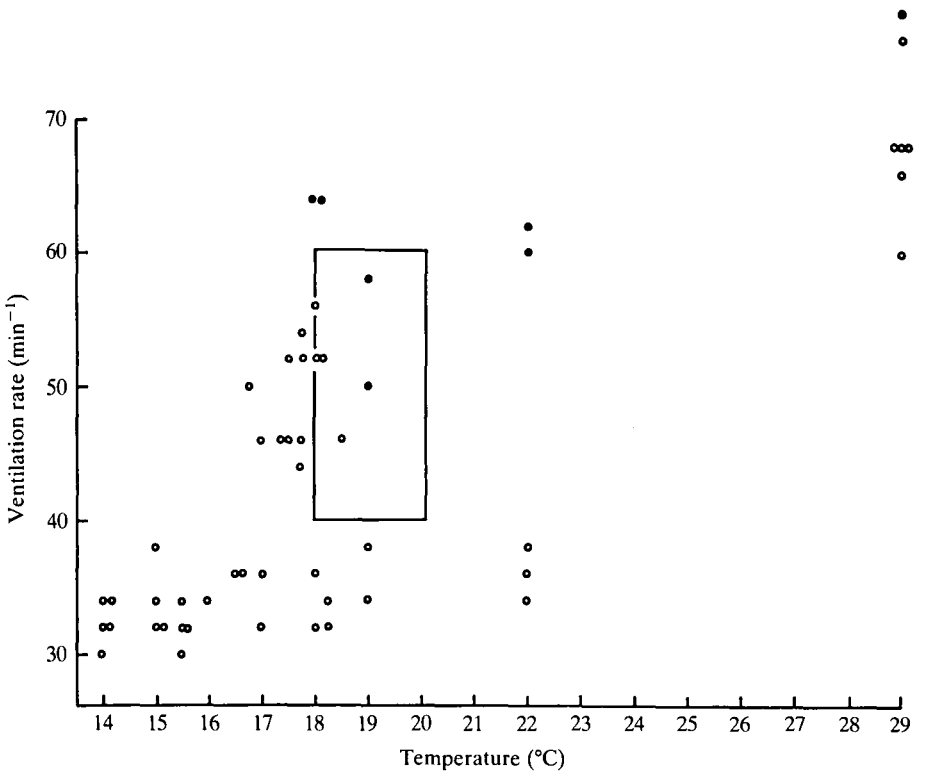

Fig. 4. Ventilation frequency and temperature in *Nautilus*. The animals observed at 29 °C died within a few hours. (●) Active animals, (○) resting animals. The box shows the ranges quoted by Johansen, Redmond & Bourne (1978).

uptake varied between 0·22 and 0·46 ml kg^{-1} min^{-1}, the latter record from a period that included intermittent, jet-propelled swimming. We have no records from continuously active animals. Most of the animals were fasted for at least 12 h before testing. A single *Nautilus*, tested within 2 h of feeding, consumed 0·75 ml kg^{-1} min^{-1}.

Oxygen extraction

Oxygen extraction was measured by comparing the tensions recorded through cannulae attached close to the inlet of the mantle cavity, and within the mantle cavity below the gills, as shown in Fig. 3B.

Sampling through one cannula or the other was continuous at about 20 ml min^{-1}. This is little more than one-tenth of the estimated ventilation flow rate (see later) and was deemed unlikely to interfere with the normal ventilatory flow. Oxygen extraction was very variable, depending mainly on the animals' activity (Fig. 6). At rest, sitting quietly on the bottom, or anchored by a few tentacles to the side of the tank, it was commonly in the region of 5–10 %, rising a little as the external P_{O_2} fell (Fig. 5). The lower figure is typical also of active animals, where the ventilation frequency is increased to produce the propulsive jets. In animals at rest after periods of activity, extraction rises to 20 % and more (Fig. 6). The highest figure that we obtained was 43 % from an animal at 19 °C.

DISCUSSION

Oxygen extraction and the regulation of oxygen uptake

Our *Nautilus*, tested at least 12 h after their last meal, consumed between 0·22 and 0·46 ml kg^{-1} min^{-1} oxygen; a single animal, tested immediately after feeding, consumed 0·75 ml kg^{-1} min^{-1}. In comparing these figures with those from other cephalopods, it has to be remembered that a high proportion (in our specimens 31 %) of the weight in *Nautilus* is shell. Because of this it is more realistic to compare *Nautilus* and other cephalopods in terms of O_2 uptake kg^{-1} flesh weight, which gives an average of 0·50 ml O_2 kg^{-1} min^{-1} for our unfed *Nautilus* at 17 °C. Johansen *et al.* (1978), working with slightly larger animals (400–600 g against our 350–400 g) at 18–20 °C found the same value. This is about half the oxygen uptake that one would find in *Octopus vulgaris* and a little less than one-third of the standard metabolic rate that we would expect from squid, *Loligo opalescens*, at similar sizes and temperatures (squid data, see O'Dor, 1982; *Octopus*, and scaling factors, see O'Dor & Wells, 1985). The archaic *Nautilus* ticks over more slowly, but not much more slowly, than the coleoids.

Oxygen extraction is predictably variable, depending upon the extent to which the animal is using the jet to move about. When moving it can fall to as low as 4 %; at rest it is more commonly in the region of 5–10 %. Our highest value was 43 %. Johansen *et al.* (1978) found an average of 7 ± 4 % extraction, and comment that this figure is much lower than values reported from other cephalopods. In fact they were so doubtful about its validity that in Redmond *et al.* (1978) they

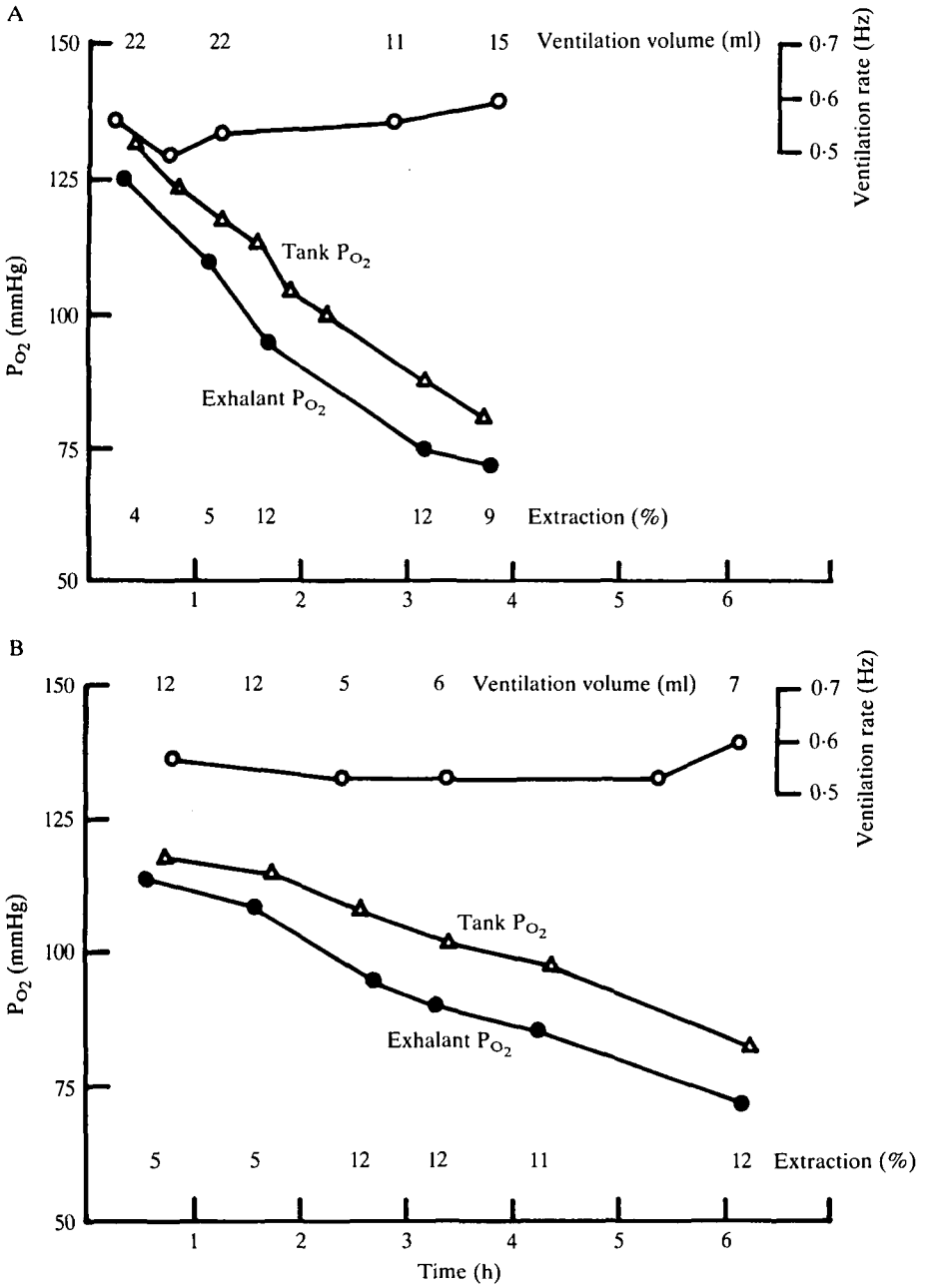

Fig. 5. Oxygen uptake in a closed respirometer; two runs with the same animal (animal 2). Ventilation stroke volume has been calculated from the percentage of oxygen extracted, tank P_{O_2} and the ventilation frequency. Sampling arrangements as shown in Fig. 3B. (A) Tank volume, 13 l; O_2 uptake, 0·37 ml kg^{-1} min^{-1} at 15 °C. (B) Tank volume, 16 l; O_2 uptake, 0·22 ml kg^{-1} min^{-1} at 15 °C.

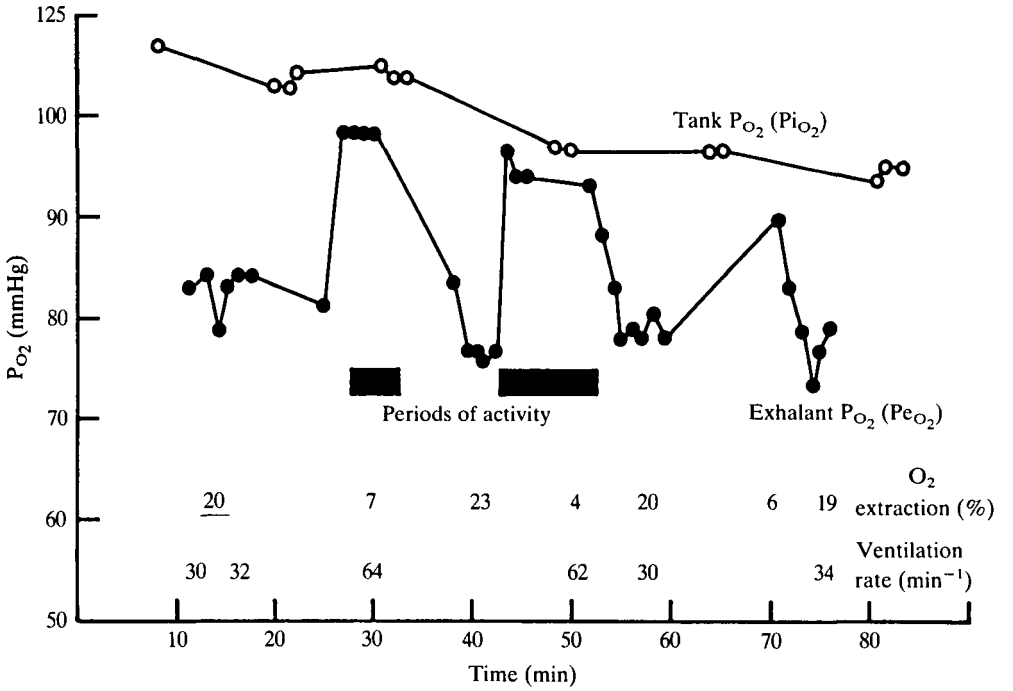

Fig. 6. Oxygen extraction and activity. When the animal is active, ventilation frequency increases and extraction falls. Sampling arrangements as in Fig. 3B.

preferred to calculate uptake (at 35 %) from total oxygen uptake and measurements of total ventilatory flow obtained in two separate series of experiments and to suggest that their cannula, entering through the funnel and sewn to the 'inside ventral wall' of the funnel, 'did not sample water of average P_{O_2} leaving the branchial chamber'. We are inclined to think that they were right first time.

Extraction did not appear to alter greatly as the external P_{O_2} fell. Oxygen uptake was maintained at a steady level down to at least 75 mmHg, without signs of distress or increase in ventilation rate. Redmond *et al.* (1978) also examined the capacity to regulate, and concluded that *Nautilus* was unable to do this, with oxygen uptake falling by two-thirds as the P_{O_2} fell from 120 to 50–70 mmHg. Their animals were, however, probably at the limit of their capacity to begin with, consuming 1·25 ml kg^{-1} min^{-1} at 24–25 °C at the start of their experiments; Johansen *et al.* (1978) have commented that the efficiency of gas exchange seems to be reduced above 21 °C, and in our experience 24–25 °C is approaching lethal limits. Their oxygen dissociation curve for *Nautilus* blood at 18 °C indicates full arterial saturation down to about 50 mmHg, so we would not expect the animals to be in difficulties over the range that we tested. Where records of ventilation frequency, oxygen uptake, tank Pi_{O_2} and extraction were all available (e.g. in Fig. 5) our calculated ventilation stroke volumes showed no correlation with Pi_{O_2} over the range 130 to 80 mmHg. Johansen *et al.* (1978) measured ventilation flow

rate directly by putting a mask over the front part of the animal. At 18–20 °C and 50 ventilatory cycles min^{-1}, they found stroke volumes in the region of 3 ml $cycle^{-1}$. Our calculated volumes, for an animal smaller than any of theirs, at 15 °C and around 33 ventilation cycles min^{-1}, were three or four times (exceptionally almost 10 times) greater. Packard *et al.* (1980) measured the mantle capacity of a fixed *Nautilus* of 470 g, with the shell muscles contracted, as 75 ml. Intuitively a 3-ml through-put per cycle seems very low for a system with such a large capacity and we believe that our present values, at around 11 ml, obtained at temperatures where the animals are relatively unstressed and in the absence of a mask (and a condom) that might have impeded the very low pressures driving the flow, are more likely to reflect normal physiology.

The ventilatory stream

The flow of water across the gills depends on quite small pressure gradients generated by the activities of the wings formed from the fused collar and funnel folds: these extend backwards on either side, as far as the vertical wall provided by the viscera, and overlap below. The mantle, applied to the shell, plays no part in generating the ventilatory stream. Large muscles (the 'shell' muscles of Packard *et al.* 1980), presumed homologous with the head retractors of coleoids, also play a part when the animal is jetting vigorously, and perhaps also when it is breathing deeply. On these occasions the *Nautilus* rocks gently back and forth as the head shield is drawn down and springs, or is pushed back, by the contraction of transverse fibres in the shell muscles. Whether the shell muscles always play a part in ventilation is more doubtful. The hood of a resting animal at 15 °C scarcely moves and we are inclined to Bidder's (1962, 1970) view that the wings are by themselves able to propel a sufficient stream for ventilation when the animal is at rest, and even perhaps a sufficient stream to drive the neutrally-buoyant animal gently backwards by jet propulsion.

From a variety of evidence, summarized in Table 1, we deduce that the sequence of events in a ventilation cycle with minimal hood movement is as follows.

(1) The margins of the funnel folds move inwards. The wave of movement spreads back rapidly along the wings which start to move forward, stroking the gills.

(2) An early effect of this forward movement is to pull down the upper margins of the collar folds, behind the eyes. This opens the region between the wings and the mantle to the outside, and water flows in from above as the wing margins move inwards and forwards.

(3) As the forward movement continues, pressure builds up in front of the wings, expanding the collar pockets and forcing water down through the gills. The gills move downwards and towards the mid-line of the animal. The total volume of the prebranchial cavities – water in front of the wings plus water drawn in behind – increases, while that of the postbranchial cavity decreases.

(4) Water flows out in a jet through the funnel.

Table 1. *Events in the ventilation cycle of* Nautilus

EXHALANT STREAM	Steady outflow								Stops
INHALANT STREAM	Valves open			Valves shut					
HOOD	Draws down (not evident in very quiet respiration)								
VIEW DOWN FUNNEL	Gills move together and down			Gills draw apart and move up					
VIEW THROUGH WINDOWS:									
Wings, above the gills	Curl inwards and move forwards						Press against mantle and sweep backwards		
Funnel margins, below the gills	Contract inwards and upwards					Expand outwards and down			
MANTLE BULGE THROUGH WINDOWS:									
Above the gills	Minimum			Maximum					
Below the gills	Minimum			Maximum					
PRESSURE TRANSDUCER:									
Below the gills	Positive pressure build up rapidly to plateau								Brief negative phase
DEDUCED FLOW ACROSS GILLS	Contraction of wing forces water down through gills					Expansion of funnel folds draws water down through the gills			?Inertial flow
Corresponding number in description of sequence in the text	10/1	2	3	4	5	6	7	8	9

(5) As the water trapped in front of the wings escapes through the gills, the volume of the prebranchial cavities decreases, the gills draw apart and move upwards and the upper margins of the collar folds relax to close the inlet valves.

(6) As the wings approach the limit of their forward movement, a wave of expansion begins in the funnel folds and spreads backwards. Expansion draws water down through the gills and maintains the pressure differential across the gills.

(7) The wings begin to return backwards, sweeping along the sides of the mantle cavity to enclose the water that flowed in behind them on the previous forward movement. Flow out through the funnel stops.

(8) Flow across the gills nevertheless continues while the funnel folds are still expanding, the postbranchial cavity is still increasing in volume, while the volume of the prebranchial cavities continues to decrease.

(9) The wings are now fully extended, almost touching the hind wall of the mantle cavity. The funnel folds, fully expanded, press against the ventral wall of the mantle. There must be a brief period during which there is no muscular contraction to generate a pressure difference across the gills.

(10) Contraction begins with the funnel folds and spreads backwards. The cycle has begun again.

It should be noted that although the inflow to the mantle, and the outgoing jet are both pulsatile, flow across the gills is in all probability continuous or very nearly so in quiet ventilation.

As with coleoids, this explains what is otherwise a paradox. The heart beat rate bears no obvious arithmetic relationship to ventilation rate. In *Nautilus* the heart beat rate is considerably slower than ventilation rate; in coleoids it is always faster (Bourne *et al.* 1978). Neither makes sense unless the blood flowing through the gills is always provided with oxygenated water.

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