

BLOOD FLOW AND PRESSURE CHANGES IN EXERCISING OCTOPUSES (*OCTOPUS VULGARIS*)

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SUMMARY

Pressure and flow were recorded from the dorsal aorta of freely moving *Octopus vulgaris* at rest and in exercise. Mean blood pressure, the amplitude of pressure pulses and flow all double as the animal moves about. Frequency changes little in exercise, indeed the increased pulses may be associated with a small drop in heartbeat frequency. There is little or no scope for expansion of arteriovenous oxygen content difference. So the increase in cardiac output necessitated by exercise must be achieved almost solely by an increase in the stroke volume of the systemic heart.

Jet propulsion is accompanied by cardiac arrest. Measurements of internal mantle pressures during jetting and of the pressure pulses generated by peristalsis of the great veins suggest that the venous system is incapable of returning blood against the gradients produced by the rise in mean mantle pressure. Since the oxygen debt that can be sustained by *Octopus* is quite small ($\approx 22 \text{ ml O}_2 \text{ kg}^{-1}$), jet-propelled movement is impossible for distances of more than a few metres.

Problems of the maintenance of a circulation in an animal with a high metabolic rate and the basic body plan of a mollusc are discussed, and the situation in squid is compared with that in octopuses.

INTRODUCTION

Most cephalopods are large by invertebrate standards, and some are large even in comparison with fish. All are predators, and many can move rapidly by jet propulsion. The combination of large size and high metabolic rate requires a well-developed circulatory system. However, the basic body plan of molluscs is far from ideal as a basis for the evolution of such a system for the following reasons. (1) Movement is dependent upon a hydrostatic skeleton; muscle can only be extended by pressure from antagonists, so that blood flow through the muscles cannot be helped by locomotion. (2) The gills are upstream of the heart and the high rate of oxygen uptake in the cephalopods necessitates fine vessels in the gills. This

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creates a second capillary bed following the main systemic peripheral resistance. (3) Cephalopod gills and hearts are inside the mantle cavity. Thus, if the mantle cavity is used to generate a jet, there will be large pressures resisting the venous return to the hearts from the head and arms. (4) Finally, most molluscs and all cephalopods use a high molecular weight blood pigment, haemocyanin, in solution though never, for reasons of viscosity, present in concentrations that result in an O₂-carrying capacity much in excess of 4 vols%.

Despite these apparently considerable difficulties, the cardiovascular systems of squids such as *Illex* (Webber & O'Dor, 1985) and *Lolliguncula* (M. J. Wells, R. T. Hanlon, P. di Marco & P. G. Lee, in preparation) manage to deliver oxygen at rates in excess of 11 O₂ kg⁻¹ h⁻¹; rates fully comparable with those of mammals, when differences in temperature are taken into account.

Squids are, however, difficult to maintain in good physiological condition in captivity. *Octopus vulgaris*, although not as active metabolically, is easier to handle, comes in large sizes, has major vessels which are accessible to surgery and can be readily induced to walk (and sometimes swim) in a confined space without damaging itself; it is therefore more appropriate for an initial study of the responses of a cephalopod circulatory system to stress. The following account describes the blood pressure and flow changes that occur when an octopus is active. A parallel study of the blood oxygen and carbon dioxide contents in animals exercising under the same conditions has been reported by Houlihan *et al.* (1986).

MATERIALS AND METHODS

Octopus vulgaris Cuvier was used in this investigation. Seven of the eight animals were mature males, between 785 and 2516 g, the eighth a ripe female of 1130 g. They were caught in trawls or by scuba divers. The animals were kept and fed on crabs at the Laboratoire Arago, Banyuls, France from July to September 1983. Exercise runs were made in a plastic paddling pool, 1.8×1.2×0.2 m deep. In most cases spontaneous movement around the pool occurred, and this was the most satisfactory way of obtaining records, since attempts to force the animals to move by touching them were liable to result in their adopting a defensive position, suckers uppermost, with intermittent cessation of ventilation, or jetting powerfully at the intruding hand, all responses that interfere with the regular heartbeat (see below). A compromise was to induce the animals to move by wading barefoot in the tank, or by presenting a white plastic bucket lid with a black 'eye' painted on it.

Probes to monitor pressure or flow were placed in the dorsal aorta. For pressure, Radiospares RS303-343 pressure transducers were modified for use underwater by filling the air-space below the piezoelectric element with liquid paraffin, open to the outside through a short length of capillary. The pressure side was connected to the aorta through a stainless-steel T-piece, as in the piped pressure-recording system used by Wells (1979). Back-filling with paraffin might be expected to slow the

response of the transducers, but the events of interest, at around 1 Hz, are far too slow for this to be significant; the shapes of the pressure pulses obtained were the same as those reported previously using conventional SE4-82 or Statham transducers. The electrical output from the RS303-343 transducers was fed to an oscilloscope and, *via* an amplifier, to a modified Cambridge type 72125 cardiograph.

Flow was measured using FW series permanent magnet transducers (*In vivo* Metric Systems, Healdsburg, California), again connected to an oscilloscope display and cardiograph.

Calibration of the pressure transducers was done manometrically. Flow transducers were calibrated as described in Wells & Wells (1986) who found that mean pulse area \times frequency showed a good correlation with measured flow over periods of a minute or so ($r = 0.92$ for the smaller bore of the two probes used and 0.93 for the larger). In the present series it was further noted that amplitude \times frequency correlates well with the total area over such series of pulses ($r = 0.98$ and 0.95 for the two probes, see Fig. 1). This simpler way of estimating flow, which has the advantage that it can be applied to records made at slow speeds where it is difficult to measure area, was used in the analysis of most of the data presented here.

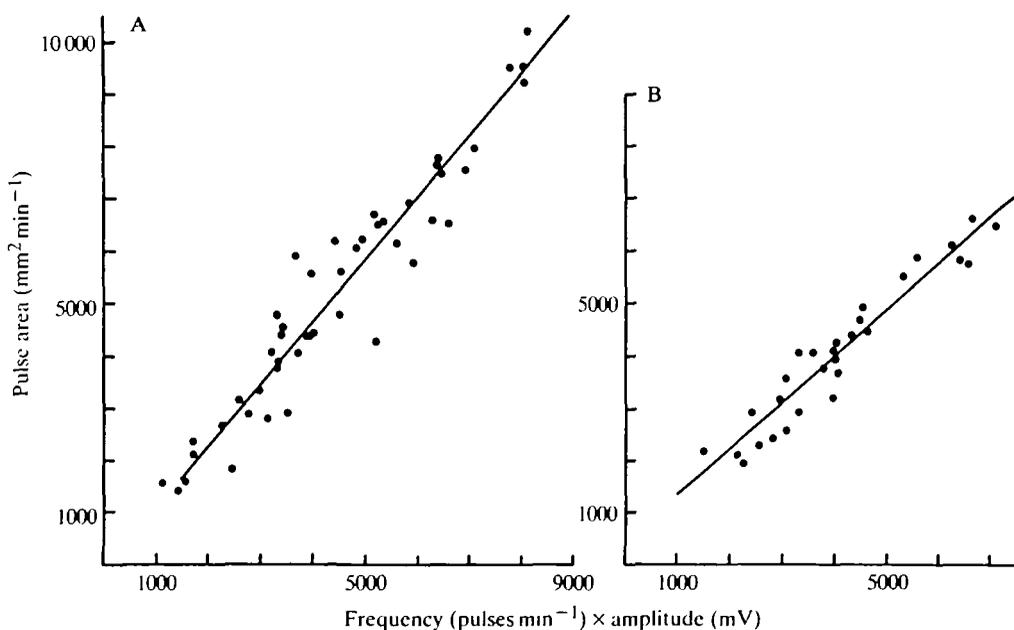


Fig. 1. The output from a flow transducer is a series of pulses in which amplitude represents instantaneous flow rate. The area of a series of pulses shows the volume passing during that time. Maximum frequency (pulses min^{-1}) \times amplitude (mV) correlates well with total pulse area min^{-1} , is quicker to measure and can be used to derive flow from records made at slow speed where measurement of area is difficult. (A,B) Measured area plotted against the product of frequency and amplitude for a series of experiments. To obtain a wide range of values the animals were subjected to progressive acute hypoxia as in Wells & Wells (1986).

RESULTS

The shape of flow and pressure pulses and their relationship at rest and in movement

Two of the largest animals used had both flow and pressure monitors inserted in series into their aortas, with the pressure probe immediately downstream of the flow probe. At rest, flow and pressure both showed a rapid rise, with flow peaking before pressure, and then a two-stage fall, with the rate of decline slowing after the closure of the exit valve from the heart at the end of systole (Fig. 2A). Shadwick, Gosline & Milsom (1987) have made a more detailed analysis of this relationship in the large *O. dofleini*; the aorta acts as an elastic reservoir, so that flow continues between beats, ceasing only momentarily in diastole. When the animal shown in Fig. 2A was moving spontaneously over the ground at around 10 cm s^{-1} , walking and sometimes jetting, but not strongly, flow along the aorta averaged around 92 ml min^{-1} , with pressures of around 3 kPa in diastole and 5 kPa in systole and occasional peaks of up to 7 kPa

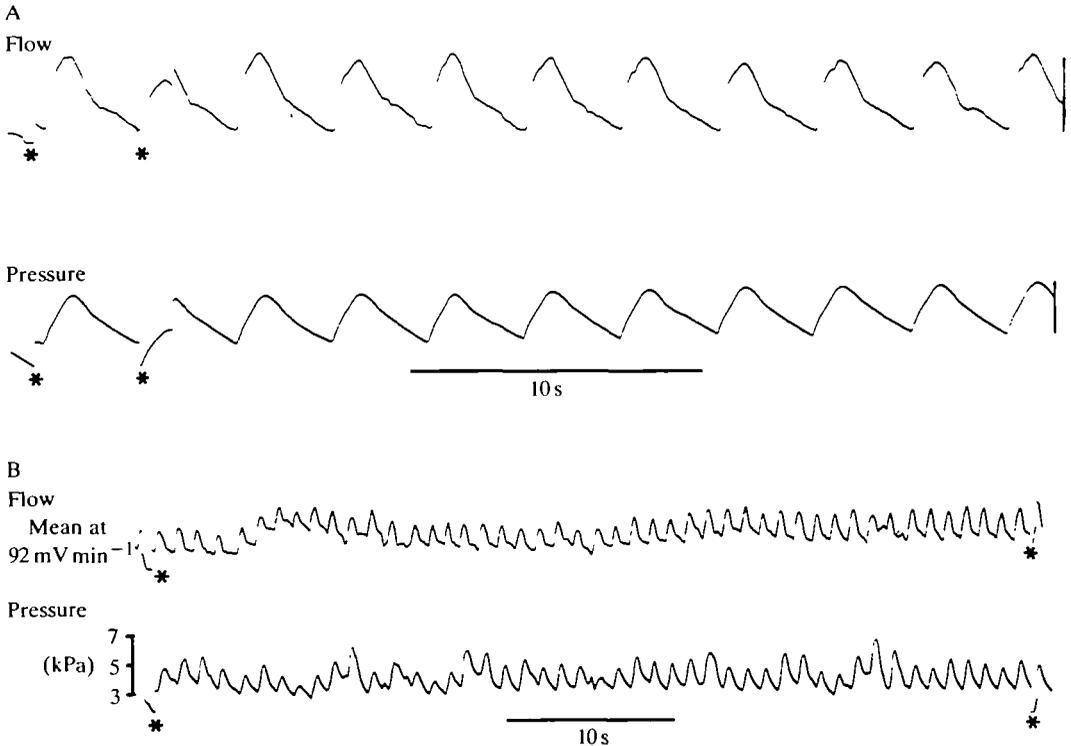


Fig. 2. Simultaneous flow and pressure records from the aorta of X12, 2387g. (A) Animal at rest. Flow peaks before pressure: both show a change in slope as the valve from the systemic heart closes in diastole; after this the flow and pressure are maintained by the elasticity of the aorta. (B) Animal moving slowly and spontaneously about its tank, walking, with occasional weak jets. The flow record baseline fluctuated for reasons unknown but unrelated to flow. Changes to the baseline of the pressure record represent real changes in pressure, which is more variable than flow (here averaging 92 ml min^{-1}). Events indicated with an asterisk are markers inserted to synchronize the records.

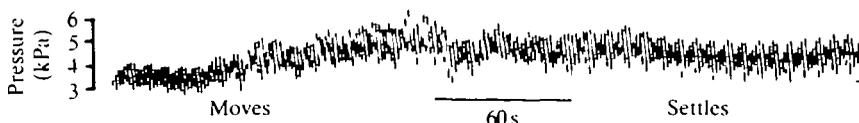


Fig. 3. Pressure changes during a movement sequence induced by putting a hand in the tank near to the octopus; X46, 1133 g, moved away and settled down when the hand was removed. Mean pressure increased by about 50% and pulse amplitude almost doubled during the active period. Heartbeat frequency remained steady at 0.7 Hz throughout.

(Fig. 2B). At rest prior to movement, the same animal pumped just over 67 ml min^{-1} along the aorta.

Pressure changes in exercise

Octopus can walk or swim and often uses a combination of crawling and jet propulsion. The speed at which it moves can vary from a slow exploratory walk forwards, at around 5 cm s^{-1} , to a jet-propelled escape, backwards at 1 m s^{-1} or more. Maldonado (1964) recorded similar speeds for jet-propelled forward attacks on crabs. The present report covers movement at the slow end of the range. Sustained jet propulsion is not seen in *Octopus* in aquaria, and occasional observation of animals in the sea (by M. J. Wells) suggests that they rarely, if ever, travel for more than a few metres in this manner (i.e. backwards, with the arms spread out in a flat horizontal plane, at a more leisurely pace than seen in escape or attack).

Fig. 3 shows a sequence from a slowly moving octopus, in which aortic blood pressure pulses rose from 3–4 kPa at rest to 6.5–8 kPa during the movement, returning to 3.5–5 kPa as the animal settled down again. The heartbeat frequency remained steady at 0.70 Hz throughout.

More vigorous responses to stimulation interfered with and sometimes stopped the pressure pulse. Fig. 4 illustrates two such sequences when the animal showed the 'dymantic' response (i.e. it flattened out, expanded the interbrachial web and paled, with dark rings around the eyes and at the edge of the web) and discharged ink through the funnel. The octopus then moved away, walking and jetting, settling down again only after removal of the stimulus. Most of these events are traceable from the pressure records, with very high pressure peaks associated with ink discharge (Fig. 4). These very high peaks probably reflect mantle pressures rather than the performance of the systemic heart. Vigorous jet production during escape responses can produce abrupt pressures of 20–40 kPa (Trueman & Packard, 1968). It is assumed that pressures of this magnitude were produced during ink ejection and were too fast for the fluid-damped RS303-343 probe to compensate fully for the ambient pressure of the mantle cavity.

Cessation of movement was followed by an increase in mean blood pressure and pulse amplitude, from 2–3 kPa at rest to 4–7 kPa at peak. The heartbeat frequency fell from an initial 0.73 Hz to 0.63 Hz during the 'recovery' period, returning to 0.73 Hz 90 s after the movement. It seems reasonable to suppose that the animal was paying off an oxygen debt (Wells, O'Dor, Mangold & Wells, 1983; Wells & Wells,

1984) that had been accumulated during the period of exercise when the pulse was irregular or stopped.

Table 1 summarizes the effects of exercise on pressure pulses for the five animals used in similar experiments.

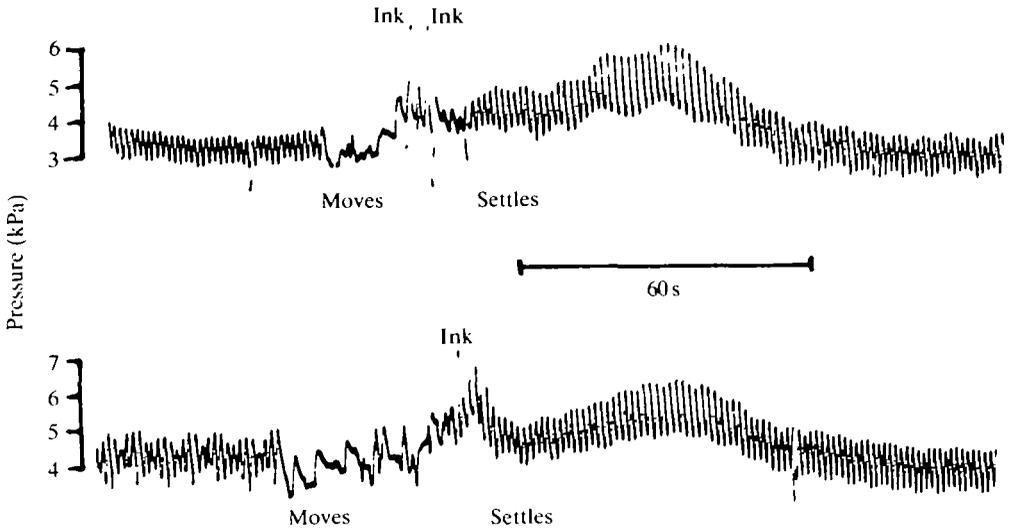


Fig. 4. Response of X46 to a white bucket lid placed in the tank; pressure records. This apparently alarming stimulus caused the animal to spread its web in the 'dynamic' display, direct jets at the lid and, on three occasions, to squirt ink while moving away. This performance interrupted the normal pressure pulse in the aorta and was followed by a period of much greater pressure pulses, presumably discharging metabolic debts run up during the period of interrupted flow.

Table 1. *Blood pressures and pulse rate in the aorta of freely moving Octopus vulgaris*

Animal	Mass (g)	Diastolic, systolic pressures (kPa*) and frequencies (Hz)			
		Recovery from anaesthetic (max)	At rest (min)	In exercise (max)	In recovery after exercise (max)
X12	2387	5, 7 0.87	4, 6 0.83	7, 9.5 0.81	4, 5 0.88
X26	1745	3.5, 5.5 0.71	2.5, 4 0.62	3, 6 0.58	4.5, 7 0.57
X46	1133	—	2, 3 0.67	6, 8 0.68	6, 7.5 0.60
X40	1130	2.5, 4 0.60	2, 3.5 0.70	3.5, 8 0.67	3, 5.5 0.70
X42	755	4, 6 0.72	2, 4 0.62	4, 8 0.68	3.5, 6 0.67

* Values maintained for periods of several (usually 10–20) beats; very high transient values are found in jetting, but last only for a beat or two and are ignored here.

Flow changes in exercise

Flow changes parallel pressure changes. Fig. 5 summarizes flow changes during a 20-min movement sequence, in which the octopus was continuously active. During this time the animal moved 64 m at 5.3 cm s^{-1} , a speed that an octopus might well maintain in the sea, moving over rocks and groping for food. Flow doubled over the first 4 min of exercise, remained steady at around 100 ml min^{-1} and then declined to 'resting' values over the 5 min following the end of the exercise period. This sequence closely parallels the rise and fall in oxygen uptake noted for *Octopus* moving in an exercise wheel (Wells *et al.* 1983).

In the experiment illustrated in Fig. 5 the animal moved slowly and evidently remained in oxygen balance, thus accumulating a small oxygen debt at the start of the run that was paid off within a few minutes of the end. In other cases, more vigorous movement was followed by a prolonged enhancement of flow, during which rates could transiently exceed those achieved during exercise (Table 2).

Blood flow recordings also confirmed that vigorous jetting was incompatible with normal blood flow, particularly when powerful jets occurred in the course of a prolonged period of movement, for flow ceased on these occasions (Fig. 6).

Cardiac performance: a summary

Blood pressure, blood flow and heartbeat frequency are not, of course, independent parameters and their interactions (summarized in Fig. 7) allow us to assess other aspects of cardiovascular performance. Thus, changes in the ratio relating the pressure required to drive blood through the systemic vascular bed (in N m^{-2}) to the mean stroke volume (in m^3) reflect alterations in resistance (Shadwick *et al.* 1987). This might be expected to increase when the animal moves, for the vascular system is part of the hydrostatic skeleton. The mean aortic pressure was calculated as

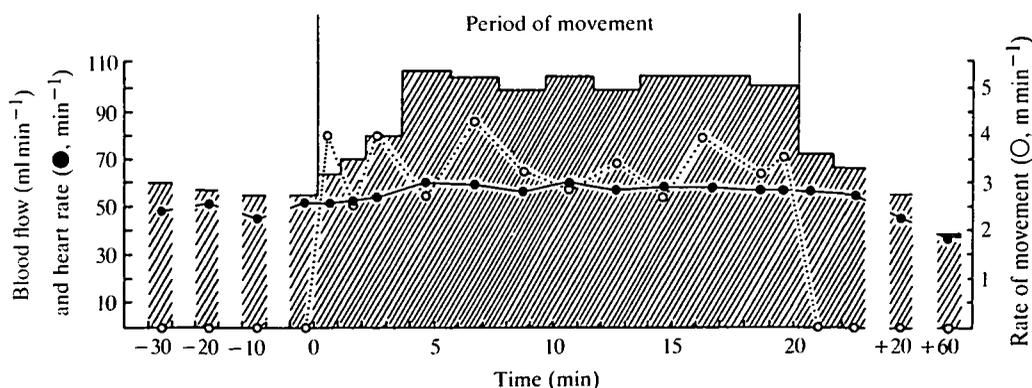


Fig. 5. A summary of flow changes over a 20-min exercise period, X47, 1016 g. Flow increased over the first 4 min, reached a steady value at almost double the resting rate and declined back to the resting value within a few minutes of the end of movement. In this slow amble around a paddling pool (the animal walked 64 m in 20 min) flow remained steady, except for occasions when the animal was touched, when there was likely to be a brief interruption of the pulse.

Table 2. *Blood flow along the aorta in freely moving Octopus vulgaris*

Animal	Mass (g)	Recovery from anaesthetic (max)	At rest (min)	In exercise (max)	In recovery after exercise (max)
X3	2516	31 (0.90; 0.57)	25 (0.80; 0.53)	43 (0.78; 0.92)	35 (0.87; 0.79)
X12	2387	34 (0.86; 0.65)	28 (0.77; 0.60)	48 (0.85; 0.94)	44 (0.85; 0.86)
X26	1745	42 (0.73; 0.90)	32 (0.58; 0.91)	36 (0.57; 1.04)	48 (0.57; 1.40)
X44	1735	67 (0.83; 1.34)	50 (0.83; 0.99)	56 (0.80; 1.16)	57 (0.78; 1.01)
X51	1117	80 (0.75; 1.77)	47 (0.78; 1.00)	111 (0.95; 1.95)	89 (0.95; 1.57)
X47	1018	59 (0.87; 1.14)	38 (0.63; 1.01)	104 (0.98; 1.76)	78 (0.83; 1.57)

Values are in $\text{ml kg}^{-1} \text{min}^{-1}$ (frequency in Hz; stroke volume in ml kg^{-1}). Extract from Wells & Smith, 1987.

$\frac{1}{3}$ (systolic + $2 \times$ diastolic pressure); the pressure in the lateral venae cavae at around 0.15 kPa (Wells & Smith, 1987) was considered negligible for these purposes. The product of stroke volume (m^3) and the pressure difference across the systemic heart [N m^{-2} ; which is very small at 0.2 kPa, see Wells & Smith (1987)] yields stroke work. The power output per gram (*O. vulgaris* hearts are close to 1.0 g kg^{-1} body mass, Wells & Smith, 1987) can thus be derived from the stroke work and the heart rate.

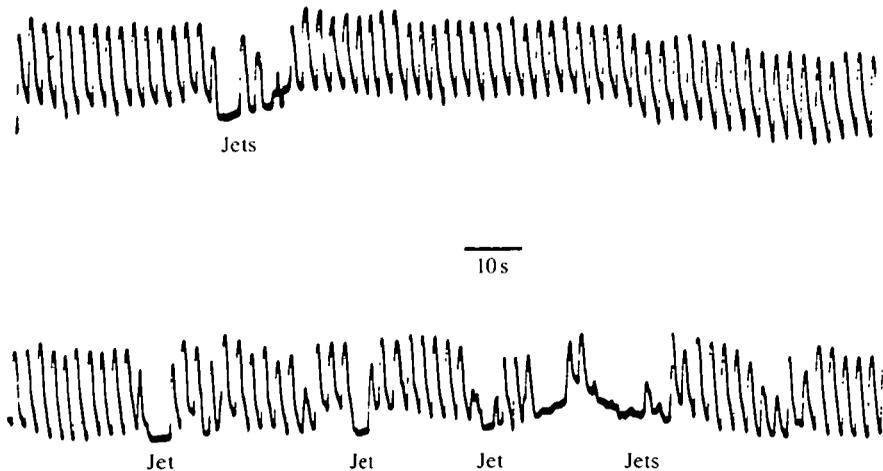


Fig. 6. Flow during exercise runs that included propulsive jets. Animal X51, 1117 g. These sequences show the effect of jet production on flow, which is temporarily interrupted. As with Fig. 1B, fluctuations in the baseline do not denote changes in flow which are signalled by pulse amplitude and frequency only; in the upper record, flow during uninterrupted pulses was about 90 ml min^{-1} , and in the lower trace about 80 ml min^{-1} .

There are several points of interest. Power output increases predictably, almost entirely due to the increase in stroke work, since the heartbeat rate alters so little. More surprisingly, the ratio of mean aortic pressure to stroke volume scarcely changes, which implies that resistance remains almost constant as the animal changes from rest to exercise. This is not what would be expected from an animal that is obliged to extend its muscles under pressure. Somehow vascular changes are taking place which facilitate the passage of blood during exercise. Such changes might include an increase in active pumping by the arteries and veins (many of which are muscular and innervated and show active peristalsis) and/or the active regulation of arterial capacitance.

It should be borne in mind that the changes summarized in Fig. 7 arise from experiments involving only rather gentle exercise. The three-fold increase in stroke work found here is certainly not a maximum. Smith (1985), using data from experiments involving more rapid walking in an exercise wheel (Wells *et al.* 1983), calculated a five-fold increase, and the animals were able to maintain this performance for at least 2 h.

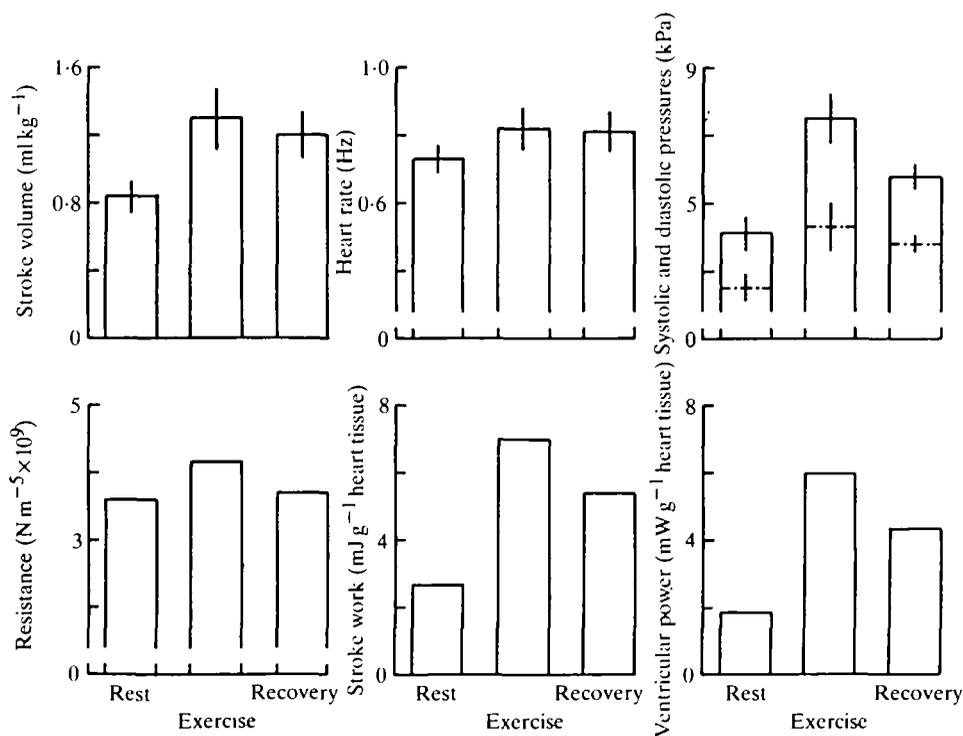


Fig. 7. Peripheral resistance changes, heart work and power output at rest, in exercise and in recovery from exercise. Values for stroke volume, heart rate and pressures are taken from Tables 1 and 2; bars show \pm S.E.M. Resistance changes are considered by comparing the ratio of aortic pressure to flow ($\text{N m}^{-2} \div \text{m}^3 \times 10^9$). Stroke work per g of heart is derived from stroke volume multiplied by the pressure difference across the systemic heart ($\text{m}^3 \times \text{N m}^{-2} = \text{J}$) and power output per g from this and the heart rate ($\text{J} \times \text{Hz} = \text{W}$).

DISCUSSION

Previous reports on the effect of exercise in *Octopus* have been hampered by pressure recording systems that included a pressure pipe from the animal to a transducer. It was possible to follow the development of pressure during slow movements by the very large *O. dofleini* (Johansen & Martin, 1962) but for *O. vulgaris* the evidence that pressure rises was based on recordings made immediately after the animal had stopped moving (Wells, 1979). Records made during any rapid movement were marred by the vibration produced when towing the pressure pipe through the water.

An implanted pressure transducer, of the sort used here, solves this problem. The results were more or less what was expected. Pressure is doubled by even quite gentle exercise, remains high while the animal is active, and often for a period afterwards. Frequency, in contrast, altered little. Often the increased pulse that accompanies a rise in mean pressure was actually slower than at rest (Tables 1, 2). This finding contrasts with Johansen & Martin's (1962) results with *O. dofleini*, where the onset of exercise was accompanied by a 30% increase in heartbeat frequency (from 0.1 to 0.13 Hz in this very large cold-water animal).

Flow, which has not been examined before in any active cephalopod, also increases during gentle exercise. In the present experiments it doubled, which is compatible with the 2.4-fold rise in oxygen uptake observed in an exercise wheel, where the animals ran more rapidly (Wells *et al.* 1983). At the onset of exercise, there is a short-term fall in arterial P_{O_2} lasting for some tens of seconds (Smith, Duthie, Wells & Houlihan, 1985: in fig. 4 of this paper the x-axis is an order of magnitude too large) followed by a return to resting values. P_{vO_2} is very low, even at rest, so there is no scope for a significant expansion of the $Pa_{O_2} - P_{vO_2}$ difference during exercise (Houlihan *et al.* 1986). Since heartbeat frequency remains unchanged, the extra oxygen delivery in exercise depends almost entirely upon increases in the stroke volume of the heart (Smith, 1985; Wells, 1979).

The experiments reported here included continuous activity lasting for 20 min at a time. Records of the track followed as animals were induced to move around ($N = 4$, including X47, summarized in Fig. 5) showed average speeds of 0.15–0.19 km h⁻¹ (2.5–3.2 m min⁻¹). This is half the speed (0.34 km h⁻¹) that can be maintained for periods of up to 2 h during forced exercise in a wheel (Wells *et al.* 1983; Wells & Wells, 1984). This would suggest that the exercise taken in the present experiments was by no means extending the animals to their limits. However, it should be borne in mind that five out of the six octopuses used here for flow experiments were larger (in four cases considerably larger) than any of the dozen octopuses run in the wheel. The latter showed a factorial aerobic scope (active ÷ routine O_2 uptake) averaging 2.38 (size range 420–1040 g). The factorial scope of the four largest animals used for the experiments reported here averaged 1.45 (size range 1735–2516 g) indicating that scope may decline with increasing size.

If the octopus needs to move at higher speeds, jet propulsion must be used. Vigorous jetting can increase the animals' speed by an order of magnitude, but the

evidence available suggests that such a performance always stops the hearts. Jet propulsion, at anything approaching the maximum speeds observed, can only be managed on oxygen debt. Since the possible oxygen debt seems to be very limited (about 22 ml kg⁻¹; Wells & Wells, 1984), vigorous jet propulsion is impossible as a regular means of transport.

Even at slower speeds, jet propulsion may be a very marginal operation for an octopus. At rest, the internal mantle pressure averages only 0.04–0.06 kPa as the animal ventilates (Wells & Smith, 1985). These very low pressures contrast with those measured in jetting. *Eledone*, which commonly swims rather than walking around its tank, showed internal mantle pressures, while jetting, in the range of 4–8 kPa; a few observations with *Octopus* yielded similar values (M. J. Wells, unpublished observations). These peak figures for slow, jet-propelled swimming (but not escape responses, where pressures can rise to 20–40 kPa, Trueman & Packard, 1968) are well in excess of the peak pressures found in the lateral venae cavae of *Octopus*, which (at rest) rarely exceed 0.2 kPa (Wells & Smith, 1987). Even if it is the mean rather than the peak pressures that matter (because the pulsations in the great veins are normally more frequent than the mantle contractions), it is not surprising that any resort to jetting stalls the venous return to the vessels inside the mantle supplying the branchial hearts. If the branchial hearts have insufficient blood to pump, the supply to the systemic heart, which contracts only when filled, is reduced, and the aortic pulse ceases or becomes erratic.

For *Octopus* this limitation on jet transport is unlikely to be important. The capacity of the octopod circulatory system is suited to the life style of a predator whose feeding forays require frequent stops to grope into crevices and among the substrate. Jetting is used to get from one patch of cover to the next or, more vigorously and perhaps comparatively rarely, for escape or a sudden jet-propelled attack on prey seen at a short distance.

In squid, which move continuously by jet propulsion, the situation must be different. Squid must somehow remain in oxygen balance during routine jet-propelled swimming. Two factors seem likely to contribute to this capacity. One is the relatively low pressures associated with routine jet propulsion in cruising squid. The other is the possible contribution of elastic recoil following compression of the collagenous tunics in the squid mantle wall. With regard to the former, Webber & O'Dor (1985) recorded peak mantle pressures of 1.5 and 3.0 and means of 0.43 at 0.99 kPa from a 550-g *Illex*, swimming freely in a large tank. The higher figures were recorded during a sequence when the animal was pursued by a net 'but did not exhibit a full escape response'. These pressures are less than half those found in jet-swimming octopods (see above). Webber & O'Dor's squid were cruising at 11.5°C at 37 and 40 jets min⁻¹, a ventilation rate some 50% higher than that of similar-sized *Eledone* or *Octopus* at 21.5°C. The squids are streamlined and evidently able to propel themselves at cruising speed with jet pressures substantially below those needed to move the more rounded octopods.

Only one attempt to record venous pressures in a squid has so far been reported. Bourne (1982) found a pulse from 0.07 kPa in diastole to 0.63 kPa in systole in the

anterior vena cava of *Loligo*. This would be sufficient to return the blood to the hearts during jetting. But the values are suspect, as Bourne points out, because the pulse coincided with ventilation and probably recorded mantle rather than blood pressures. Superimposed upon the larger pulses were smaller, more frequent, oscillations of around 0.2 kPa which perhaps represented the pressures generated by peristalsis of the great veins. This would be similar to the value found in *Octopus*, with a lower mean mantle pressure. The problem of how the venous return is achieved while the animal is jetting is evidently not as great in squids as in octopods, but the pressure available still seems inadequate to ensure the venous flow from the head and arms.

In this situation, the possibility of help from negative pressures within the mantle arising from the elastic recoil of the collagen tunics in the mantle wall becomes important. Such a possibility was inherent in Gosline & Shadwick's (1983) demonstration that the circular muscles are not simply expanded by the radials, as was at one time believed; powerful jets are associated with contraction beyond the point found in quiet ventilation and the connective tissue tunics in the mantle wall then contribute to re-expansion.

Actual demonstration of negative pressures in the mantles of swimming squids has had to wait until quite recently. Webber & O'Dor (1986) have shown negative pressures in the region of 0.3 kPa in 490-g *Illex* jetting at submaximal speeds and M. J. Wells (in preparation) has obtained similar values from 12-g *Lolliguncula* during escape responses. Negative pressures of this magnitude would appear to solve the problem of how the blood gets back into the mantle from the head and arms. But there are two difficulties. One is that the negative phases of the jet pulses seem to be of very brief duration, lasting for only a small fraction of each jet cycle. A second is their near disappearance at normal cruising speeds. Webber & O'Dor (1986; figs 4, 6) show irregular values of 0.1–0.2 kPa for around half of the cycles illustrated; the results with *Lolliguncula* imply even smaller negative pressures, often absent for many cycles on end. So the problem remains unresolved, pending the development of techniques for measuring the evidently very small pressure differentials between veins and mantle in cruising squid.

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