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# The cephalopod heart: The evolution of a high-performance invertebrate pump

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*Abstract.* Cephalopods typically have high metabolic rates. They have blood in which the oxygen carrier is haemocyanin, a pigment that is found only in solution and which never seems to be present in concentrations that will transport more than 4–5 vols % of oxygen. Their hearts must in consequence have very high cardiac outputs. In this account the performance of the heart of *Nautilus*, the only surviving ectocochleate, is contrasted with the performance of the hearts of coleoids, *Octopus* which has a relatively low metabolic rate (for a coleoid) and squids which have very high oxygen uptakes by any standards. In all these animals, heartbeat frequency is temperature-dependent and the additional oxygen demand in exercise is met very largely by a 2–3-fold increase in stroke volume. With the exception of *Nautilus*, cephalopods tend to utilise nearly all of the oxygen transported in the blood even at rest; they show very limited factorial scopes. Specific power output has, however, increased dramatically from 2.7 mW $g^{-1}$ in an active *Nautilus* to 5.5 mW $g^{-1}$ in *Octopus* and up to 20 or 30 mW $g^{-1}$ in species of *Loligo*. The increase is almost entirely due to a 10-fold increase in heartbeat frequency. It is argued that frequency cannot be used as a means of responding to extra demand in an animal that must also carry automatic compensation for changes in metabolic rate dependent upon the ambient temperature, and that the use of frequency in some squid may be associated with a reduced temperature tolerance. Cephalopod systemic hearts do not scale directly with body mass, like the hearts of fish and the higher vertebrates. Smaller cephalopods have relatively larger hearts (as Mass$^{0.9}$). A typical 100-g coleoid would have a heart mass of 0.15 g. Oegopsid squids appear to be exceptional with hearts twice as large.

*Key words.* Cephalopod evolution; cardiac performance; scaling of hearts.

## *Introduction*

Cephalopods include the largest invertebrate animals. They are active predators, preying on fish and invertebrates. With the single known exception of *Nautilus*, which lives for 10 to 20 years, they grow very rapidly, breed in a single season at an age of one to three years and then die (for summaries of the life histories of the better-known species, see Boyle[4]).

Growth rates that can raise an animal like *Octopus cyanea* from a few milligrams to several kilograms within a matter of ten months (Van Heukelem[30], but see Boyle[4] for many other examples) are associated with high metabolic rates. These in turn imply high capacity ventilatory and circulatory systems. A great deal of oxygen must be extracted and distributed through bodies that are often of very considerable size.

Distribution is made difficult by the low oxygen carrying capacity of cephalopod bloods. The pigment is always haemocyanin and this is always in solution, never in cells. Concentration is presumably limited by viscosity and the blood oxygen capacity, even in the most active squid, seems never to exceed 4 or 5 volumes per cent. Cardiac outputs have to be enormous by the standards of invertebrate animals or fish, reaching levels more typical of mammals than molluscs. This paper considers the changes in performance of the systemic heart that must have come about in the course of cephalopod evolution, and contrasts the situation in *Nautilus*, as a possible model for the situation in primitive ectocochleate cephalopods, with the state of affairs that we find in modern coleoids.

## *The animals concerned and the information available*

Information about the performance of the systemic heart of *Nautilus* comes almost entirely from two sources: data collected in the course of the 1976 *Alpha Helix* expedition to the Philippines by the late Kjell Johansen and his colleagues (Bourne, Redmond and Johansen[3]; Johansen, Redmond and Bourne[12]) and data, most of it as yet unpublished, collected by the present author and colleagues in 1989 and 1991 at the Motupore Island Research Department of the University of Papua New Guinea. The heart of *Nautilus* is readily accessible through a hole in the shell (see operational details given below). Compared with other cephalopods the animal appears remarkably phlegmatic; it scarcely reacts to visual stimuli and seems unperturbed by confinement or heart cannulation, continuing to feed, mate and show the same cyclic activity as unoperated animals in large tanks. The metabolic rate does not change as a result of operation.

Among the coleoids, *Octopus vulgaris* has been the subject of a wide range of experiments dating from Ransom[24] onwards; Wells and Smith[41] is a recent review. Most of this work was carried out at the Naples and Banyuls marine laboratories in the Mediterranean. From an experimental point of view *Octopus* has the advantage of being quite large, with a wall to the mantle cavity that can be folded back, under anaesthetic, to reveal the hearts; the dorsal aorta is accessible through a dorsal mantle space that is not present in decapods. The convenient anatomy means that elements of the circulatory system can be cannulated readily so that pressures and frequencies can be recorded from animals able to move freely about their aquaria. Once again, there appears to be little or no change in behaviour as a result of operation provided that care is taken to lead the cannulae out through the body wall and not via the mantle aperture; the latter irritates the animal and stimulates hyperventilation. If care is taken with the surgery the animals will continue to feed and mate and females will continue to brood their eggs; if deaths occur, they are generally attributable to octopus's pulling out the cannulae; the tips of the arms continually explore the environment and will grasp and pull on unfamiliar objects. Signs of stress have, however, been noted in one series of experiments. Houlihan, Innes, Wells and Wells[10] placed cannulae both in the dorsal aorta and in the branchial heart to study oxygen levels in progressive acute hypoxia. Their animals did not regulate their oxygen uptake as efficiently as unoperated octopuses.

Decapods are generally more difficult to maintain in laboratories than the littoral octopods. Some, like *Sepia officinalis*, live well and can be bred and reared in the laboratory; Forsythe, Hanlon and DeRusha[7], for example, have reported on four successive generations reared at the Marine Biomedical Institute in Galveston between 1976 and 1990. The animal's habits of burying itself, lying on the floor of its tank or hovering for long periods just above the substrate mean that it is not obliged to behave abnormally in a confined space. The hearts, unfortunately, are relatively inaccessible because the mantle cannot be folded back as in *Octopus*, and the circulatory system is screened from above by the cuttlebone.

Squids generally require a great deal of space and are prone to damage themselves against the sides of their tanks. Several species have been kept, even reared successfully from eggs in the laboratory, but most are unsatisfactory animals from a physiologist's point of view, because they move about too fast and respond too violently to disturbance. A restrained squid is almost certainly a heavily stressed squid, and we should bear this in mind when considering the few experiments that have been carried out on cardiac performance. A compensating advantage is that the smaller species tend to be transparent so that the heartbeat of a squid like *Lolliguncula* (which incidentally hovers like *Sepia* and appears more tolerant than most of confinement) can be observed without surgical interference.

Because of these limitations, the nature and reliability of the information available on cardiac performance tends to be different for different cephalopods. Direct records of cardiac output are available only for *Octopus* (Wells, Duthie, Houlihan, Smith and Wells[37]; Wells and Wells[44]). In all other cases flow has had to be estimated from Fick calculations. Blood oxygen carrying capacity and arterio-venous oxygen content differences have rarely been measured in the same individuals as were used to measure heartbeat frequency, or blood pressure. Blood pressures and frequencies have been measured through cannulae in the aortae and efferent branchial vessels of *Nautilus*, *Octopus* and *Loligo* only (for references see below, with the descriptions of experiments on individual species), so that in some instances estimates of cardiac output and power developed have even had to be based on figures derived from more than one species.

### *Anatomy*

Cephalopods have a double circulation and in this respect resemble the higher vertebrates rather than fish. The single systemic heart generates the high pressures necessary to push blood through an arterial system running to all the major organs of the body. This connects to a venous return through fine blood vessels that are commonly described as 'capillaries'. Unlike the situation in vertebrates, however, there is no size limitation on the finer vessels, because there are no blood corpuscles to be accommodated. The veins, like the arteries, are contractile. There is a very extensive innervation of the blood vessels and large numbers of neurons in the brain appear to be concerned exclusively with the detailed control of the blood vessels. It must be remembered that cephalopods have hydrostatic skeletons, so that the venous return is generally obstructed rather than assisted by the action of the locomotor musculature. By the time the blood has returned to the gills the venous pressure is very low and insufficient to drive the blood through a further set of capillaries. Cephalopods always have accessory pumps to overcome this second set of resistances. In *Nautilus* the contractile elements responsible appear to be the renal and pericardial appendages. In coleoids a large but not very muscular branchial heart is developed at the base of each gill (Wells[35] reviews the anatomy of the circulatory system).

### *Blood pressures in the vessels leading to the systemic heart*

The contractile structures upstream of the four gills of *Nautilus* generate pressures averaging 0.42 kPa and peaking at about 1.0 kPa (Bourne, Redmond and Johansen[2,3]). In *Octopus vulgaris*, the branchial hearts generate similar pressures but only in exercise; at rest prebranchial pressures are only about half those reported from the ectocochleate (Wells[34]; Wells and Wells[36]). Bourne[1], working with the squid *Loligo pealei*, found peak pressures of 0.9 kPa.

Efferent branchial pressures again seem to be much the same throughout the cephalopods, 0.1 to 0.2 kPa in *Nautilus*, octopuses and squids (Bourne[1]; Bourne, Redmond and Johansen[3], Wells and Smith[41]).

Heartbeat frequency is a different matter. The heartbeat of *Nautilus* is much slower than that of octopods, and this in turn is slower than the heartbeat of squids. Since the frequency of the pulse in the afferent and efferent branchials is always the same as the beat frequency of the systemic heart, this matter will be considered below when describing the performances of the much more powerful systemic hearts.

### *The performance of the heart of* Nautilus pompilius

The systemic heart of *Nautilus* can be approached from below by cutting a hole in the shell with a hole saw. The heart is clearly visible within the pericardium. The pericardium drains to the mantle cavity through a pair of papillae in the soft flexible wall forming the posterior limit of the mantle cavity. Puncturing the wall of the pericardium has no visible effect upon the heartbeat, and a silicone rubber or 'Portex' cannula (1–2 mm internal diameter) can be inserted through the wall of the heart and held in place by purse-string suture. The cannula is led out through a rubber membrane (part of a surgical glove) which is then glued to the shell to prevent the soft tissues from bulging out of the hole in the shell when the powerful head retractor muscles contract in jet propulsion. In the experiments to be described the cannula was connected to a pressure transducer (Elcomatic EM 750, Glasgow, Scotland, or Vemco V3D-IL-R, Shad Bay, Nova Scotia) or used to take blood samples for blood oxygen measurements. Recording of ventricular pressures and frequencies were made on a modified Cambridge Instrument Company cardiograph, or transmitted (Vemco system) to a remote hydrophone for recording on an Apple PC, as described in O'Dor, Wells and Wells[22].

Survival was excellent. Animals normally survived for a week or more, being discarded only when pressures began to drop, presumably as a result of leakage around the cannulae which eventually worked loose from the purse string sutures. Recordings were made from animals in respirometers, swimming freely in a large tank, and from a cage, returned to the animal's natural habitat. A full report of these experiments is in preparation.

Figure 1 shows a typical recording; every heart observed cycled in the manner shown. The mean systolic pressure in animals at rest in normoxic waters at 15–21 °C averaged 2.3 kPa. Diastolic pressures were close to 0 kPa.

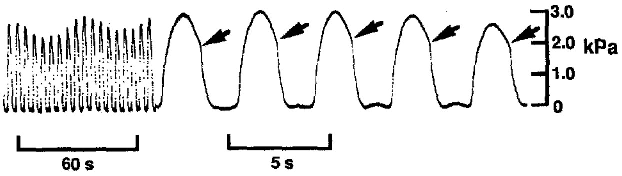

Figure 1. Pressure record from the ventricle of *Nautilus pompilius* E47, flesh weight 428 g at 15 °C. All the hearts tested cycled in this manner, pressures adopted to calculate stroke work and power output were mean values. Arrows show a sudden change of slope, assumed to indicate the closing of the aortic valve in diastole.

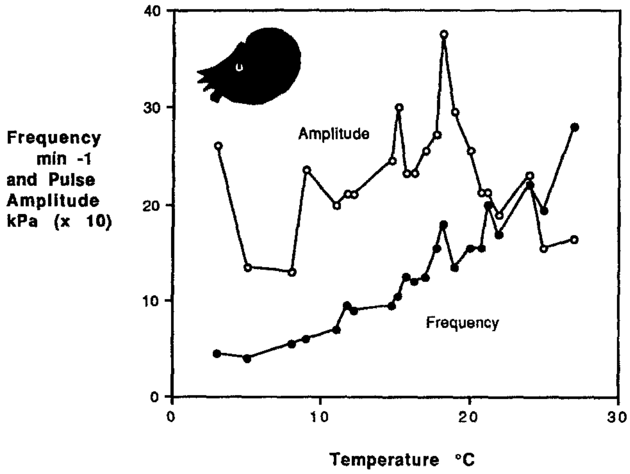

Figure 2. *Nautilus*; the effects of temperature on heartbeat frequency and pulse amplitude. Summed results from three animals.

Heartbeat frequencies in the same 7 animals varied from 0.21 to 0.36 Hz; temperature had a very marked effect on heartbeat frequency (fig. 2). The Q10 for frequency computed from the experiments summarised in figure 2 was 2.1; Wells[35] found that oxygen uptake in *Nautilus* increased with a Q10 of about 4. Heartbeat amplitude was, in contrast, little affected by temperature (fig. 2); only at the extreme ends of the range tested did the average amplitude fall off a little; *Nautilus* will not survive for more than a few hours at 25 °C, and 5 °C is probably well below the temperature that it ever encounters in its natural environment.

In exercise, both frequency and amplitude increase, the former by about 30%, with the most notable increase at the transition between inactivity and the onset of jet propulsion. Amplitude, in contrast, almost doubles at the modest speed of 0.1 $\mathrm{m\,s^{-1}}$ (fig. 3), well below the aerobically sustainable speed of around 0.16 $\mathrm{m\,s^{-1}}$ (O'Dor, Wells and Wells[22]).

Blood oxygen levels have been observed in animals at rest in normoxic water. Johansen, Redmond and Bourne[3] reported 2.0 vols % in arterial and an average of 1.3 vols % in the venous return. Our own measurements showed less oxygen in samples taken from the heart, but a considerably greater utilisation: 1.6 vols % in the arterial blood and 0.6 vols % in the venous return to the gills (Wells et al. in prep.).

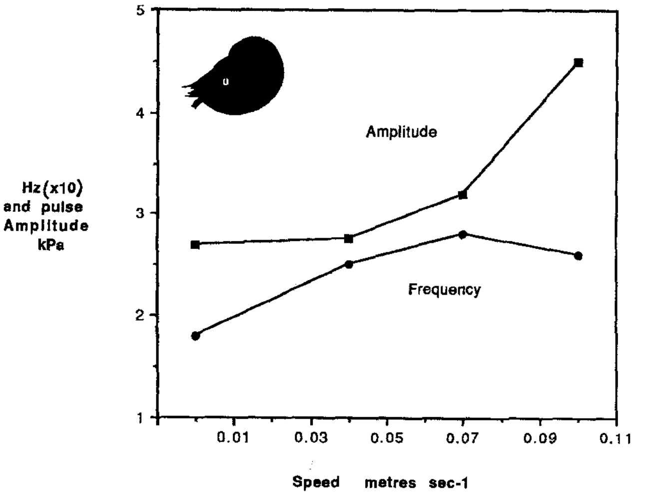

Figure 3. *Nautilus* E 19, 417 g at 17 °C. Heartbeat frequencies and amplitudes swimming in a flume at a range of speeds, 3 days after cannulation of the ventricle. Pressures telemetered as described in O'Dor, Wells and Wells[22].

The oxygen uptake of *Nautilus* at rest is close to 0.5 ml kg$^{-1}$ (flesh wt) min$^{-1}$ at 16–18 °C (Redmond, Bourne and Johansen[3]; Wells and Wells[43]), rising to 1.7 ml kg$^{-1}$ min$^{-1}$ when swimming at the maximum aerobically sustainable speed of 0.15–0.16 m s$^{-1}$ (O'Dor, Wells and Wells[22]; Wells[36]).

Cardiac output can be calculated from these figures, assuming no cutaneous oxygen uptake, as:

$$\dot{V}O_2 \times \frac{100}{\text{A-V difference in } O_2 \text{ content vols \%}} \quad \text{(equation 1)}$$

On this basis Johansen, Redmond and Bourne[11] found 62.5 ml kg$^{-1}$ (flesh wt) min$^{-1}$, while our own figures yield 50 ml kg$^{-1}$ min$^{-1}$. At 0.21 Hz (their frequency at 17 °C) this would require a stroke volume of 4.96 ml kg$^{-1}$. The corresponding figure from our own observations at 0.23 Hz (fig. 2) was 3.7 ml. 10 *Nautilus* hearts averaged 1.72 g kg$^{-1}$; the heart is large and thin-walled compared with the hearts of most coleoids.

Estimates of stroke work and ventricular power output require additional information about aortic and efferent branchial blood pressures. The former is difficult to measure because the aorta lies within a very large blood sinus, which is squeezed when the powerful head retractor muscles contract. Attempts to cannulate the aorta almost inevitably lead to extensive blood loss. Bourne, Redmond and Johansen[3] state 'many animals died'; their values come from animals that survived for at least half on hour, were still capable of swimming and had stable blood pressure. They found that the aortic systolic and diastolic pressures averaged 3.5 (range 0.8–8.0) and 1.6 (0.4–4.5) kPa respectively. The corresponding peak efferent branchial pressure was 0.2 kPa (range 0–0.5), with a mean pressure, filling the heart, of around 0.1 kPa. A mean aortic systolic pressure of 3.5 kPa is greatly in excess of the 2.3 kPa systolic ventricular pressure found in our own animals, where survival was typically for several days. In our experience pressures as high as those reported by Johansen et al. are to be expected in recovery after operation, or in exercise; they are, I suggest, typical of highly stressed animals. More realistic figures for the likely aortic pressures in unstressed resting animals can be derived from the ventricular systolic pressure and an assumption that the aortic diastolic pressure will bear the same relation to the systolic as Johansen et al. reported, that is 1.6/3.5 × 2.3 = 1.0 kPa.

Taking the mean aortic pressure as
1/3 × (systolic + 2 × diastolic) (equation 2)

Stroke work per g of heart
= stroke volume kg$^{-1}$ × (mean aortic pressure – mean efferent branchial pressure)
÷ heart weight kg$^{-1}$ (equation 3)

$$\text{S.W.} = \frac{4.96 \times 1.43 \times 1000\,(\text{Pa})}{100^3 \times 1.72} = 4.12 \times 10^{-3}\ \text{Joules g}^{-1}$$

And the power output from the heart
= J × Hz W g$^{-1}$ (equation 4)

$$\text{P.O.} = 4.12\ (\text{J}) \times 0.21\ (\text{Hz}) = 0.86 \times 10^{-3}\ \text{W g}^{-1}$$

Using our own figures for S.V. and Hz, S.W. = 3.07 mJ and P.O. = 0.69 mW g$^{-1}$.

In exercise, oxygen uptake rises to 1.7 ml kg$^{-1}$ min$^{-1}$. If one assumes *no* expansion of the arterio-venous oxygen content difference, this would raise the cardiac output to 167 ml kg$^{-1}$ min$^{-1}$ (our figures) or 213 ml kg$^{-1}$ min$^{-1}$ (Johansen's). Corresponding S.Vs (taking Hz at 0.26 from fig. 3 at 0.1 m s$^{-1}$) would be 10.70 and 13.65 ml kg$^{-1}$ b. wt, too large, one would have thought, even for the very expandable heart of *Nautilus*. It seems more reasonable to assume that the A-V difference would increase in the circumstances. If one assumes that 84% of the oxygen is removed (adopting a figure found for *Octopus* from Houlihan, Innes, Wells and Wells[10]) S.Vs = 8.0 and 6.5 ml kg$^{-1}$ (the greater change in the volume based on Johansen et al.'s figures arising from the very high resting venous oxygen levels reported in that study). Estimates of stroke work depend upon guesses about the aortic pressures in exercise. Our figures for ventricular pressure show that the systolic pressure can double; if one assumes (piling up the assumptions!) that the diastolic pressure also doubles, S.W. = 10.3 and 8.4 mJ and P.O. = 2.7 and 2.2 mW g$^{-1}$, a threefold increase from the resting condition, achieved very largely by an increase in the stroke volume of the heart.

## *The performance of the heart of* Octopus vulgaris

In *Octopus*, cardiac output and blood pressures have been measured directly both at rest and in exercise. Wells, Duthie, Houlihan, Smith and Wells[37] measured blood flow and blood pressure in the same five octopuses at rest and in exercise. The mean stroke volume at rest was 0.84 ml kg$^{-1}$. Mean systolic and diastolic pressures in the aorta were 4.1 and 2.5 kPa. Frequency in this study was 0.69 Hz; in *Octopus*, as in *Nautilus*, heartbeat frequency is temperature-dependent (Wells[34]). *Octopus* heart weights in animals of the size used for the blood flow experiments (1–2.5 kg) averaged 1.08 g kg$^{-1}$ b. wt. Using equations 1–4 above, stroke work for the heart of *Octopus vulgaris* at rest is found to be 2.26 mJ g$^{-1}$ and the power output 1.56 mW g$^{-1}$.

In exercise the stroke volume rises to 1.30 ml kg$^{-1}$, while systolic and diastolic pressures increase to 7.9 and 4.7 kPa. There is a modest increase in heartbeat frequency, from 0.69 to 0.82 Hz. Stroke work rises to 6.68 mJ g$^{-1}$ and power output to 5.49 mW g$^{-1}$.

These figures will underestimate the performance of the *Octopus* heart because they depend on measurements of flow made downstream of branches of the aorta running to the digestive system, to the mantle musculature and to the heart itself. The exercising animals, moving around in a paddling pool were, moreover, not crawling at their maximum sustainable speed. Smith[28], using data on *Octopus* oxygen consumption in an exercise wheel (Wells, O'Dor, Mangold and Wells[40]), calculated a fivefold increase in stroke work between rest and exercise, a 50% increase on the values given here that would yield a power output close to 8.5 mW g$^{-1}$.

As with *Nautilus*, it should be noticed that the increased cardiac output in exercise is achieved mainly by an increase in stroke volume which rises by more than 50%. Frequency increases by less than 20%.

### *The performance of squid hearts*

Bourne[1] cannulated the aortae of 6 *Loligo pealei* and found mean systolic and diastolic pressures of 7.18 and 2.72 kPa at 1.7 Hz at 19–22 °C. He also measured efferent branchial pressures at 0.18 kPa ($n = 5$) and weighed the hearts, 1.6 k kg$^{-1}$ b. wt for animals of 100 g ($n = 14$). He did not measure the oxygen consumption of his animals.

Table 1 shows the resting and active oxygen uptakes from a range of squid, including *L. pealei* in the same size range and at the same temperature as the animals used by Bourne. The oxygen uptake of *L. pealei* is 5.0 ml kg$^{-1}$ min$^{-1}$ at rest rising to 15.8 ml kg$^{-1}$ min$^{-1}$ when active (see O'Dor and Webber[21]).

The arterio-venous oxygen content difference has been measured as 3.9 vols % at rest (Redfield and Goodkind[25]). This figure was obtained from squid pinned to a board, with a slit in the mantle. The proportion of oxygen extracted from the blood, 91% removed from an arterial oxygen content of 4.3 vols % is, however, not greatly different from that found in *Octopus*, 84% from 3.3 vols %, under much less stressful conditions (Houlihan, Innes, Wells and Wells[10]). It is the only available figure for oxygen uptake from the blood of a squid.

These values allow us to calculate cardiac output as 132 ml kg$^{-1}$ min$^{-1}$ and stroke volume as 1.29 ml. It is, however, unlikely that all the oxygen enters by the gills. Cutaneous uptake has been measured in *Octopus vulgaris* in the 1 kg range and was found to be in the region of 13% of the total uptake (Wells and Wells[42]). The *Loligo* used to make blood pressure and oxygen uptake measurements weighed 100–150 g. With a much greater relative surface area it seems reasonable to guess that the proportion of cutaneous uptake will be greater in *L. pealei*, despite the much higher metabolic rate of the smaller animal. If cutaneous uptake were to account for 20% of the total uptake, cardiac output and stroke volume estimates would be reduced to 106 and 1.02 ml.

Taking these values together with Bourne's blood pressure measurements, stroke work and power output can be calculated as before. S.W. = 2.62 mJ g$^{-1}$ and P.O. = 4.45 mW g$^{-1}$.

Nobody has yet succeeded in measuring blood pressures in active squid. The likelihood is that Bourne's animals were already stressed and the pressures that he recorded may be characteristic of 'active' as of 'resting' animals. Oxygen uptake has, however, been measured in *L. pealei*

Table 1. The performance of the hearts of squids. $VO_2$s and cardiac output in ml kg$^{-1}$ min$^{-1}$ (figures in brackets are estimated values)

| Animal | Mass (g) | T° C | Resting $VO_2$ | Active $VO_2$ | Stroke vol. (ml kg$^{-1}$) Rest/active | Cardiac output$^{+}$ Rest/active | References |
|---|---|---|---|---|---|---|---|
| *Lolliguncula brevis* | 10 | 14–15 | 6.83 | (23.2)* | 1.50 (4.59)* | 131 (444)* | 38 |
| | | 20 | 8.98 | (30.5)* | 1.38 (4.22)* | 171 (584)* | |
| | | 25 | 10.32 | (35.1)* | 1.13 (3.46)* | 197 (671)* | |
| | | 27–30 | 12.73 | (43.3)* | 1.05 (3.21)* | 243 (827)* | |
| *Loligo opalescens* | 40 | 14 | 3.98 | 14.4 | | 82/295 | 20 |
| | 30 | 12 | 3.35 | 13.2 | 1.67/2.92 | 100/350 | 27 |
| *Loligo pealei* | 125 | 22 | 5.00 | 15.8 | 1.00 (2.71)** | 103/325 | 8, and pers. comm. to O'Dor and Webber[21] |
| *Illex illecebrosus* | 400 | 15 | 3.37 | 17.5 | | 86/295 | 33 |

$^{+}$ Cardiac output, assuming 20% cutaneous oxygen uptake. * Values estimated on the basis that active oxygen uptake is 3.4 times the resting uptake (the average from the other two myopsids in this table) and that frequency rises by 10%. ** Assuming frequency doubles as in *L. opalescens*.

(and two other species, see table 1). It is reported as 15.8 ml kg$^{-1}$ min$^{-1}$ at 22 °C, 3.17 × the resting uptake. Heart rate in *Loligo opalescens* doubles in exercise (Shadwick, O'Dor and Gosline[27], see below) and it seems reasonable to assume that the same is true of *L. pealei*. If one assumes the same blood pressures as at 'rest', stroke work for active *L. pealei* will rise to 7.88 mJ g$^{-1}$ and the power output to 27.1 mW g$^{-1}$ in exercise.

Shadwick, O'Dor and Gosline[27] made similar calculation for 20–40 g *Loligo opalescens* swimming in a Brett respirometer at 12 °C. They adopted Redfield and Goodkind's extraction figure and 5.0 kPa (higher than the 4.2 kPa measured by Bourne) as the mean aortic pressure. They made no allowance for cutaneous uptake. They estimated stroke work at 4.2 mJ g$^{-1}$ at rest, 8.8 mJ g$^{-1}$ at 0.34 m s$^{-1}$ (the aerobically sustainable speed) and 20.9 mJ g$^{-1}$ from values extrapolated to the maximum speed of 0.6 m s$^{-1}$. Corresponding power outputs were 4.2, 15.3 and 41.1 mW g$^{-1}$.

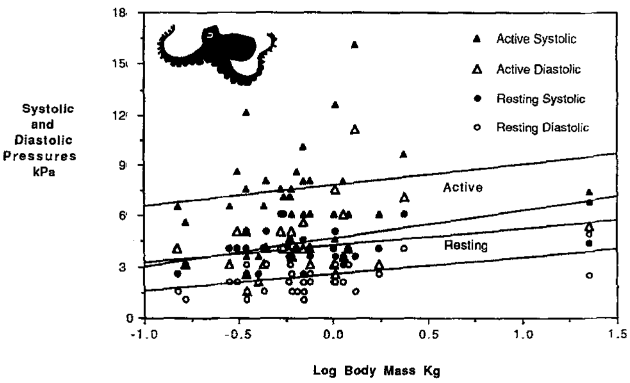

Figure 4. *Octopus*; relation between body mass and aortic pressures at rest and in exercise. Data from *O. dofleini* (very large animals to the right of this figure) from Johansen and Martin[13]. The rest, *O. vulgaris*, from Wells[34], Wells, Duthie, Houlihan, Smith and Wells[37], and Wells, unpublished.

### *Comparing the performance of* Nautilus *and the coleoids*

The results reported above came from animals of widely different size, in experiments carried out at widely different temperatures. We know that size affects metabolic rate in cephalopods; Wells, O'Dor, Mangold and Wells[39] found that specific oxygen uptake decreased as weight$^{-0.3}$ in *O. vulgaris*; Maginnis and Wells[17] found that it decreased as weight$^{-0.2}$ in *O. cyanea* over five orders of magnitude. Scale effects in other species have generally been based on a smaller range of weights, but yield similar results; Webber and O'Dor[33], working with *Illex illecebrosus* found that mass specific oxygen uptake fell as weight$^{-0.25}$ in animals over the range 0.2–0.7 kg. These scaling effects must be taken into account, particularly when comparing the squid results with the rest, because some of the squids tested were as small as 20–40 g and these must be compared with *Nautilus* and *Octopus* at 10 or 20 times the mass. A tenfold increase in size would reduce the mass-specific oxygen uptake (and thus work and power output) by about 40%.

There are indications that blood pressures may increase a little with size in *Octopus* (fig. 4); there is no information available about other genera.

Temperature must also be considered. Table 1 shows how critical temperature is to the cardiac output of *Lolligun-*

Table 2. Heart performance and the effect of compensating for temperature and body mass

| Animal | Mass g | T °C | Stroke work J/kg | Hz | Power W/kg | Power at 20 °C | Power at 20 °C and 400 g |
|---|---|---|---|---|---|---|---|
| *Nautilus pompilius* | | | | | | | |
| R1 | 500 | 17 °C | 4.12 | 0.21 | 0.86 | 1.06 | 1.12 |
| A1 | | | 8.40 | 0.26 | 2.20 | 2.71 | 2.87 |
| R2 | 400 | 17 °C | 2.99 | 0.23 | 0.67 | 0.82 | 0.82 |
| A2 | | | 10.30 | 0.26 | 2.70 | 3.32 | 3.32 |
| *Octopus vulgaris* | | | | | | | |
| R | 1750 | 23 °C | 2.26 | 0.69 | 1.56 | 1.26 | 1.82 |
| A | | | 6.68 | 0.82 | 5.49 | 4.46 | 5.70 |
| *Loligo pealei* | | | | | | | |
| R | 125 | 22 °C | 2.62 | 1.70 | 4.45 | 3.87 | 2.89 |
| A | | | 7.88 | 3.40 | 27.10 | 23.59 | 17.64 |
| *Loligo opalescens* | | | | | | | |
| R | 30 | 12 °C | 4.20 | 1.00 | 4.20 | 7.31 | 3.83 |
| A | | | 8.80 | 2.00 | 15.3 | 26.64 | 13.94 |

Compensation for temperature difference, assuming a Q10 of 2,

$$W g^{-1} 2 = W g^{-1} 1 \times 2^{((t1 - t2) \div 10)}$$

Scaling for mass, assuming W g$^{-1}$ will change in line with metabolic rate, as $Mb^{0.75}$

$$W g^{-1} 2 = \left(W g^{-1} 1 \div \frac{Mb1^{0.75}}{Mb1}\right) \times \frac{Mb2^{0.75}}{Mb2}$$

Two sets of figures for *Nautilus* are given. The first R1,A1) uses Johansen, Redmond and Bourne's[12] figures for arterio-venous difference and heartbeat frequency at rest, the second (R2,A2) uses unpublished data from Wells et al. in prep. (see text).

Table 3. Comparing the performance of fish, cephalopod and mammalian hearts

| Animal | Mass (g) | T °C | Cardiac output ml min$^{-1}$ Resting | Cardiac output ml min$^{-1}$ Active | Heart (g) | Cardiac output ml g$^{-1}$ min$^{-1}$ Resting | Cardiac output ml g$^{-1}$ min$^{-1}$ Active |
|---|---|---|---|---|---|---|---|
| Rainbow trout *Salmo gairdneri* | 1200 | 10 °C | 21.1 | 63.1 | 2.65 | 8 | 24 |
| *Nautilus pompilius* | 400 | 17 °C | 34.4 | 50.0 | 0.69 | 50 | 73 |
| *Octopus vulgaris* | 1750 | 23 °C | 34.8 | 64.0 | 1.89 | 18 | 34 |
| Mammal | 400 | 37 °C | 89.0 | 356.0 | 2.32 | 38 | 153 |
| *Loligo pealei* | 125 | 22 °C | 12.9 | 40.6 | 0.20 | 64 | 203 |
| *Loligo opalescens* | 30 | 12 °C | 3.0 | 10.5 | 0.054 | 56 | 184 |
| Mammal | 30 | 37 °C | 10.9 | 43.7 | 0.19 | 59 | 235 |

Trout data from Kiceniuk and Jones[13]. Mammal, two masses, from scaling factors given by Stahl[26]; cardiac output = $187\ M_b^{0.81}$ ($M_b$ in kg); heart mass = $0.0058\ M_b^{0.98}$. Mammalian cardiac output in exercise is estimated on the basis of a 10-fold increase in oxygen uptake coupled with a 2.5 x expansion of the arterio-venous blood oxygen difference. When comparing the specific outputs it must be remembered that the heart weights for cephalopods are the systemic heart weights, equivalent to the ventricle only in the fish and the left ventricle only in mammals.

*cula brevis* which, as a species able to survive under estuarine conditions, appears to be tolerant of a wide range of temperatures; in this species oxygen uptake shows a resting Q10 of 1.47. Demont and O'Dor[6] have reported a Q10 as high as 6 for *Illex*, but are inclined to believe that the real figure is closer to 2 or 3 (see O'Dor and Webber[21]). Wells, O'Dor, Mangold and Wells[39] found 1.8 for *Octopus*.

Table 2 includes comparisons of stroke work, heartbeat frequency and power output from *Nautilus*, *Octopus* and *Loligo* showing the data as collected, and with the results scaled for a 'standard' animal of 400 g at a 'standard' temperature of 20 °C. Scaling and allowance for temperature make no difference to the overall conclusion that cephalopod hearts have shown a fivefold increase in specific power output in the course of evolution.

In table 3 a comparison is made between the cardiac outputs of cephalopods, fish (rainbow trout) and a small mammal. The cardiac outputs even of comparatively slow-moving species like *Nautilus* or *Octopus* exceed that of the (comparatively athletic) fish while those of the squids reach almost mammalian levels. Power output is, of course, less than that of mammals because mammalian blood pressures and heartbeat frequencies are higher. Mammalian mean aortic pressure is about 13.3 kPa at rest, regardless of mass (Schmidt-Nielsen[26]), five times that of a 125 g squid. Mammalian heartbeat frequencies (using scaling factors from Stahl[26] – 6.75 Hz for a 125 g animal) are about four times those of the squid. The corresponding power outputs for 125 g squid and mammal are 2.9 and 36.6 mW g$^{-1}$ at rest and, assuming a 4-fold increase in cardiac output and a 20% increase in blood pressure for the mammal, 17.6 and 182.8 mW g$^{-1}$ in exercise.

### Heart weights and body weights

Figure 5 shows heart weight plotted against body weight for a number of cephalopods. Two matters may be noted. One is that cephalopod hearts, unlike the hearts of vertebrates (Schmidt-Nielsen[26]), do not scale directly with body mass. The slope is closer to 0.9 than 1.0; larger cephalopods have relatively smaller hearts. A second matter worth attention is that the oegopsid hearts so far sampled have proved to be significantly larger than the hearts of myopsids, which are not themselves different from the hearts of the less active octopods or the sepiolid *Rossia* (fig. 5). Whether *Illex* and *Architeuthis* are exceptional remains to be seen. *Illex* is known to have a very high metabolic rate (Webber and O'Dor[33]) and while it is unlikely that we shall ever discover much about the

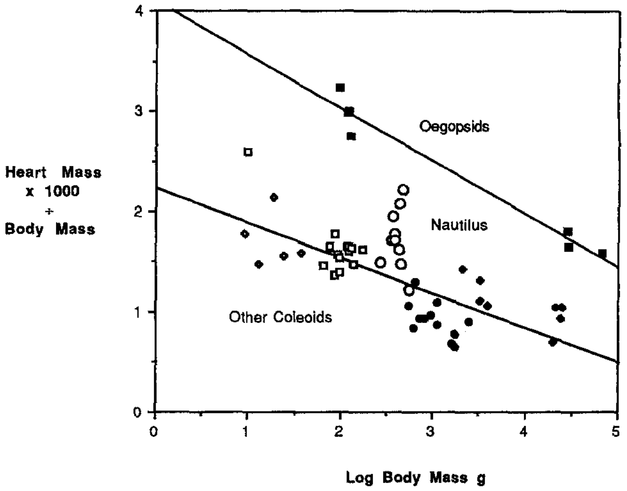

Figure 5. Heart to body mass ratios in a range of cephalopods: ◇, data from *Rossia pacifica* (sepiolid); ●, data from *Octopus vulgaris* and ◆, *O. dofleini*; □, data from *Lolliguncula brevis* and *Loligo pealei* (myopsids); ■, from *Illex illecebrosus* and *Architeuthis giganteus* (oegopsids), and ○, data from *Nautilus pompilius*. Data on *Architeuthis*, *Illex*, *O. dofleini* and *Rossia*, from Martin and Aldrich[19]; *L. pealei* from Bourne[1]; *Lolliguncula* from Wells, Hanlon, Lee and DiMarco[38], *Nautilus* and *O. vulgaris* from Wells, unpublished. The lower regression line plotted here is for all coleoids except oegopsids. Linear regressions of heart mass against body mass were compared using the method of Snedecor and Cochran[29]; octopods and the sepiolid do not differ significantly from myopsids (F = 3.71 for 1 and 37 d.f., $p > 0.25 < 0.1$), but the oegopsids have significantly larger hearts than the other squid, or octopods (F = 125.73, 1 and 19 d.f. $p < 0.005$).

metabolic rate of *Architeuthis*, it is to be hoped that uptake records from other oegopsids will soon be available.

As pointed out above, the systemic heart of cephalopods is the functional equivalent of the left ventricle of a mammal, and of the ventricle only in the heart of a fish. Cephalopod heart sizes range from 0.09% of the body weight in the very large *Octopus dofleini* through to 0.35% in a 100 g *Illex*. The latter forms about the same proportion of the total body weight as the systemic ventricle of a mammal (where the total heart weight averages 0.58% of the body weight, irrespective of size, Prothero[23]). It is considerably larger than the average fish heart, the whole of which constitutes only 0.22% of the body weight, again irrespective of size (Crile and Quiring[5]).

### *Discussion*

Table 2 shows the source of the power increase that has taken place in the course of cephalopod evolution; stroke work, per gram, has not changed much. The difference between the situation in *Nautilus* and the more active coleoids is almost entirely due to a very considerable increase in heartbeat frequency.

It should be noted that what has increased is the baseline, resting frequency. The frequency in an active *Nautilus* is only about 30% greater than the resting frequency. In *Octopus* it is less than 20%. In *Loligo opalescens* it is still only 100%, a small matter compared with the 5-fold difference in the rate at rest between *Nautilus* and the squid, rates recorded, incidentally, at very similar temperatures. In *Loligo*, as in *Nautilus*, most of the change in frequency occurs at the transition between rest and exercise, rather than progressively as the level of activity increases (Shadwick, O'Dor and Gosline[27], and fig. 3 above). Changes in cardiac output, to meet any additional oxygen demand, are brought about very largely by progressive increases in stroke volume, which typically expands by 2–3 times. Cephalopods seem to be driven to rely on increasing stroke volume rather than frequency to meet any additional oxygen demand because frequency changes are apparently reserved to deal with temperature changes, an automatic compensation upon which any short-term adaptive changes must be superimposed. It would be interesting to know whether there is a relation between the capacity to make an adaptive change in frequency and the temperature range in which a given species is able to operate. One might predict that species like *Loligo opalescens*, which shows a large frequency response in exercise, will be restricted in ecological range compared with species like *Lolliguncula brevis* which apparently shows little or no change in heartbeat frequency in exercise (n = 2 only) but large changes in response to temperature (Wells, Hanlon, Lee and DiMarco[38]).

Having pushed frequency and stroke volume to the limit, the only option left to a squid would be to increase the size of the heart. There is some evidence that the open-water squids may have done this; the heart of *Illex*, for example, is almost twice as large as those of *Loligo* of similar mass (fig. 5). This is a solution to the problem of increased oxygen demand found also in the very smallest birds and mammals, which appear to run up against a frequency barrier (see Schmidt-Nielsen[26]).

A final set of similarities to mammals is shown in table 4. The total number of heartbeats occurring during the lifetime of a cephalopod is in the region of $2.5 \times 10^8$, compared with $1.5 \times 10^9$ in a mammal, the smaller number in the invertebrate reflecting, perhaps, a life history in which the attainment of sexual maturity and subsequent single spawning is terminal (*Nautilus*, alone, does not show this pattern). There are indications that, in cephalopods as in mammals, the lifetime total may decrease with increasing body mass.

The heart muscles of cephalopods are plainly a very interesting set of tissues, working at rates within an order of magnitude of those of mammals, despite very large differences in operating temperatures. A comparative study of mitochondrial densities and other aspects of the fine structure of the two could be rewarding.

Table 4. Heartbeats in a lifetime

| | Weight (g) | Life expectancy (years) | Heartbeats ($\mathrm{min}^{-1}$) | Heartbeats (in a lifetime) |
|---|---|---|---|---|
| Mammal | 10 | 4.62 | 762 | $1.9 \times 10^9$ |
| | 100 | 7.32 | 428 | $1.7 \times 10^9$ |
| | 1000 | 11.6 | 241 | $1.5 \times 10^9$ |
| Cephalopod | 10 (*Lolliguncula*) | 1.0[a] | 169 | $1.1 \times 10^8$<br>(1 g–$3.3 \times 10^8$) |
| | 150 (*Loligo pealei*) | 1.5[b] | 102 | $8.0 \times 10^7$<br>(1.5 g–$2.4 \times 10^8$) |
| | 400 (*Nautilus*) | 10 +[c] | 15 | $7.8 \times 10^7$<br>(200 g–$1.0 \times 10^8$) |
| | 1000 (*Octopus*) | 1.5[d] | 45 | $3.5 \times 10^7$<br>(10 g–$1.1 \times 10^8$) |

Scaling factors for lifespan and heartbeat frequency in mammals from Lindstedt and Calder[16]. Figures in brackets for coleoids take body mass at halfway through the lifetime and a heartbeat rate appropriate for that size. *Nautilus* alone is iteroparous and may live for a further 10 years after attaining sexual maturity and ceasing to grow. The growth curve for *Nautilus* is still largely speculative. Cephalopod longevity estimates from [a] Hixon[9], [b] Summers[31], [c] Landman and Cochran[15], [d] Mangold[18].

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