THE HEARTBEAT OF *OCTOPUS VULGARIS*

By M. J. WELLS

Department of Zoology, Cambridge, England

SUMMARY

Heartbeat frequencies and blood pressures were monitored in free-moving *Octopus vulgaris*. Typical resting frequencies (for animals of 500 g ± at 22° C) were 40–50 beats min^{-1}, with resting pressures measured at the dorsal aorta of 40 cm H_2O in systole and 15 cm in diastole, rising to 100 cm or more with a pulse of 50 cm in exercise. Beat frequency changes very little and any increased oxygen demand results mainly in an increase in stroke volume. Temperature affects heartbeat frequency with a Q_{10} of about 3 over the range 7–27 °C. Systemic heartbeat rate and pulse amplitude also change with the oxygen content of the water, slowing as this decreases and stopping, reversibly (at least for short periods), at about 2·5 parts O_2 per million.

INTRODUCTION

There is a considerable literature on the performance of the *Octopus* systemic heart *in vitro* (for a review see Krijgsman & Divaris, 1955; a recent study of hormonal effects on heartbeat is reported in Froesch & Mangold, 1976) and there are some early accounts of the circulation in acute preparations (Ransom, 1884; Fredericq, 1914). The only papers reporting conditions in intact animals are those of Johansen & Huston (1962), Johansen & Martin (1962), Smith (1962) and Johansen (1965), on *Octopus dofleini* under conditions essentially similar to those reported below. *O. dofleini* is, however, a veritable giant among octopuses, 10–12 kg and some 30 times the weight of *O. vulgaris*. Furthermore, *O. dofleini* is a cold water species and laboratory experiments were carried out at about 8 °C, compared with the 20–24 °C normal for *O. vulgaris*.

These very large differences make it hard to predict the cardiac performance of *O. vulgaris* from that of *O. dofleini*. The published data, moreover, give little information on individual variation or on the effect of changes in temperature or oxygen saturation. A knowledge of these factors is necessary for an understanding of the changes in cardiac performance resulting from brain lesions, interference with the peripheral nervous system, or manipulation of the animals' hormonal system, all matters to be reported later. The present account is an attempt to establish baselines for intact, immature *O. vulgaris*, against which to compare the results of a variety of experimental procedures.

METHODS

Experiments were made at the Stazione Zoologica, Naples (in July and August, 1975), and at the Laboratoire Arago, Banyuls-sur-mer (in August 1976 and 1977). The animals ranged in weight from 150 to 1300 g and included both males and females. The females were all immature; the males all had ripe spermatophores in their sex ducts, but none had the big suckers, enlarged rather flabby testes and large orange optic glands found in fully mature pre-senescent octopuses (see Van Heukelem, 1973).

Operations were carried out on animals that had been in the laboratory for several days, were feeding well, and without visible damage. A pressure pipeline and/or electrodes from two sorts of recording device were implanted under 3 % urethane (Naples) or 2·5 % ethyl alcohol (Banyuls) anaesthesia.

One of these devices monitored pressure, usually at a point in the dorsal aorta a few centimetres anterior to the systemic heart. To install this a cut was made through the skin and muscle of the abdomen and through the connective tissue sheath surrounding the digestive gland. The dorsal aorta was fished out through the incision using a blunt glass hook, was clamped on the systemic heart side, and a stainless steel T piece inserted through a cut and tied in; the diameter of the T was matched in each case to the likely diameter of the aorta in systole (established by measuring aortae under suitable pressures *in vitro*) in the resting animal. The clamp was removed and the aorta pushed back through the hole in the connective tissue sheath and the T piece sewn in tightly (the connective tissue sheath surrounds a blood sinus and it is important to avoid leaks). This leaves one end of the T, which runs into a short length of rubber pressure-tubing with a temporary plug in the free end, protruding through the connective tissue sheath, across the upper part of the mantle cavity and out of the middle of the back of the animal. The tube, and the T piece below it are kept from rotating by a wire brace stuck through the rubber at right angles to the long arm of the T. This is pushed into the muscle on either side of the cut and the sides of the cut sewn together by stitches through the muscle (it is important to avoid the sensitive skin, or the animal will pick at the stitches). Finally the plug in the tube is removed and replaced by a 2–3 mm diameter nylon pipe running upwards and out of the animal's tank to a piezo-electric pressure transducer (SE4-82; from SE Laboratories Ltd, Feltham, Middlesex). The piezo-resistance effect is used in a wheatstone bridge circuit to provide an output voltage that is fed through a pair of amplifiers into a conventional electrocardiograph (Gulton TR711 in Naples, Cambridge Instrument Company type 72125 in Banyuls).

Branchial heartbeats were monitored using an impedance unit (The Scientific Instrument Centre Ltd, Liverpool). This device generates a high frequency a.c. signal and detects changes in the distance apart of two thin wire electrodes by measuring the impedance of the tissue between. The wires (0·2 mm diameter resistance wire was used, with the insulation scraped off the ends) were threaded into the heart (or mantle) musculature, looped and sewn in to prevent the octopus from removing them and led out alongside the pressure line to the transducer.

Installed in this manner the tube and wires seem to irritate the animals remarkably little. Some individuals will struggle with the tube from time to time and may even pull on it so strongly as to twist the T and interrupt the blood flow. It is easy enough to

see when they are doing this (it is anyway obvious from the record) and to discard any measurements obtained in these circumstances. Since the animals will walk, swim, catch crabs and even copulate with the recording leads installed, it seems reasonable to assume that the pressures and heart-rates observed are truly representative of those occurring in unstressed, unoperated octopuses.

The animals can survive for two or three days, but most experiments lasted for only a few hours. Between recording sessions the pressure pipe can be removed and the T-piece plugged, but most animals eventually succeed in removing the plug or in loosening the stitches that seal the T into the sinus around the gut. It seems probable that the octopuses would soon die even in the absence of leaks, because the operations, carried out under seawater, can hardly be kept sterile, and the bloods of individuals examined after two or three days were nearly all infected with bacteria.

Because of uncertainty about the condition of octopuses kept for more than a few hours, only measurements made within five or six hours of operation have been included here.

<div align="center">RESULTS</div>

<div align="center">*Accuracy of the measurements and interpretation of the records*</div>

The pressure transducer was placed close to the octopus tank, with the face of the transducing element level with the surface of the tank water. Calibration was achieved by turning a tap from the octopus pressure pipe to a pipe from a column of seawater that could be raised and lowered to establish and record further values in the expected range. Calibration was frequently repeated between recording runs, because it was convenient later to read off from a nearby scale. Otherwise re-calibration was unnecessary; once the scale was set the apparatus would perform reliably for hours without drift.

The accuracy of the pressure transducer itself was not limiting in the present experiments. The device registered pressure changes of a few mm H_2O. Such changes fall within the range of variation introduced by ripples on the surface of the octopus tank. Individual heartbeats, moreover, often differ in pressure by as much as two or three centimetres even when the heart is beating 'steadily', and in most of the report that follows, pressures are quoted only to the nearest 5 cm H_2O.

The impedence device used to record mantle and branchial heart movements is reliable over a period of hours only as an indicator of frequency. The amplitude that it records varies with the distance apart of the electrodes and with the rate at which the gap between the electrodes is opening or closing. The device will show changes in the form of the heartbeat but is not adapted to give unequivocal information about the precise nature of these changes. Over a longer time scale there is an additional problem that the electrodes may work loose and/or damage the tissues in which they are embedded; the insulation may flake as it is fatigued by continuous movement, and so on. It is not always easy, and indeed sometimes not possible to distinguish changes brought about in these ways from changes due to alterations in the form of the heart or mantle beats, and in the account that follows no attempt has been made to do so; the device is used as an indicator only of when a beat takes place, and to measure beat frequency.
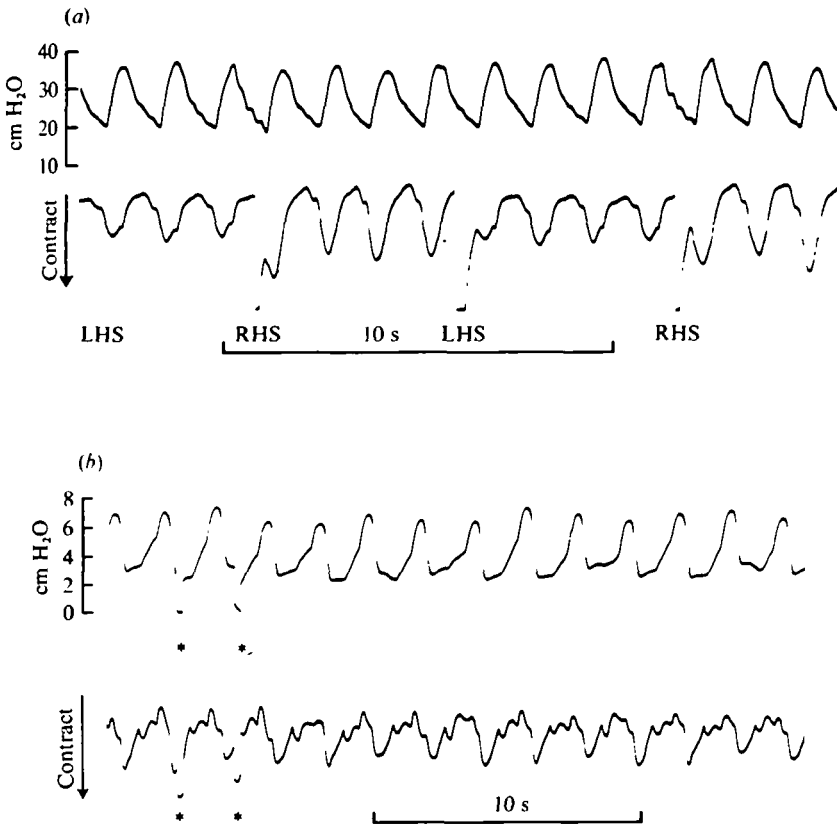
Fig. 1. (a) The aortic pressure pulse (upper trace) and branchial heart contractions (lower trace) from an octopus at rest (B32♂, 1030 g). Recording was switched from one heart to the other at the points indicated; the two hearts are plainly in phase with one another and with the systemic heart. (b) Shows the relationship between the branchial heartbeat, as recorded by the impedence unit, and pressure in the afferent branchial (C127♀, 1200 g). In this and in all subsequent records an upward deflection of the pressure trace indicates a rise in pressure. A downward deflection of the branchial heart (or mantle) record shows that the gap between the electrodes is closing; rapid contraction does not necessarily imply a rapid rise in pressure (see text). Deflections at points marked * here and in other records are produced by a manual override operating on both traces simultaneously, so that the timing of the two may be matched precisely. All traces read from left to right.

The relation between the aortic pulse, branchial heartbeats and respiratory movements

The appearance of the aortic pulse (Fig. 1 a) is very similar to that found in recordings from our own blood system. There is an abrupt rise and then a fall in pressure that is subdivided into two distinct phases. The rapid rise and fall, comprising approximately the first half of each cycle, presumably represents the systolic beat of the systemic heart up to the point when the valves into the aorta close. The slower decline found in the second half of the cycle shows the pressure drop as the blood is expelled from the elastic aorta.

Fig. 1 a shows (successively) the beats of the two branchial hearts recorded at the same time as the aortic pulse; the record was made by switching rapidly from one
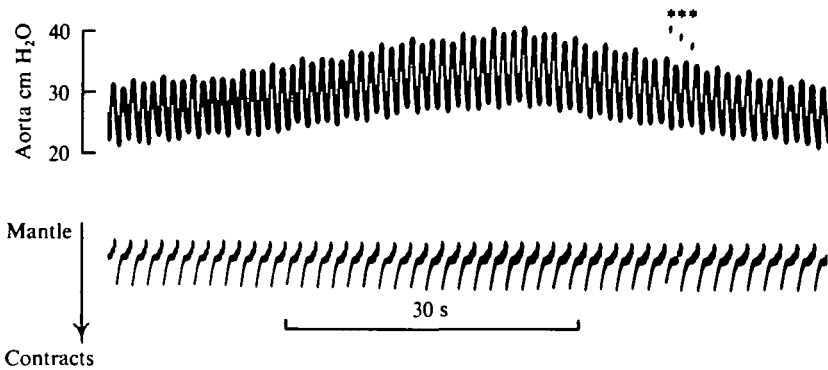
Fig. 2. The aortic pulse and mantle movements from an animal of 700 g (B22♀). In this instance the systemic heart was beating at 57 per min with respiration at 36. This trace illustrates an instance where there was a long slow fluctuation in blood pressure (the cycle was repeated many times) unaccompanied by any change in the respiratory rhythm and apparently in the absence of any external stimulus. ** Deflections for the synchronization of records (see Fig. 1).

pair of electrodes to the other. The two hearts beat at the same rate and show the same relationship to the aortic pulse.

The probable relationship between the branchial and the systemic heartbeat is revealed by the data illustrated in Fig. 1b. Here the pressure pulse in the afferent branchial is shown together with an electrical record made simultaneously from the corresponding branchial heart. The pressure pipeline (without the usual ⊥ piece) was threaded into the tip of the afferent branchial, the open end facing towards the branchial heart; ligatures holding the cannula in place would eliminate circulation from the distal quarter of the length of the gill, which tapers to a blunt point. The electrodes from the impedence unit were threaded across the heart, at right angles to the afferent branchial. They thus record longitudinal contraction of the heart, which will tend to be most rapid (giving maximum downward deflection of the record) while the heart is filling the thick-walled afferent branchial vessel and before the full resistence of this and the gill capillaries is felt. Maximum pressure is developed later in the cycle, while the heart muscle, though contracting strongly, is moving comparatively little. The pulse of blood to the gills is thus delivered about half a cycle before the corresponding aortic pulse appears.

The relationship between the gill hearts (which always contract simultaneously) and the systemic heart (which always contracts a little later than the branchials) is preserved over a wide range of pressure and frequency changes. It breaks down only under conditions of extreme oxygen depletion, or when the nervous connexions between the hearts are severed.

Fig. 2 shows the aortic pulse and the respiratory rhythm, recorded by electrodes threaded into the mantle just anterior to the gill on each side. Heartbeat is here (and nearly always, the exception again being the performance in low oxygen conditions) more rapid than the movements of the mantle (Table 1, see also Fig. 6). No simple arithmetic relationship between heartbeat frequency and respiratory movements was found.

Table 1

(Maximum, and typical resting values for F, systemic heart frequency; S, systolic pressure; D, diastolic pressure and R, respiratory frequency for a range of animals. S and D are rounded off to the nearest 5 cm H_2O. In this list animals with a prefix B were used in Banyuls at a temperature of 22 ± 1 °C, the rest were tested in Naples at 24.5 ± 1 °C. The last column indicates the conditions under which the maximum readings were obtained.)

Animal	Weight (g) and sex	Resting				Maxima				Conditions producing maxima
		F	S	D	R	F	S	D	R	
210	150♀	66	25	15	—	70	65	40	38	After exercise – chased for 15 s
613	165♀	61	30	10	30	66	55	30	—	After exercise – chased and handled for 15 s
547	280♀	67	40	20	51	70	65	30	48	Apparently at rest
543	310♀	52	40	20	32	66	85	50	40	After exercise (spontaneous movement)
546	350♀	48	40	15	35	65	75	25	34	Recovery from anaesthetic
630	430♀	47	40	15	40	57	65	30	39	After exercise – chased for 60 s
629	445♀	52	50	30	37	47	80	40	—	Recovery from anaesthetic
509	530♀	60	60	40	32	62	75	50	28	Recovery from anaesthetic
508	550♂	64	60	40	21	47	70	40	30	Apparently at rest
609	590♀	51	45	30	48	53	70	45	—	After exercise – chased for 10 s
599	640♀	43	40	15	35	53	85	40	32	Recovery from anaesthetic
560	700♂	46	45	20	42	69	100	55	—	After exercise – chased and handled for 120 s
574	760♀	42	35	25	—	43	60	30	35	Recovery from anaesthetic
B30	350♂	46	50	30	—	34	120	50	—	Return to water at 22 °C from 18 °C
B31	350♀	45	25	10	—	50	35	15	—	Both resting
B34	400♀	40	25	20	—	52	35	20	—	After exercise – chased for 10 s
B17	c500?	42	25	15	32	—	—	—	—	
B29	580♂	35	35	20	—	56	70	40	—	Apparently at rest
B1	600♀	50	35	15	28	46	75	50	—	Apparently at rest
B23	c600♂	50	35	25	—	45	60	35	30	Recovery from anaesthetic
B20	700♂	34	20	10	20	53	80	40	—	Transfer from 35% to 100% Satn. O_2
B22	700♀	50	25	15	—	50	60	40	21	Recovery from anaesthetic
B28	800♂	46	40	20	—	—	—	—	—	
B14	820♂	48	30	15	—	—	—	—	—	
B37	1010♂	42	40	20	—	43	60	30	—	After exercise – chased for 15 s
B32	1030♀	45	35	20	—	37	45	25	—	Apparently at rest
B39	1030♂	48	50	30	—	45	125	75	—	Recovery from anaesthetic
B40	c1200♀	37	40	30	—	36	60	40	—	After exercise – chased for 10 s
B3	1300♀	41	35	15	—	47	160	110	—	Recovery from anaesthetic

These results with *Octopus vulgaris* closely parallel those of Johansen & Martin (1962) for *O. dofleini*. They too found that the pulse in the afferent branchial precedes that in the aorta, by a period that ranges from one half to one complete beat cycle and that the respiratory rhythm is always slower than the heartbeat.

Recovery from anaesthesia and the blood pressure of animals at rest

Very high systolic pressures and large amplitude pulses occurred immediately after respiration returned during recovery from anaesthesia (Fig. 13, p. 102). The pattern was similar in octopuses anaesthetized in urethane and ethyl alcohol. Table 1 lists some further instances and other high values observed after periods of exercise or following a return to well-aerated water after a period in oxygen deficient conditions. Systolic pressures can reach 100+ cm of water with a pulse of more than 50 cm.

The records include several instances where a large rise in systolic pressure was not accompanied by any significant change in diastolic pressure. The aortic pressure rise in these instances must be due to an increase in the volume of blood delivered by the heart rather than to any increase in peripheral resistance (the same probably applied to the high pressures observed after exercise – see later – but here the matter is always complicated by an increase in peripheral resistance). Since the frequency in most cases remained close to the values observed in resting animals (and may even fall – animals such as 629 and B30 in Table 1) the very large increases in mean pressure and pulse amplitude found during recovery from anaesthesia (and by implication, elsewhere) must be due to substantial increases in the stroke volume of the individual heartbeats.

Typical frequencies associated with high blood pressures ranged from 45 to 60 beats per minute. Values obtained in Naples at 25 °C tended to be higher than those found in Banyuls at 22 °C.

The same octopuses at rest in their tanks (*ca.* 30 min after recovery from anaesthesia or between periods of exercise) showed a modest reduction in heartbeat frequency (range now typically 40–50 per min) but very considerable reductions in pulse amplitude and mean blood pressure. Typical systolic values ranged from 25–50 cm H_2O, with as little as 10 or 15 cm H_2O in diastole.

There was no obvious correlation between heartbeat frequency or blood pressure and size over the range considered (Table 1). The highest pressures recorded, 160 cm and 125 cm of water, were from large octopuses of 1300 g and 1030 g respectively; but an almost equally impressive value of 120 cm H_2O was recorded from an octopus of only 350 g and a spattering of other high values (noted as transients but not recorded and therefore omitted from Table 1) suggest that pressures well in excess of 100 cm H_2O can be generated by animals throughout the size range used. In general large animals seemed to show greater pressures and a slightly slower heartbeat at rest than small specimens at the same tank temperatures. But the effect is not well marked and difficult to quantify because it requires subjective estimates of when the animal is truly at rest. The resting values given in Table 1 are the lowest steady pressures observed during the first hour or so after the beginning of an experiment, while the animals were still clearly in good condition and subsequently able to raise much higher pressures in exercise.

Spontaneous fluctuations in blood pressure and cardiac arrest

It is difficult to establish resting pressure in *Octopus* because considerable variations seem to occur in the absence of any obvious stimulation. One such instance is illustrated in Fig. 2. Shorter cycles also occur (Fig. 3) and may continue with great
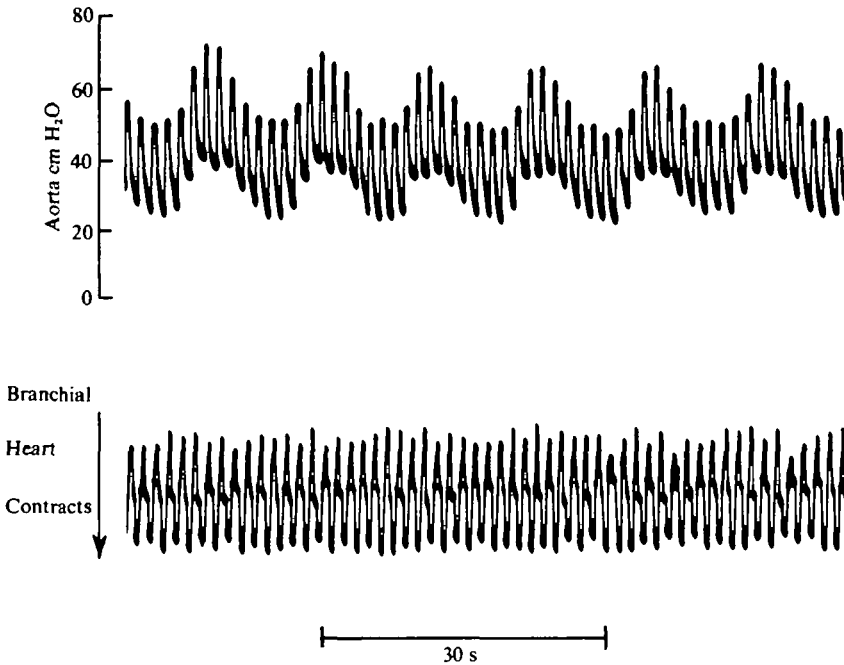
4

Fig. 3. A short term cyclic fluctuation in blood pressure in animal B29, a male of 580 g. The lower trace records the branchial heartbeat. Mean blood pressure is slowly falling after a period of exercise some 5′ before this record.
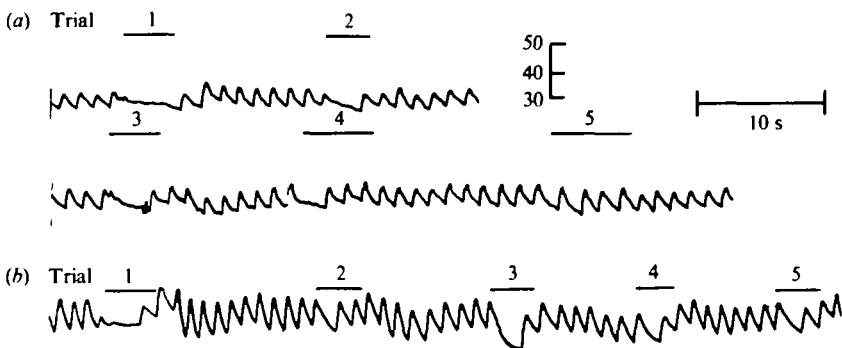

Fig. 4. Cardiac arrest and habituation to a repeated stimulus. Female 574 of 760 g. In (a) the octopus was startled by putting a hand into its tank; there was a break of 2 min between trials 2 and 3. In (b) the same octopus was shown a previously unseen 10 × 2 white perspex rectangle, presented on the end of a plastic rod by an observer who remained as far as possible out of sight of the animal. (The pressure scale in this series is half that in (a).)
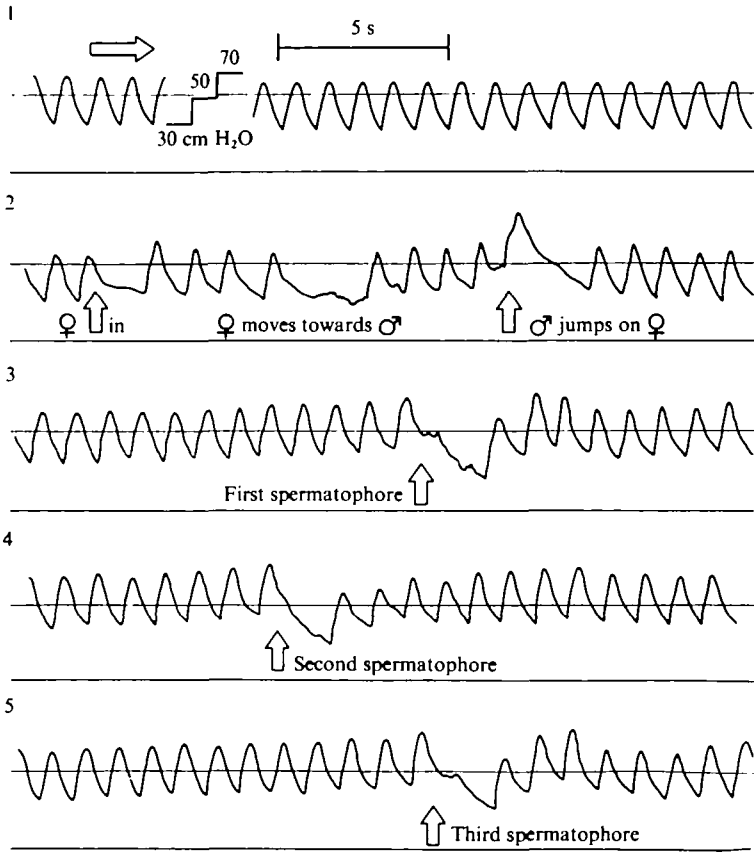
Fig. 5. Cardiac arrest and the sex life of *Octopus vulgaris*. This animal, (508) a male of 560 g, had a female introduced into his tank. His heart missed one beat then and two more as she moved towards him. Copulation followed, with further beats missed each time a spermatophore was passed from the mantle into the groove along the hectocotylized arm. There were no changes in beat frequency or mean blood pressure.

regularity for many min. Alternatively, or additionally, the mean blood pressure may rise and fall over periods that range from a few min to 1 h or more.

As well as varying in amplitude, the systemic heartbeat can cease altogether. Cardiac arrest can be induced by almost any sudden stimulus. The response habituates if the stimulus is repeated (Fig. 4).

Fig. 5 shows a sequence in which a male octopus heart missed a beat when a female was introduced into his tank. Copulation followed, with a further beat omitted at each ejaculation.

As well as these instances, where cardiac arrest is plainly the result of an external stimulus, one can observe cases where the heart stops beating, apparently in the absence of stimulation, while the animal is sitting quiet, breathing regularly and doing nothing obvious with its arms or body. These 'spontaneous' arrests usually last for a few seconds only in *Octopus vulgaris*. Johansen & Martin (1962) observed cardiac arrest in *O. dofleini* and reported that the systemic heart could stop for an hour or
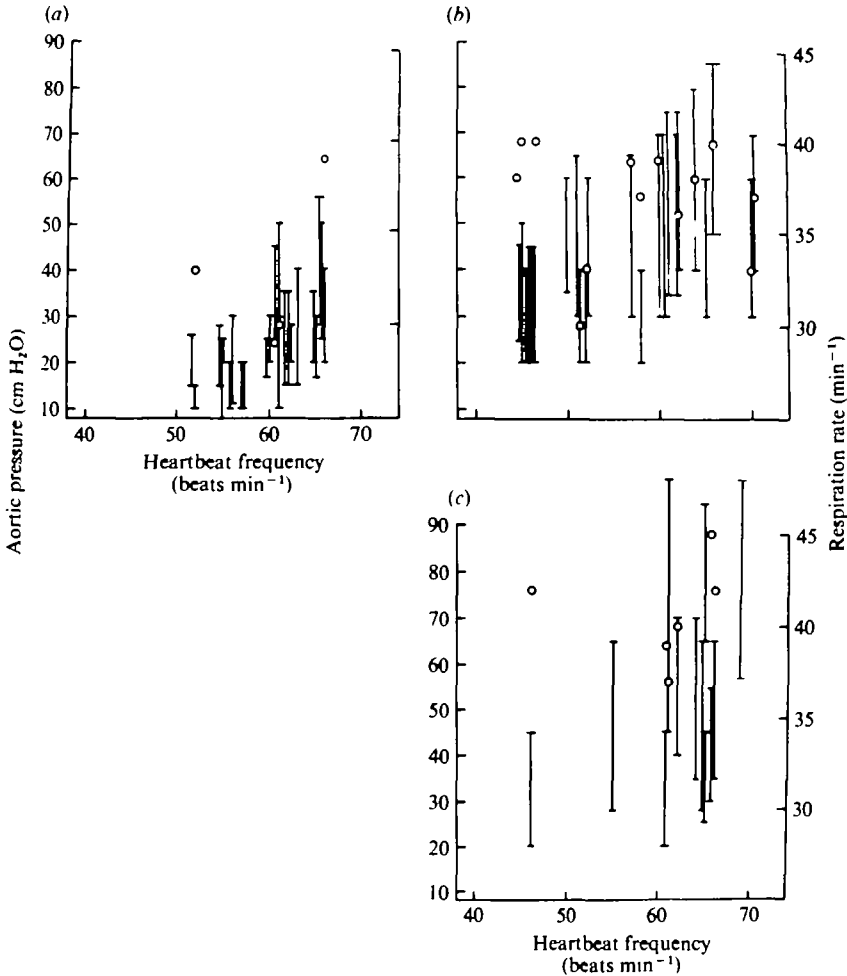
Fig. 6. Blood pressure, heartbeat frequency and respiration rate (o) from the three octopuses measured on a number of occasions after exercise and, with the individual at rest: (a) female of 165 g (613), (b) female of 310 g (543) and (c) male of 700 g (560). All records at 25 ± 1 °C. Each bar shows the pulse at the stated frequency. In general high pressures and large pulses are associated with high frequencies; there is no obvious correlation with respiratory frequency.

more without apparent ill effects, a sufficient circulation being maintained by the branchial hearts alone, which beat more vigorously than usual on these occasions.

The relation between beat frequency and blood pressure

By analogy with the system of regulatory reflexes in mammals one might have expected some fairly straightforward relationship between heartbeat frequency and blood pressure. In fact the relationship is complex. Fig. 6 shows the range of frequencies and pressures observed in 3 typical animals. In general high pressures and large pulses are associated with high frequencies of heartbeat. But there were also occasions when high pressure and/or large amplitude pulses were found at comparatively low frequencies (Fig. 6 and Table 1).
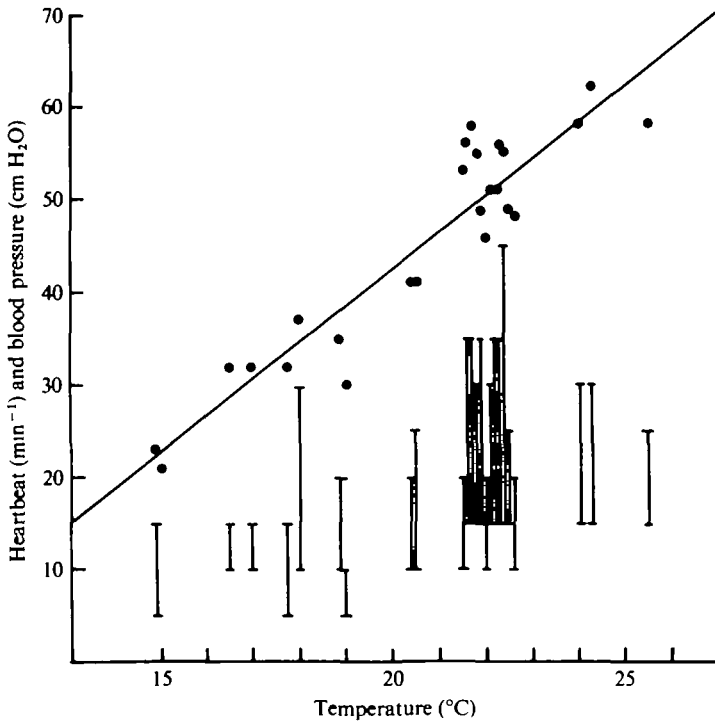
Fig. 7. Resting blood pressure, pulse and heartbeat frequency (●) in octopus B31, a female of 350 g. Trials at different temperatures were made in a random order with a reversion to 22 °C between each.

Temperature and heartbeat

At laboratory temperatures (i.e. 24 ± 2 °C in Naples and 22 ± 2 °C in Banyuls) heartbeat frequency was usually in the range 40–60 beats per min rising a little in exercise but in general varying far less than pulse amplitude or blood pressure. The frequency is, however, very dependent upon temperature and in the sea, where the water (particularly at depth) is generally colder than in the laboratory circulation, beat frequencies must be lower.

Fig. 7 shows a series of measurements made at Banyuls with a single individual of 350 g (B31♀). To obtain each reading the animal was moved out of its tank into a bucket (water level the same as in the home tank) and allowed to settle down for five min before a recording was made. It was then returned to the home tank, and the oxygen content of the water in the bucket checked; it never fell below 5·2 parts per million, a level at which it was unlikely to have a significant effect upon the heartbeat frequency (see below). The range of frequencies observed at 22 °C gives an idea of the variation that can be expected at any one temperature. With this amount of scatter it is impossible to be certain that the relation between temperature and heartbeat frequency is linear, as it appears to be from Fig. 7; it could equally well be geometric. The Q^{10} appears to be about 3. Fig. 8 shows some samples from this series of recordings.

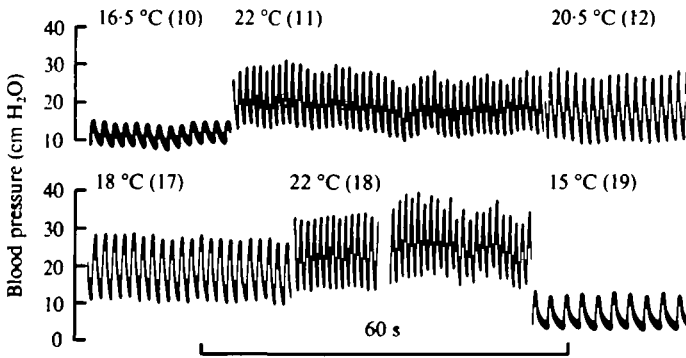The initial response to a change in temperature is very rapid. Fig. 9 shows a case

Fig. 8. Samples from aortic pulse records made with B31♀ (350 g) in the course of the series of transfers summarized in Fig. 7. Systemic heartbeat is very regular, at a different frequency for each temperature. Numbers in brackets (10) show the position in the testing sequence; each recording was made 5 min after transfer to water at the temperature specified.
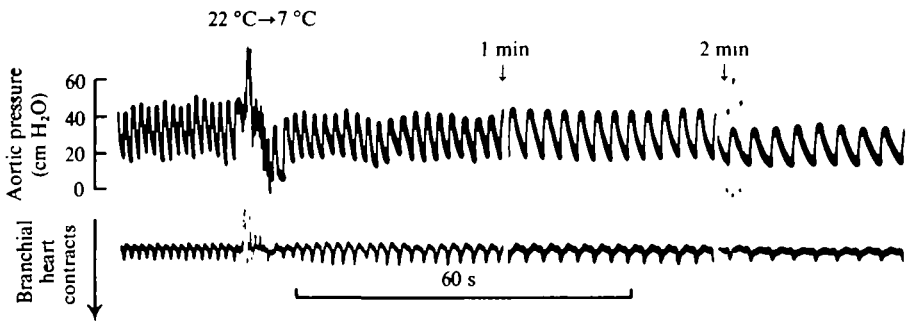

Fig. 9. Aortic pressure and branchial heartbeat following a transfer from water at 22 °C to 7 °C; octopus B30♂, 350 g. The trio of markers just after the 2 min break are to allow synchronization of the systemic and branchial heartbeat records. The two remain in phase throughout. (Interpretation of the branchial heartbeat record, see Fig. 1.)

where an octopus was transferred from 22 °C to 7 °C; the slowing of the heartbeat from 50 to about 30 beats per min was almost instantaneous. Thereafter the rate declined progressively so that by the end of 5 min it had fallen to 17 beats per min, at which level it appeared to have stablized. A constant rate is reached much more rapidly after less extreme changes in temperature.

Oxygen saturation and the heartbeat

Octopus cyanea can regulate its oxygen uptake over the whole of the range that it is likely to encounter in nature. Consumption in closed vessels remained steady at a rate varying as $Weight^{0.833}$ over the range 6·4 parts per million (saturated at 26 °C) down to 2 p.p.m. Below this oxygen consumption declined (Maginnis & Wells, 1969).

In the present series of experiments animals were kept in buckets of seawater (at room temperature) and allowed to deplete the oxygen, or they were transferred to buckets of water that they had already depleted. To demonstrate that the effects
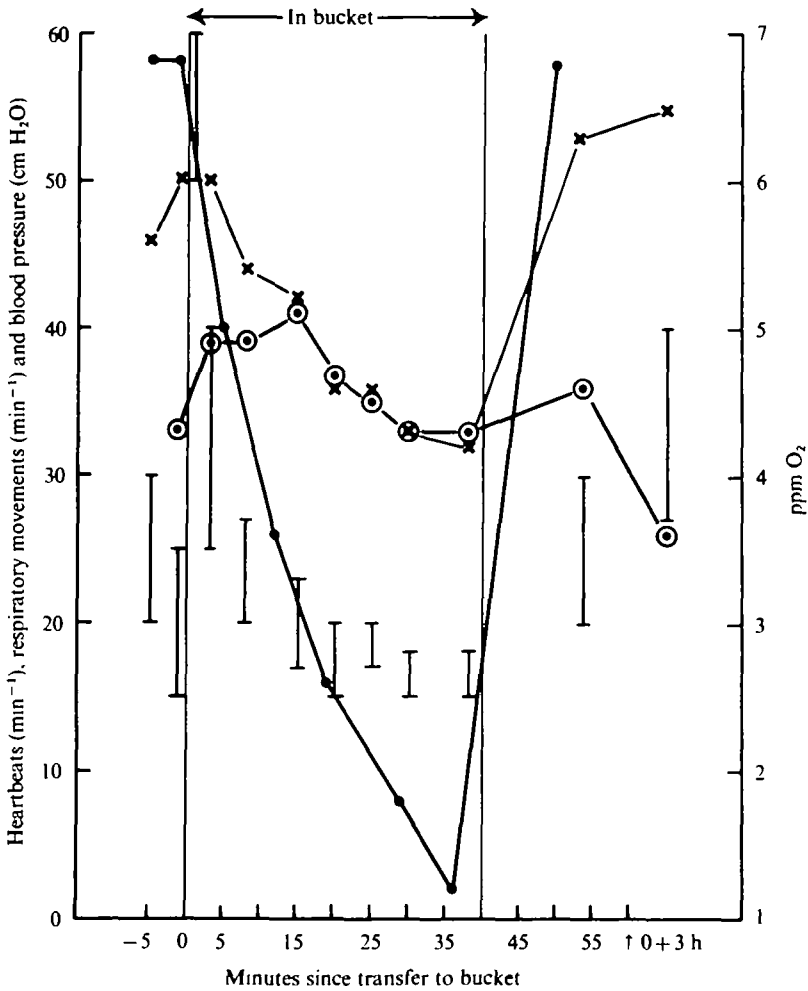
Fig. 10. Oxygen content of seawater (●) and the heartbeat of octopus B22♀ (700 g). The animal was transferred to a bucket (producing an initial sharp rise in blood pressure with little change in heartbeat frequency – ✕) and allowed to deplete the oxygen content of the water. At a little under 3 p.p.m. of O_2 the octopus became restive and tried to climb out. Its blood pressure and heartbeat frequency fell to levels where the pulse was probably driven by the respiratory movements – (⊙), which altered comparatively little in frequency throughout the experiment. After 40 min the bucket was gently tipped onto its side, allowing fresh seawater to enter.

shown were truly due to oxygen lack rather than the accumulation of CO_2 or other metabolites, some experiments were run in seawater where the gases had been driven off by boiling. No differences were found in the two series. Oxygen tensions were measured using an E.I.L. model 15A dissolved oxygen meter.

Octopus vulgaris for the most part sat quiet until the oxygen content in the bucket fell to between 2 and 3 p.p.m. At this stage the animals became restless and tried to climb out.

As the oxygen tension fell, the heartbeat slowed and the pulse amplitude declined. Blood pressure dropped progressively. At 2·5 p.p.m. or thereabouts, at just about the
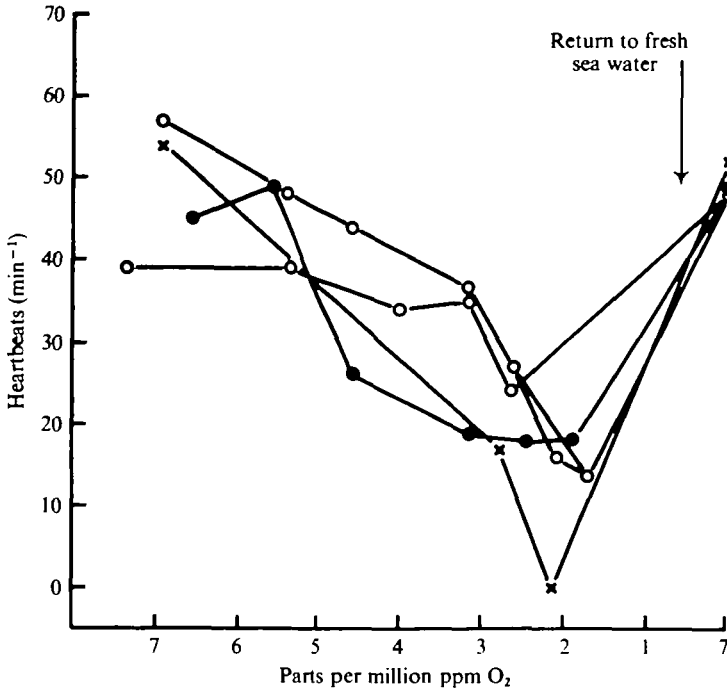
Fig. 11. Oxygen tension and heartbeat; a summary of four further experiments of the type detailed in Fig. 10. O – from B1♀ (600 g; two experiments a.m. and p.m. of the same day). X – from B3 (1300 g ♀) and ● – from B9 c. 800 g, sex not recorded.
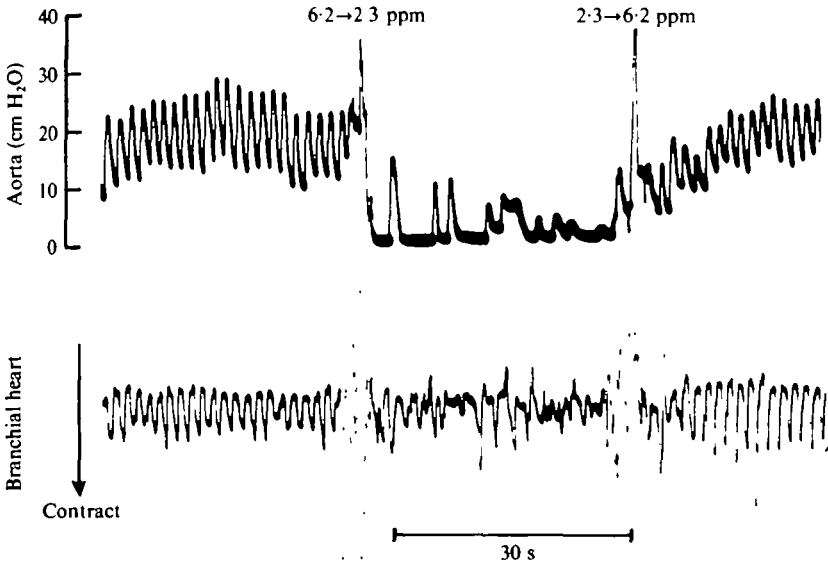

Fig. 12. Transfers from water of high to low oxygen content (6·2 and 2·3 p.p.m.) and return. Octopus B17 (c. 500 g, sex not recorded). The record here ran continuously; the lower trace shows the beat of a branchial heart. At 2·3 p.p.m. the heartbeat rapidly becomes disorganized; regular beats begin again as soon as the octopus is returned to water with a normal O_2 content.

stage at which the animals began to show signs of distress, the heart sometimes stopped altogether; pressure recordings showed only a feeble pulse in phase with the respiratory movements and possibly attributable to these (Figs. 10 and 11). Respiratory movements continued steadily after the heart had stopped; they probably increased in amplitude, drawing more water in to the mantle and across the gills at each stroke (Winterstein, 1925).

Cardiac arrest produced in this manner is reversible and, as with the effect of changing the temperature, the alteration in heart rate is very rapid (Fig. 12). In a later report, in which the effect of interference with the nervous control of the heartbeat are examined, it will be shown that both seem to be direct effects upon the performance of the branchial heart musculature.

The effects of exercise

Johansen & Martin (1962) showed that exercise increased both pressure and frequency in *O. dofleini*. When the animal moved slowly down its tank the systolic pressure (measured, as here, from a cannula in the aorta) rose from 50 to 70 cm (diastolic 40 to 60) and the heart beat rate rose from 6 to 8 per min. Even very modest exertion had prolonged effects on the pulse which took from 10 to 15 min to return to its resting value after 3 min of gentle exercise.

It is difficult to evaluate recordings made from octopuses moving about their aquaria, whether 'spontaneously' or in provoked exercise. *Octopus vulgaris*, at least, moves about very little (and then mostly at night) once it has settled down in an aquarium, and an immature animal that is restlessly moving about is exceptional. On the other hand, animals provoked into exercise are also suspect, because their heartbeats may be affected by 'psychological' effects which could vary with the previous experience of the individual concerned – an octopus that has already spent a period in the aquarium may even choose to approach the hand that feeds it, rather than running away. And we know that spontaneous fluctuations in pulse amplitude can occur in the apparent absence of disturbance, so that it is never entirely certain that any observed effect is attributable to the effects of exercise *per se*.

Despite these uncertainties about the causes of changes in any single instance certain generalizations about the effects of exercise can be made on a basis of the 40 or so records now available for *O. vulgaris*.

These are: 1. Exercise, even gentle exercise (an unhurried walk down a 1 m tank or a chase lasting for as little as 10 s) is always associated with a rise in blood pressure and pulse amplitude. Both of these commonly rise by as much as 100%.

2. Exercise is usually, but by no means always, associated with a rise in heartbeat frequency. Exceptionally this may rise by as much as 50% but the increase is usually much more modest and it is often negligible. Any substantial increase in the volume of blood moved must be achieved by an increase in the stroke volumes of the hearts.

3. Records made within a minute or so of the end even of short (10–15 s) periods of vigorous movement nearly all show continued elevated blood pressures and a greatly increased pulse. Often the effects seem to last much longer than this. Since the animals have by now come to rest, it seems unlikely that 'psychological' factors still dominate the performance of the hearts (if indeed they ever did so). The continued
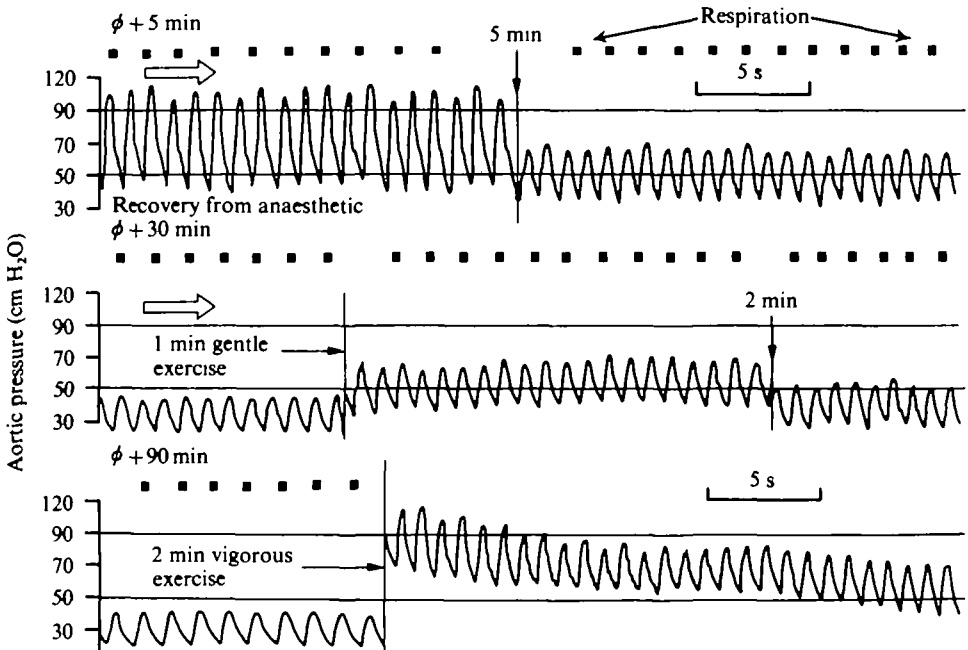
Fig. 13. Recovery from anaesthetic, resting pulse and the effect of exercise in animal 560, 700 g ♂. Runs (0+ 5 min, etc.) are timed from the moment when respiration began in recovery from the anaesthetic (in this case 3 % urethane). At the first exercise period the octopus was touched and it then moved slowly once up and down its tank, a total distance of about 1·5 m. On the second the animal was handled, struggled to escape and swam away, blowing jets of ink. On this occasion the heartbeat frequency and pulse amplitude was still dropping towards the pre-exercise level 15 min after the event.

elevation of pulse and pressure presumably relates to the need to disperse metabolites. The most obvious possibility (which is indicated by the very similar effects of returning the animals to fresh seawater after a period in low oxygen conditions) is that *Octopus* begins to accumulate an oxygen debt as soon as it moves at all rapidly.

Oxygen consumption and cardiac output

The resting oxygen consumption was measured at 21 ± 2 °C for nine animals ranging in weight from 230 to 760 g. For each series of measurements an octopus was placed in a 15 l aquarium filled with water to the level of a tight-fitting lid and supplied with a brisk circulation. When the animal had settled down quietly in one corner of the tank the circulation was shut off and the oxygen content of the water measured (E.I.L. Model 15A dissolved oxygen meter) at intervals during the next 30 to 60 min, depending upon the size of the animal. The seawater was always saturated and sometimes super-saturated at the beginning of an experimental run, and it was never allowed to fall below 4·5 p.p.m., a level well above that at which octopuses begin to show signs of respiratory distress; plots of oxygen consumption against time all yielded straight lines, indicating that *O. vulgaris* (like *O. cyanea*, Maginnis & Wells, 1969) is capable of regulating its oxygen uptake over the whole of the range in question.

The results obtained are summarized in Table 2; an octopus of 500 g may be ex-◀

Table 2. *Oxygen consumption of* Octopus vulgaris *at rest*

Animal	Weight	Temperature	O_2 consumption (ml g^{-1} h^{-1})
C89	220	21·6	0·071
C87	230	21·5	0·073
(Same day)	230	21·5	0·094
(19 days later)	280	19·8	0·074
C119	250	20·7	0·108
C77	290	21·6	0·060
C124	300	20·2	0·073
C107	460	21·6	0·082
C45	490	21·4	0·084
C17	640	20·0	0·077
C30	710	21·0	0·092

Oxygen consumption was measured over periods of 30–90 min in a closed 15 l aquarium. Each animal was allowed to settle down for at least one h before the circulation was turned off and records of the oxygen consumption began. In every case the animal remained sitting quietly in a darkened corner of the tank throughout the measured period. The oxygen content was never allowed to fall below 4·5 p.p.m. which is well above the level (about 2·5 p.p.m.) at which the animals show any signs of respiratory distress.

pected to consume about 0·08 ml O_2 h when at rest at 22 °C. This is close to the value given by Montuori (1913) for the larger of the two *O. vulgaris* that he tested at 24 °C, and rather less than the 0·09 ml/g/h found in *O. cyanea* at 25–28 °C (Maginnis & Wells, 1969).

Once the oxygen consumption is known, the cardiac output can be calculated provided the amount of oxygen extracted from the blood as it passes through the tissues is also known.

The oxygen capacity of *Octopus vulgaris* blood has been measured a number of times (references, see Redfield, 1934) with results that range from 3 to about 5 vols %. Differences between arterial and venous blood have not been monitored as frequently and the most recent and numerous (and probably the most accurate) measurements have been made with *O. dofleini*, not *O. vulgaris*. Johansen (1965) found between 3·2 and 4·3 (exceptionally 1·8) O_2 vols % in blood from the dorsal (cephalic) aortae of 15 *O. dofleini*, with corresponding values of 0·7–0·8 vols % in the venous return.

If one accepts 3 vols % as a likely figure for the delivery of oxygen to the tissues during one circuit of the blood, the cardiac output from a resting *Octopus vulgaris* of 500 g, consuming 0·08 ml g^{-1} h^{-1} would be about 22 ml min^{-1}. At a frequency of 45 beats per min, this gives a stroke volume of 0·49 ml per beat.

DISCUSSION

There are only three ways in which the circulatory system of an animal can meet a substantial increase in oxygen demand. These are 1. Increasing the heartbeat frequency. 2. Increasing the stroke volume of each beat (s.v. increase). 3. Increasing the oxygen utilization as the blood circulates around the body so that the venous return is more depleted of oxygen than before (a.v. difference increase). Additionally and exceptionally (in birds, for example, see Jones & Johansen, 1972) increased ventilation may allow the animal to raise its arterial blood O_2 saturation a little.

Octopus vulgaris shows no substantial increase in heartbeat frequency above resting levels when stressed by exercise, or in recovery from anaesthetic or low oxygen conditions; indeed the frequency may even drop in these circumstances (Table 1). With an oxygen carrying capacity of less than 5 vols %, there is little scope for an increase in the a.v. difference (and the only available measurements, from *O. dofleini*, show no measurable difference, Johansen, 1965). This leaves an increase in stroke volume as the only means by which the animal could substantially increase oxygen delivery to the tissues. *In vitro* the systemic heart can show up to a three-fold increase in stroke volume (P. Smith, pers. comm.). This would limit the animal to a sustainable oxygen consumption of only three times the resting value, a metabolic scope that compares poorly with that of fish, such as salmonids, which can step up the oxygen consumption by four or five times. Even so, salmonids readily run up a long-lasting (several hours) oxygen debt (Brett, 1972). It would seem inevitable that *Octopus* with its even more limited metabolic scope must begin to accumulate an oxygen debt as soon as it starts to move around at all actively, a conclusion that is consistent with the prolonged increase in pulse amplitude that follows even very short periods of enforced exercise.

REFERENCES

BRETT, J. R. (1972). The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. *Respiratory Physiol.* **14**, 151–170.

FREDERICQ, H. (1914). Recherches expérimentales sur la physiologie cardiaque d'*Octopus vulgaris*. *Arch. int. Physiol.* **14**, 126–151.

FROESCH, D. & MANGOLD, K. (1976). On the structure and function of a neurohemal organ in the eye cavity of *Eledone cirrosa* (Cephalopoda). *Brain Res.* **111**, 287–293.

JOHANSEN, K. (1965). Cardiac output in the large Cephalopod *O. dofleini*. *J. exp. Biol.* **42**, 475–480.

JOHANSEN, K. & HUSTON, M. J. (1962). Effects of some drugs on the circulatory system in the intact non-anaesthetised cephalopod *Octopus dofleini*. *Comp. Biochem. Physiol.* **5** 177–184.

JOHANSEN, K. & MARTIN, A. W. (1962). Circulation in the cephalopod, *Octopus dofleini*. *Comp. Biochem. Physiol.* **5**, 161–176.

JONES, D. R. & JOHANSEN, K. (1972). The blood vascular system of birds. In *Avian Biology*, vol. 2, ch. 4 (ed. D. S. Farner and J. R. King), pp. 158–285. New York: Academic Press.

KRIJGSMAN, B. J. & DIVARIS, G. A. (1955). Contractile and pacemaker mechanisms of the heart of molluscs. *Biol. Rev.* **30**, 1–39.

MAGINNISS, L. A. & WELLS, M. J. (1969). The oxygen consumption of *Octopus cyanea*. *J. exp. Biol.* **51**, 607–613.

MONTUORI, A. (1913). Les processus oxydatifs chez les animaux marins en rapport avec la loi de superficie. *Arch. ital. Biol.*, **59**, 213–214.

RANSOM, W. B. (1884). On the cardiac rhythm of invertebrates. *J. Physiol.* **5**, 261–341.

REDFIELD, A. C. (1934). The Haemocyanins. *Biol. Rev.* **9**, 269–275.

SMITH, L. S. (1962). The role of venous peristalsis in the arm circulation of *Octopus dofleini*. *Comp. Biochem. Physiol.* **7**, 269–275.

VAN HEUKELEM, W. F. (1973). Growth and lifespan of *Octopus cyanea*. (Mollusca: Cephalopoda). *J. zool. Lond.* **169**, 299–315.

WINTERSTEIN, H. (1925). Uber die chemische Regulierung der Atmung bei dem Cephalopden. *Z. vergl. Physiol.* **2**, 315–328.