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CARDIAC OUTPUT IN THE LARGE CEPHALOPOD *OCTOPUS DOFLEINI**

BY KJELL JOHANSEN
From Department of Zoology, University of Washington, Seattle 5, *Washington, U.S.A.*

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The high level of structural organization displayed by the cardiovascular system of cephalopods promises a similar complexity in its functional organization. In spite of an extensive literature on this subject most of the work is old and inadequate in techniques and experimental procedures (Fuchs, 1895; Fredericq, 1914). The only physiological parameters hitherto recorded of any value for the evaluation of cardiovascular dynamics have been arterial and venous blood pressures (Johansen & Martin, 1962).

The present paper attempts to describe measurements of the cardiac output making use of the Fick principle. Simultaneous measurements of blood pressure and analyses of blood gases provide data for calculation of stroke volume and stroke work as well as oxygen saturation of arterial and venous blood.

MATERIALS, METHODS AND EXPERIMENTAL PROCEDURES

The species used for the experiments was *Octopus dofleini*. The species is one of the larger living cephalopods reaching weights up to 50 kg. It is distributed along the Asian coast, extending over to the Gulf of Alaska and down the Pacific coast of North America to California.

The animals used were obtained from the waters of Puget Sound and brought to the laboratory in Seattle in plastic bags cooled down in crushed ice. Upon arrival they were transferred to aquaria connected to a recirculating sea-water system. The sea water was kept at 7–9° C. and constantly aerated. The animals used ranged in weight from 5·4 to 15·2 kg.

In preparation for an experiment the animal was transferred to an operating tank filled with cold sea water. It was anaesthetized by adding ethyl alcohol to the water. Details of the method of anaesthesia are described by Johansen & Martin (1962).

After induction of anaesthesia the following operative procedures were performed. The cephalic aorta was cannulated by an incision in the midline of the body wall on the dorsal side. This area can be reached from the upper margin of the mantle opening without cutting through the mantle wall. In cutting through the body wall one will invariably rupture the wall of a large abdominal blood sinus. Care was exercised to make a small incision and to suture the sinus wall and body wall after cannulation, thereby preventing post-operative bleeding. Polyethylene catheters, P.E. 50, were used for cannulation. The catheter was passed in through a small

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incision in the vessel wall in the upstream direction. A ligature was placed around the catheter and the cut tissue edge in the vessel wall, tying these closely together. The size of the catheter was small enough not to cause any obstruction of normal blood flow. The large vena cava cephalica was cannulated slightly proximal to the anus in a similar way. The lengths of the two catheters were adjusted to allow undisturbed swimming movements after the animal was transferred back to the aquarium. Arterial and venous blood could now be drawn simultaneously and pressures could be recorded continuously through the same catheters with the use of Statham pressure transducers

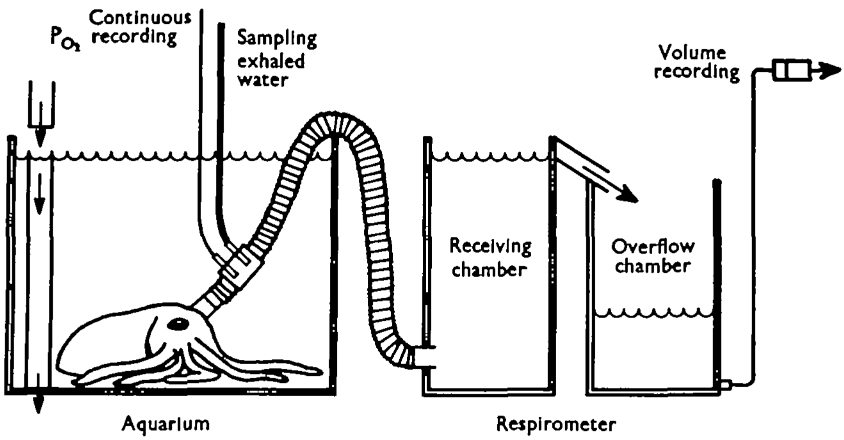

Fig. 1. The animal connected to the respirometer. The receiving chamber is connected to the octopus via a flexible hose. A plastic holder for mounting the polarographic oxygen electrodes and tubes for water sampling are shunted into the connecting hose. The overflow chamber receives the expired water, whose volume is recorded continuously.

and a system of amplifiers and a recorder. The respiratory exchange was measured according to the method described by Johansen (1965). With the use of a respirometer (Fig. 1) the volume of the exhalant water current could be measured. The oxygen tension in the inhaled and exhaled water as well as in arterial and venous blood was also measured with a Beckman model 160 polarographic oxygen analyser. The oxygen content of the same samples was analysed manometrically according to the method of Scholander & Van Dam (1956) with slight modifications. The oxygen capacity of blood samples from all the experimental animals was measured using the same method after equilibrating the blood to air in a temperature controlled tonometer. The pH of the blood and tank water was measured with a microelectrode. The haemocyanin content was derived from measurement of the refractive index. Haemocyanin is known to be the only protein in significant concentration in octopus blood.

The measured quantities listed above permitted calculations of the oxygen consumption and cardiac output of the animals. The values of blood pressure and heart rate further gave values of stroke volume and stroke work.

It should be emphasized that all the measured parameters were obtained from unrestrained animals free to swim and move about in large tanks after complete recovery from anaesthesia.

RESULTS AND COMMENTS

The data obtained, and the parameters computed from these, are assembled in Table 1. The arterial oxygen tension varied from 45 mm Hg in animal 3 to 94 mm Hg in animal 10. Most animals fell, however, in the range between 60 and 80 mm Hg. Animal 3 had the mantle nerve severed on one side and was totally paralysed on that side. The results from this specimen are included in an attempt to evaluate how such an injury interferes with the cardiovascular function. The oxygen pressure for half-saturation in *O. dofleini* is around 10–15 mm Hg and fairly high in comparison with earlier reported values from other species of Octopodidae (Wolvekamp, Baerends, Kok & Mammaerts, 1942). The arterial oxygen content ranged between 3·2 and 4·3 vol. % in the healthy animals. The oxygen pressure and content in central venous blood drawn from the vena cava cephalica were less variable and ranged between 8 and 12 mm Hg, the oxygen content being 0·7 or 0·8 vol. %. Animal 15 deviates in this last respect with 0·3 vol. % oxygen in the venous blood. The oxygen capacity was measured on freshly drawn blood with air bubbling through it. It ranged from 3·5 to 4·9 vol. %. This will give oxygen saturation levels in arterial blood ranging from 80 to 100% in healthy animals, whereas the venous oxygen saturation ranged from 16 to 26%.

The values obtained for oxygen capacity compare well with values reported by Redfield (1934), by Winterstein (1909) and by Wolvekamp (1938) for other cephalopods.

The haemocyanin content in g./100 ml. of blood ranged from 8·0 to 12·6 g./100 ml. It was surprising to find several inconsistencies in the expected correlation between the oxygen capacity and the haemocyanin content (animals 10 and 15). Earlier reports emphasize a significant Bohr effect in cephalopods (Redfield & Goodking, 1929). Differences in the acidity of the blood may well explain the discrepancies between oxygen capacity and haemocyanin content in the present study. The haemocyanin content in *O. dofleini* seems to be somewhat higher than that reported earlier for other species of cephalopods (Winterstein, 1909; Redfield, Coolidge & Hurd, 1926).

The relatively large variations in oxygen consumption obtained in the present experiments are reflected in similar variations in the other computed parameters. The state of activity of the animals was impossible to standardize and great variations in this were abundantly obvious; for example, animal 6 was conspicuously active and alert with vigorous breathing movements and a high blood pressure.

Cardiac output was calculated using the Fick principle. The values obtained are listed in the table as ml./min. and ml./kg. animal/min. The output in resting healthy animals averaged around 10 ml./kg./min.

There is only one earlier reference to a measurement of cardiac output in a cephalopod. Chapman & Martin (1957) studied the weight/metabolism relationship in *O. hongkongensis*.* They report one computation where cardiac minute volume was found to be 320 ml. in an 18 kg. specimen. This compares well with values obtained in the present paper. Johansen (1962) studying cardiac output in a teleost fish, also arrived at values in the same range as for *O. dofleini*. In spite of difficulties in grading the state of activity in the animals there seemed to be a tendency towards an increased

* This is the same species as *Octopus dofleini*. The name *O. dofleini* is correct and should be used in future reference.

Table 1*

Animal no.	Weight (kg.)	Arterial oxygen (mm Hg)	Arterial oxygen (vol. %)	Venous oxygen (mm Hg)	Venous oxygen (vol. %)	Oxygen capacity (vol. %)	Venous oxygen satura- (%)	Arterial oxygen saturation (%)	Haemo- cyanin (g./100 ml.)	O_2 consump- tion (ml./hr.)	Cardiac output (ml./ min.)	Cardiac output (ml./kg./ min.)	Blood pressure (mm Hg)	Heart rate (per min.)	Stroke volume (ml.)	Stroke work (g./m.)
1	7·6	57	3·2	8	0·8	4·0	20	80	10·7	225	156	20·5	25/15	23	6·3	1·7
2	8·7	75	4·3	11	0·7	4·3	16	100	10·7	191	88	10·1	60/32	16	5·5	3·4
3	5·4	45	2·5	10	0·7	4·5	15	55	10·3	39	36	6·7	80/60	16	2·2	2·1
4	8·7	78	3·7	8	0·8	4·0	20	92	10·9	100	57	6·6	40/24	16	3·6	1·5
5	8·9	75	3·5	12	0·8	4·0	20	88	10·7	300	185	20·8	60/26	16	11·5	6·7
6	9·0	90	3·8	12	0·8	3·8	21	100	10·0	523	290	32·2	78/64	16	18·1	17·0
7	10·9	39	1·8	10	0·7	2·8	25	64	9·0	128	195	17·8	43/31	16	12·1	6·0
8	15·2	71	3·6	10	0·7	3·6	19	100	10·6	369	212	13·8	—	—	—	—
9	8·1	70	4·0	11	0·8	4·0	20	100	12·6	302	157	19·3	25/20	16	9·8	2·9
10	9·5	94	3·4	12	0·7	3·5	20	97	12·6	265	164	17·3	80/62	18	9·1	8·7
11	9·8	72	2·8	8	0·8	3·0	27	93	8·0	121	100	10·2	58/40	16	6·3	4·2
12	11·0	78	4·0	10	0·8	4·9	16	82	11·2	106	55	5·0	—	—	—	—
13	9·1	60	4·0	7	0·7	4·3	16	93	12·6	188	95	10·4	—	—	—	—
14	10·0	50	3·2	—	—	3·4	—	94	10·0	177	—	—	—	—	—	—
15	11·3	65	3·7	2	0·3	3·7	8	100	11·0	225	110	9·7	—	—	—	—

* The following are comments upon the general status of the various experimental animals:

(1) slightly injured;
(2) healthy resting;
(3) left side of animal was paralysed due to nerve injury;
(4) poor recovery from anaesthesia;
(5) healthy, active;
(6) healthy, very active;
(7) healthy, active;
(8) healthy, moderately active;
(9) healthy, moderately active;
(10) healthy, moderately active;
(11) bleeding slightly, resting;
(12) injured mantle;
(13) healthy;
(14) healthy;
(15) healthy.

cardiac output in association with exercise and particularly in the post-exercise period. Animal 6 was a striking example in this regard. The measurements were taken after more than 10 min. of vigorous swimming back and forth in the tank. Both the oxygen consumption and the cardiac output were more than doubled compared to the average for the other animals. The high level of activity is also reflected in a high blood pressure. On the other hand the heart rate showed a value of 16 beats per minute which was the average value for all the animals regardless of size and state of activity. In consequence animal 6 had a very high stroke volume of 33 ml. and also a very high stroke work calculated in gram.metres. The stroke work was also high in animal 10 which was also very active. In this animal the cardiac output was only moderately increased but a marked increase was apparent in the arterial blood pressure. In the partially paralysed animal 3 the blood pressure was high, probably in compensation for the very low oxygen saturation of the arterial blood. Animal 11 was similarly weak from bleeding, with a low haemocyanin content. The cardiac output and stroke volume were both below average in this animal.

There was no apparent relationship between weight and oxygen consumption or between weight and cardiac output. It seems reasonable to assume that any such relationship would be obscured by the different levels of activity displayed by the animals.

A more comprehensive discussion of the results so far obtained must await the results from similar investigations in the future.

SUMMARY

The cardiac output in *Octopus dofleini* has been measured, making use of the Fick principle.

The measurements were made on intact animals, resting or free-swimming, after previous chronic implantation of intravascular catheters for collection of blood samples.

The respiratory exchange was measured with a specially designed respirometer.

In addition to cardiac output the following parameters were measured or computed: oxygen consumption; oxygen tension, oxygen content and percentage saturation of venous and arterial blood; arterial pressure; heart rate; stroke volume and stroke work.

A detailed discussion of the results obtained is limited by the lack of comparable information for other invertebrates.

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