

THE RESPIRATORY RESPONSES OF *CARCINUS MAENAS* TO DECLINING OXYGEN TENSION

BY A. C. TAYLOR*

*Department of Marine Biology, University of Liverpool,
Port Erin, Isle of Man*

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SUMMARY

The degree of respiratory independence shown by *Carcinus* under conditions of declining oxygen tension is dependent on the animal's level of activity. Inactive *Carcinus* are capable of maintaining respiratory independence down to a P_{O_2} of 60-80 mmHg. This is achieved primarily by an increase in ventilation volume such that the amount of oxygen made available at the respiratory surfaces remains constant over a wide range of oxygen tension. The P_{O_2} at which this can no longer be maintained corresponds closely to the P_{O_2} at which respiratory independence is lost.

Under normoxic conditions the P_{O_2} of the post- and prebranchial blood was 97 and 18 mmHg respectively. At the high oxygen tensions prevailing in the postbranchial blood the respiratory pigment is fully saturated. Under conditions of declining oxygen tension the heart rate remains more or less constant until the P_{O_2} reaches 60-80 mmHg, the onset of bradycardia coinciding with the loss of saturation of the haemocyanin. Although cardiac output falls during hypoxia, the capacity rate ratio remains approximately constant, which enables the effectiveness of oxygen uptake by the blood to remain at a high level.

INTRODUCTION

Although the respiratory responses of *Carcinus* to hypoxia have been investigated by several workers (Arudpragasam & Naylor, 1964a; Scammell, 1971; Taylor, Butler & Sherlock, 1973), these studies have not produced a detailed analysis of respiration in *Carcinus* comparable to that by Johansen, Lenfant & Mecklenburg (1970) on *Cancer magister*. The present investigation was therefore undertaken to re-examine the cardiac and respiratory responses of *Carcinus* to hypoxia, and to extend our understanding of respiration in this species. An integral part of this study was the determination of the oxygen tensions prevailing in the pre- and postbranchial blood; this has enabled calculations to be made of cardiac output and other respiratory parameters not previously recorded for *Carcinus*.

* Present address: University Marine Biological Station, Millport, Isle of Cumbrae, Scotland KA28 0EG

MATERIALS AND METHODS

The present study was carried out between May and September on male *Carcinus maenas* (L.) weighing between 60 and 80 g. All animals were kept in the dark in constant temperature rooms for at least 14 days before the experiments were carried out to acclimatize them to the experimental temperature of 15 °C and to eliminate any interference of rhythmic changes in oxygen consumption ($\dot{V}O_2$) on the results obtained. Preliminary recordings of oxygen consumption at reduced oxygen tension were carried out using a perspex closed system respirometer, in which the animals were acclimatized overnight in flowing sea water. Recordings were carried out at different ambient oxygen tensions by replacing the water within the respirometer with water which had been reduced to the required P_{O_2} by bubbling nitrogen through it.

Further studies of the respiratory responses of *Carcinus* to hypoxia were made using a modified version of the apparatus used by Arudpragasam & Naylor (1964*a*) (Fig. 1). This method permitted the simultaneous recording of ventilation volume, oxygen utilization and oxygen consumption, as well as heart rate and scaphognathite rate. The exhalant water from the crab was collected by a hood constructed from a balloon placed over the anterior part of the animal, with a plastic mask fitted beneath to avoid impaired movement of the eyes, antennae and mouthparts. The balloon was attached to the carapace with Eastman 910 adhesive, and areas of possible leakage around the edges sealed with dental wax (Metrodent).

Since Johansen *et al.* (1970) have shown that ventilation may be sensitive to alterations in the resistance to water flow, the internal diameter of the tube leading away from the mask was kept fairly large (12 mm). The end of the balloon covering this tube was attached to another tube connecting the animal compartment to the overflow chamber. Water pumped by the crab entered the second chamber and overflowed down a narrow tube into a collecting vessel, into which three carbon electrodes, two long and one short, were suspended. As the water level rose, contact was made between the short electrode and one of the long ones, which activated a transistorized relay causing a small electric pump to operate, which pumped the water back into the circulation system until contact was broken between the two long electrodes. In this way a constant volume of water (70 ml) was pumped for each operation of the relay, and this was recorded on a chart recorder.

The P_{O_2} of the inhalant and exhalant water was monitored alternately by slowly siphoning the water past an oxygen electrode (Radiometer E5046) contained within a thermostatted cell and connected to a Radiometer pH meter and chart recorder (Smith's Servoscribe). The oxygen tension of the circulating water was maintained at the required level by bubbling nitrogen through the water contained within the reservoir tank.

Heart rates were recorded using an Impedance Pneumograph (Narco Bio-systems Inc.) connected to a Physiograph pen recorder with fine silver wire electrodes inserted through the carapace on either side of the heart. The electrodes were held in place with epoxy adhesive and connected to the Impedance Pneumograph by miniature PVC-coated wire. Changes in the rate of beating of the scaphognathites were followed from recordings of the water pressure within one of the branchial chambers, recorded with a Statham pressure transducer (P23BB) connected to a 1 mm diameter polythene cannula inserted in the same manner as the electrodes.

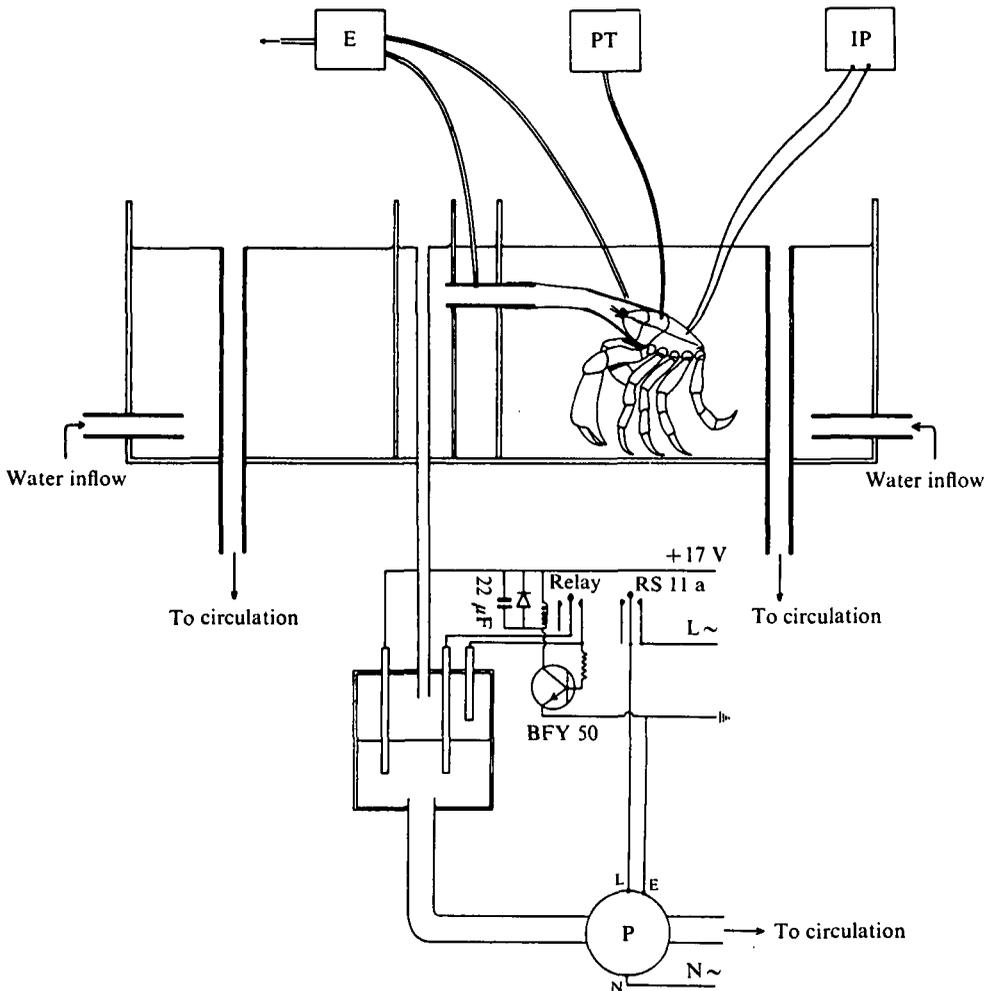


Fig. 1. Apparatus used to study the respiratory responses of *Carcinus maenas* to declining ambient oxygen tension. E = oxygen electrode; PT = pressure transducer; IP = impedance pneumograph; P = pump.

Blood sampling

Attempts to obtain samples of pre- and postbranchial blood using catheters proved unsuccessful, since these frequently became blocked or dislodged when the animal moved. A less satisfactory method therefore had to be employed in which pre- and postbranchial blood samples were taken from groups of 10–15 crabs, each group being acclimatized to different ambient oxygen tensions. Samples of prebranchial blood (0.3–0.5 ml) were taken from the bases of the walking limbs using a 1 ml syringe. Postbranchial blood was taken directly from the heart using a fine hypodermic needle (20 gauge) connected by pressure tubing to the Statham pressure transducer, and lowered vertically through a small hole drilled directly above the heart. When the characteristic pressure responses were recorded, indicating that the tip of the needle

was located in the correct position within the heart, the tubing was then removed and replaced by a 1 ml syringe into which the blood sample was drawn. This procedure often caused temporary cessation of ventilation and heart beat so, to ensure that the P_{O_2} of the blood samples was representative of crabs actively ventilating, blood samples were taken only after ventilation and heart activity had recommenced. The time taken to withdraw each blood sample from the heart was between 10 and 15 s. A further sample was normally taken from each crab after an interval of 15 min.

The P_{O_2} of the blood was determined using a Radiometer oxygen electrode contained within a thermostatted cell. Determinations of the pH of the blood samples were carried out using a Radiometer capillary pH electrode (G292A) and pH meter.

Analyses were made of the effectiveness of oxygen removal from the water (E_w), and the effectiveness of oxygen uptake by the blood (E_b). These concepts, defined as the ratios of the actual to the maximum possible oxygen removal from the water or oxygen uptake by the blood, were first derived by Hughes & Shelton (1962) for analysis of gaseous exchange in fish and have only recently been introduced into respiratory studies of invertebrates (Johansen *et al.* 1970). Other values calculated from these data include the mean P_{O_2} difference between the water and the blood entering and leaving the gills (ΔP_G), and the transfer factor (T_{O_2}) which is a measure of the relative ability of the respiratory surfaces to exchange gases (Randall, Holeyton & Stevens, 1967). The formulae used were:

$$\begin{aligned}\dot{Q} &= \frac{\dot{V}_{O_2}}{C_{a,O_2} - C_{v,O_2}} \text{ ml min}^{-1}, \\ E_w &= \frac{(P_{i,O_2} - P_{e,O_2})}{(P_{i,O_2} - P_{v,O_2})} \times 100 \%, \\ E_b &= \frac{(C_{a,O_2} - C_{v,O_2})}{(C_{i,eq} - C_{v,O_2})} \times 100 \%, \\ \Delta P_G &= \frac{1}{2}(P_{i,O_2} + P_{e,O_2}) - \frac{1}{2}(P_{a,O_2} + P_{v,O_2}) \text{ mmHg}, \\ T_{O_2} &= \frac{\dot{V}_{O_2}}{\Delta P_G} \text{ ml O}_2 \text{ g}^{-1} \text{ min}^{-1} \text{ mmHg}^{-1}, \\ C_w/C_b &= \frac{\dot{V}_G \cdot \alpha_{w,O_2}}{\dot{Q} \cdot \alpha_{b,O_2}},\end{aligned}$$

where P_{i,O_2} = oxygen tension of the inspired water; P_{e,O_2} = oxygen tension of the expired water; P_{v,O_2} = oxygen tension of the prebranchial blood; P_{a,O_2} = oxygen tension of the postbranchial blood; C_{a,O_2} = oxygen content (vols %) of the postbranchial blood; C_{v,O_2} = oxygen content (vols %) of the prebranchial blood; $C_{i,eq}$ = oxygen content (vols %) of blood in complete equilibrium with the inspired water; α_{w,O_2} = solubility coefficient for oxygen in water; α_{b,O_2} = equivalent overall solubility coefficient for oxygen in the blood; ΔP_G = difference between the mean oxygen tensions in the water and in the blood, entering and leaving the gills; \dot{V}_G = ventilation volume; \dot{V}/\dot{Q} = ventilation to perfusion ratio; C_w/C_b = capacity rate ratio; \dot{V}_{O_2} = oxygen consumption; E_w = effectiveness (%) of oxygen removal from the water; E_b = effectiveness (%) of oxygen uptake by the blood; T_{O_2} = transfer factor for oxygen.

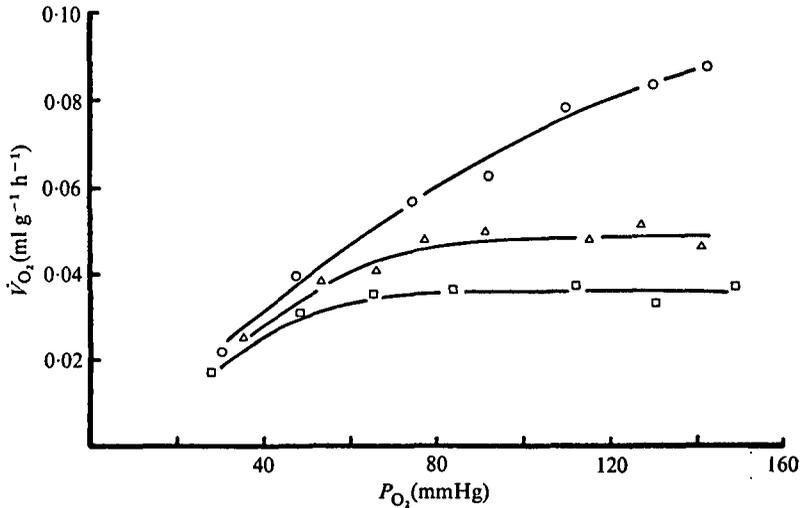


Fig. 2. Oxygen consumption (\dot{V}_{O_2}) of the same individual *Carcinus maenas* during declining ambient oxygen tension after 1 (○), 5 (△) and 10 (□) hours in the respirometer.

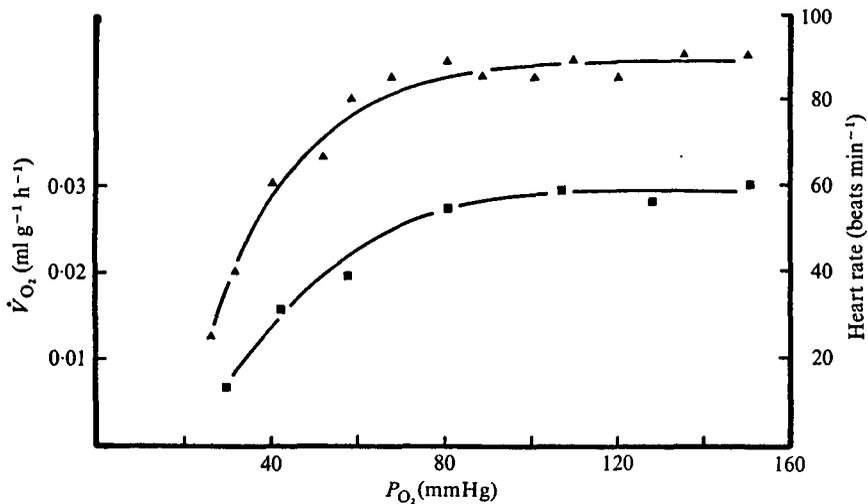


Fig. 3. Simultaneous recordings of heart rate (▲) and oxygen consumption (\dot{V}_{O_2}) (■) of *Carcinus maenas* during declining ambient oxygen tension.

RESULTS

Oxygen consumption

The degree of respiratory independence shown by *Carcinus* under conditions of declining oxygen tension was found to be dependent on the level of activity or state of disturbance of the animal. Recordings of oxygen consumption made within 1–2 h of electrode implantation showed a high rate of oxygen consumption at normal oxygen tensions, but this declined gradually as the P_{O_2} of the water was reduced (Fig. 2). Under these conditions the animal exhibited a low level of respiratory independence, but the pattern was different in crabs left undisturbed in the respirometer. In these,

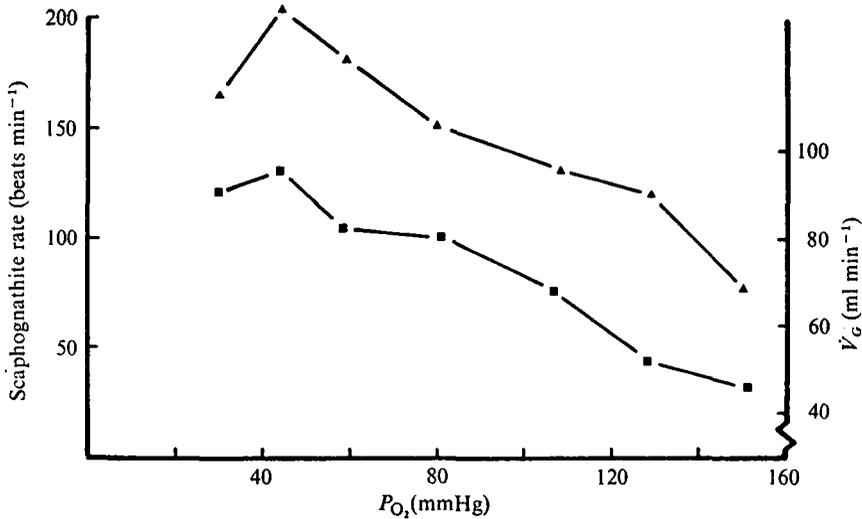


Fig. 4. Simultaneous recordings of ventilation volume (\dot{V}_G) (■) and scaphognathite rate (▲) of *Carcinus maenas* during declining ambient oxygen tension

the rate of oxygen consumption shown at high oxygen tensions was related to the duration of the period that the animal had been left in the respirometer, being lowest after 10 h (Fig. 2). In addition the degree of respiratory independence increased, since this initial rate of oxygen consumption was maintained over an increasingly wider range of oxygen tension.

To ensure that the respiratory responses to hypoxia were unaffected by the state of disturbance of the animal, all subsequent recordings were carried out only after the animals had been left for 24 h in the respirometer. When measured under these conditions, *Carcinus* showed a quite high degree of respiratory independence, with an approximately constant rate of oxygen consumption being maintained down to a critical oxygen tension (P_c) of between 60 and 80 mmHg, below which oxygen consumption decreased rapidly (Fig. 3). This value for the critical oxygen tension is similar to that obtained by Wallace (1971) and also to the P_c recorded for the heart rate (Fig. 3).

Ventilation volume and oxygen utilization

Under conditions of declining oxygen tension *Carcinus* showed a marked increase in ventilation volume (\dot{V}_G), reaching a maximum at about 40–60 mmHg (Fig. 4). At lower oxygen tensions, however, some reduction in ventilation volume was recorded. This increase under hypoxic conditions was associated, as might be expected, with a concurrent increase in the rate of beating of the scaphognathites (Fig. 4). A similar pattern was also shown in recordings of the frequency and duration of periods of reversed beating of the scaphognathites (Fig. 5), which are a well-documented, though poorly understood, feature of the ventilation activity of decapod crustaceans (Borradale, 1922; Arudpragasam & Naylor, 1964*b*; Hughes, Knights & Scammell, 1969). Values for oxygen utilization were between 10 and 25% under normoxic conditions and are similar to those obtained in previous studies (Arudpragasam & Naylor, 1964*a*;

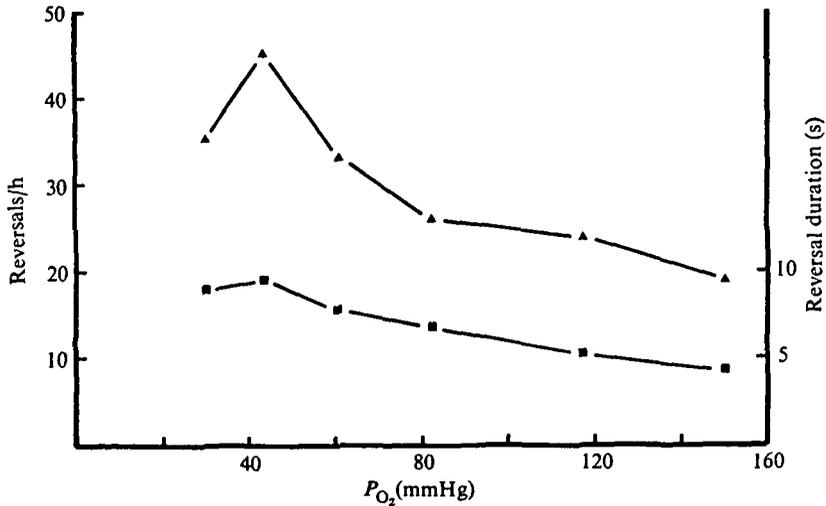


Fig. 5. The frequency (▲) and duration (■) of periods of reversal of the ventilatory current (reversals) of *Carcinus maenas* during declining ambient oxygen tension

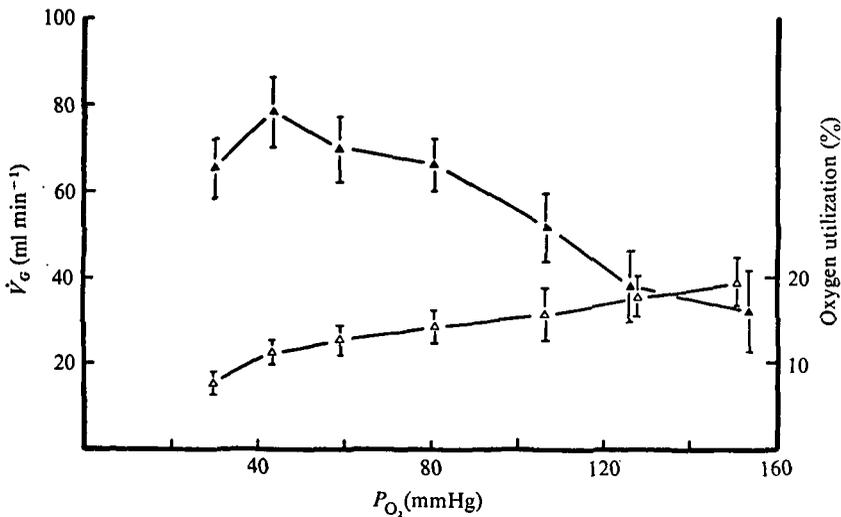


Fig. 6. Simultaneous recordings of ventilation volume (\dot{V}_v) (▲) and oxygen utilization (△) of *Carcinus maenas* during declining ambient oxygen tension. Points are means \pm 95% confidence limits.

Hughes *et al.* 1969). However, as the oxygen tension of the medium was reduced, oxygen utilization decreased, reaching values of 5–7% at 30 mmHg (Fig. 6).

The amount of oxygen made available to the animal at different oxygen tensions by this increased ventilatory activity can be estimated from the product of the ventilation volume ($\text{ml g}^{-1} \text{h}^{-1}$) and the concentration of oxygen in the water. Under hypoxic conditions the amount of oxygen made available at the respiratory surfaces remains approximately constant down to a P_{O_2} of between 60 and 80 mmHg (Fig. 7).

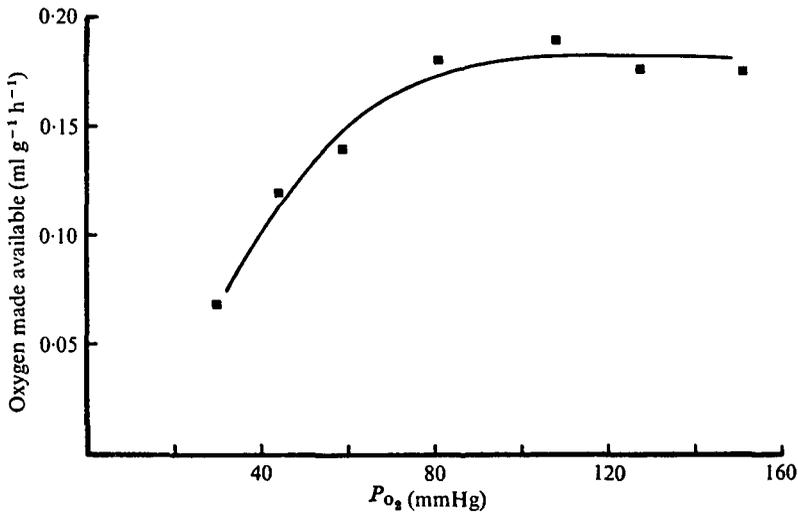


Fig. 7. The amount of oxygen made available to *Carcinus maenas* during declining ambient oxygen tension.

Blood oxygen tension and circulatory responses

The mean values for the oxygen tension of the pre- and postbranchial blood of *Carcinus* at different ambient oxygen tensions are shown in Fig. 8. Of special interest are the high values for the postbranchial blood of crabs under normoxic conditions which are in contrast to the earlier observations of Redmond (1955) on *Panulirus*, but are similar to the values recently recorded by Scammell (1971) and by Taylor *et al.* (1973) for *Carcinus*, and by Johansen *et al.* (1970) for *Cancer magister*.

Calculations of ΔP_G , the mean oxygen gradient between the blood and water at the gills, gave values of about 80 mmHg for crabs under normoxic conditions, which are slightly higher than those calculated by Johansen *et al.* (1970) for *Cancer magister*. However, as the P_{O_2} of the medium declined, ΔP_G decreased progressively (Table 1). The mean pH value of the blood was found to be 7.72 (s.d. = 0.05) under normoxic conditions and very little change (maximum 0.05 pH unit) was recorded in this value under conditions of declining P_{O_2} during the experiments.

Using previously published oxygen dissociation curves for the haemocyanin of *Carcinus* (Truchot, 1971), calculations were made of the percentage saturation of the pigment and the oxygen concentration of the pre- and postbranchial blood. At the high oxygen tensions prevailing in the postbranchial blood under normoxic conditions the blood returning to the heart is fully saturated. Although the oxygen tension of the postbranchial blood decreases as the P_{O_2} of the medium is reduced, the blood remains saturated until the P_{O_2} of the water reaches 60–80 mmHg.

Further information on the role of the haemocyanin in oxygen transport was obtained from calculations of the amount of oxygen delivered by the blood to the tissues (Fig. 9). These showed that at normal oxygen tensions over 50% of the total oxygen delivered was carried in physical solution. However, under conditions of declining oxygen tension this value decreased progressively, while the contribution of the oxy-

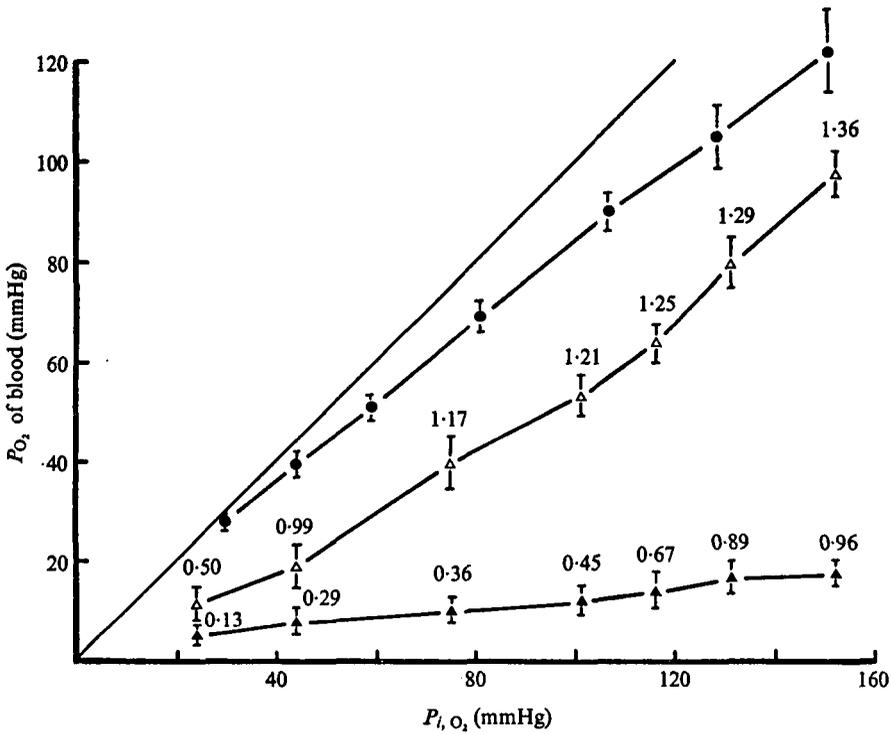


Fig. 8. Oxygen tension of the pre- (▲) and postbranchial (△) blood and expired water (●) of *Carcinus maenas* measured at different ambient oxygen tensions. Points are means \pm 95% confidence limits. Values shown represent the oxygen content (vols %) of the blood, determined using the data of Truchot (1971).

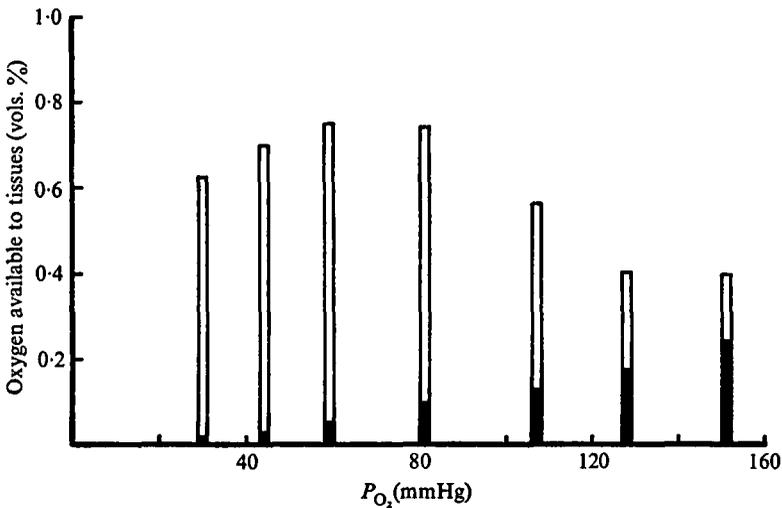


Fig. 9. The amount of oxygen delivered by the blood to the tissues of *Carcinus maenas* at different ambient oxygen tensions. Proportion from haemocyanin (□) and from solution (■).

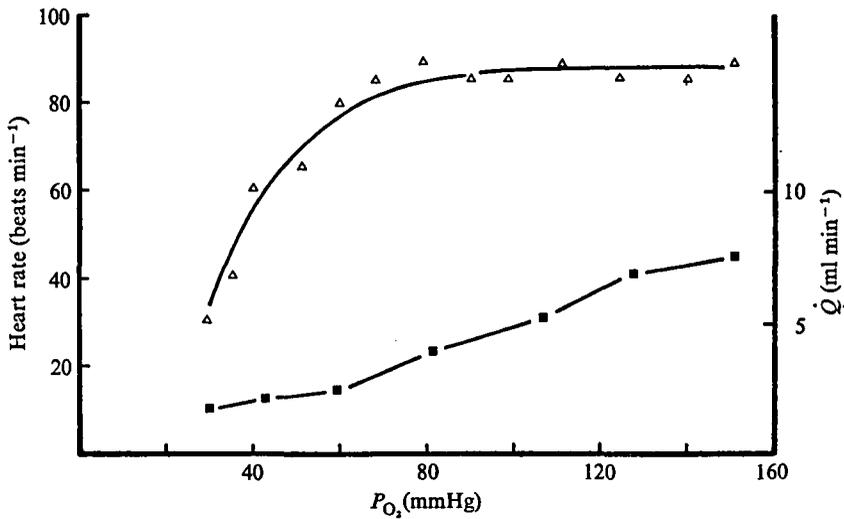


Fig. 10. The heart rate (Δ) and cardiac output (\dot{Q}) (\blacksquare) of *Carcinus maenas* during declining ambient oxygen tension.

Table 1. Analyses of respiratory data obtained from *Carcinus maenas* under conditions of declining oxygen tension. For further details see text.

P_{iO_2} (mmHg)	ΔP_{θ} (mmHg)	T_{O_2} (ml O_2 g ⁻¹ min ⁻¹ mmHg ⁻¹)	E_w (%)	E_b (%)	C_w/C_b	\dot{V}/\dot{Q}
151	80.4	5.72×10^{-6}	21.6	77.6	2.04	3.8
128	70.8	6.07×10^{-6}	20.0	71.7	2.49	5.2
107	63.9	7.19×10^{-6}	17.7	80.0	2.58	10.0
81	48.8	8.40×10^{-6}	16.8	85.1	2.37	18.0
59	36.1	8.03×10^{-6}	15.6	84.2	2.22	28.0
44	28.6	7.34×10^{-6}	10.8	77.3	2.06	42.0
30	19.2	4.01×10^{-6}	8.8	59.1	2.69	82.5

gen carried by the pigment increased from 43% at 150 mmHg to over 90% at 30 mmHg.

At normal oxygen tensions, cardiac output, calculated using the Fick principle, was approximately 5–7 ml min⁻¹, giving values of 0.07–0.09 ml g⁻¹ min⁻¹ for the animals used in these experiments. Although the heart rate remained more or less constant over a wide range of oxygen tension, cardiac output gradually decreased as the P_{O_2} of the medium was reduced (Fig. 10). The ventilation:perfusion ratio was rather low under normoxic conditions, but the increase in ventilation volume together with the reduction in cardiac output under hypoxic conditions resulted in a rapid rise in this ratio as the P_{O_2} of the water was reduced (Table 1).

The effectiveness of oxygen removal from the water (E_w) was low under normoxic conditions (21%) and decreased somewhat as the oxygen tension of the water was reduced (Table 1). The effectiveness of oxygen uptake by the blood (E_b) was, however, high (over 75%) and remained at a high level over a wide range of oxygen tension. At the same time there was an initial rise in the transfer factor for oxygen (T_{O_2}) across the

gills during hypoxia. Calculations of the capacity rate ratio (C_w/C_b) have shown that despite the large increase in ventilation volume, the capacity rate ratio remained approximately constant as the P_{O_2} of the medium declined (Table 1).

DISCUSSION

Though Fry (1957) concluded that many animals exhibit respiratory dependence only when respiring at their maximum rate, Spoek (1974) points out that some authors still state that many species of Crustacea show a resting metabolism that is dependent on the ambient P_{O_2} . In particular, Spoek demonstrated that, in contrast to the earlier study of Thomas (1954), untethered, inactive lobsters were capable of showing a high level of respiratory independence. He concluded that this was due to the fact that the animals used by Thomas (1954) were tethered, which probably caused them to be disturbed and to respire at a high rate, under which conditions they were unlikely to show respiratory independence. Further support for the conclusions of Fry (1957) is provided by the present study, which demonstrates that the degree of respiratory independence shown by *Carcinus* under conditions of declining oxygen tension is dependent on the level of activity or state of disturbance of the animal.

Recent studies on bivalve molluscs have shown that respiratory independence can be affected by a variety of physiological and ecological factors (Bayne, 1971, 1973; Taylor & Brand, 1975). Since bivalves show much intraspecific variation in the degree of respiratory independence under hypoxic conditions, it has been concluded that the division of species into 'regulators' and 'conformers' is unwarranted and that the different respiratory responses to declining oxygen tension are explicable on a quantitative basis (Mangum & Van Winkle, 1973; Taylor & Brand, 1975). The evidence presently available suggests that these conclusions are also valid for crustaceans and that the division of species into 'conformers' and 'regulators' as made by some authors (Wolvekamp & Waterman, 1960; Lockwood, 1968) is incorrect, since these terms describe only the extremes of a variable capacity to maintain respiratory independence under hypoxic conditions.

Under conditions of declining P_{O_2} inactive *Carcinus* are able to maintain their rate of respiration independent of the ambient oxygen tension down to a P_{O_2} of 60–80 mmHg. This is achieved primarily by an increase in ventilatory activity, since the ventilation volume increases progressively as the oxygen tension of the medium is reduced, although at very low oxygen tensions some reduction in ventilation volume was observed. An increase in ventilatory activity under hypoxic conditions has also been recorded in previous studies of *Carcinus* (Arudpragasam & Naylor, 1964*a*; Scammell, 1971) and appears to be a common respiratory response to hypoxia in many species of Crustacea (see review of Wolvekamp & Waterman, 1960). However, Johnson (1936) concluded that the rate of beating of the scaphognathites of *Carcinus* was independent of the gas content of the medium. In contrast to the present study, Taylor *et al.* (1973) detected little change in the rate of beat of the scaphognathites of *Carcinus* under conditions of declining oxygen tension. The present investigation has also confirmed the observation of Arudpragasam & Naylor (1964*a*) that a high correlation exists between the frequency of reversals and the ventilation volume in *Carcinus*. Since Taylor *et al.* (1973) also recorded an increase in both the frequency and duration

of reversals during hypoxia, it is rather surprising that they did not detect any increase in the rate of beat of the scaphognathites.

The significance of the critical oxygen tension at which respiratory independence is lost is not fully understood, but in fish it is thought to be due to limitations in the gas exchange system (Fry, 1957; Hughes & Shelton, 1962; Hughes, 1964). It would appear that in fish the maximum amount of water that the animal is capable of passing over the gills is the most important factor governing the appearance of respiratory dependence. The oxygen tension at which this becomes limiting will also be affected by the increasing proportion of the oxygen supplied that is needed by the respiratory pump itself. When this limiting P_{O_2} is reached, respiratory independence is lost and this is correlated with a reduction in the saturation of the postbranchial blood (Hughes, 1964). This would also explain why active animals are able to maintain respiratory independence over only a limited range of oxygen tension. Since these animals are already respiring at a high rate, only a slight reduction in the ambient oxygen tension can be tolerated before the respiratory pump is no longer able to provide sufficient oxygen to sustain this high rate of respiration.

This may also be true for *Carcinus*. Here the increased ventilation volume during hypoxia results in the amount of oxygen made available at the respiratory surfaces remaining more or less constant over a wide range of oxygen tension down to a P_{O_2} of 60–80 mmHg, below which it declines rapidly. It is perhaps significant that this oxygen tension corresponds closely to the critical P_{O_2} below which respiratory independence is lost. At this oxygen tension (corresponding to a P_{a,O_2} of 30–40 mmHg), the blood leaving the gills is no longer fully saturated and bradycardia begins. A similar relationship between the onset of bradycardia and the loss of full saturation of the respiratory pigment was found by Taylor *et al.* (1973), who also observed that it was at these oxygen tensions that unrestrained crabs began to emerge from shallow hypoxic water and bubble air through the water in the branchial chambers.

In contrast to the observations of Redmond (1955, 1962, 1968*a, b*), recent studies have recorded high oxygen tensions in the postbranchial blood of several decapods (Johansen *et al.* 1970; Taylor *et al.* 1973; McMahan & Wilkens, 1975). This discrepancy has been discussed in detail by Johansen *et al.* (1970), who were of the opinion that the low values recorded by Redmond were probably the result of the sampling procedure used, although Belman (1975) has recently supported the accuracy of Redmond's data. Taylor *et al.* (1973) have emphasized the importance of proper conditions for blood sampling, for they found that the P_{O_2} of the postbranchial blood of *Carcinus* was significantly lower in those animals in which cardiac and scaphognathite activity had spontaneously ceased immediately prior to blood sampling, as compared to animals which had continued to irrigate and perfuse the gills. For this reason heart and scaphognathite activity were monitored during blood sampling in the present study.

McMahan & Wilkens (1975) have shown that in *Homarus* over 76% of the total oxygen delivered to the tissues was carried in solution. In *Carcinus* this value was found to be in the region of 50% but, as in *Homarus*, the amount of oxygen carried in physical solution decreased progressively as the P_{O_2} of the medium was reduced, while the contribution made by the oxygen carried by the respiratory pigment increased. The increase in the total amount of oxygen delivered to the tissues at low oxygen

tensions (Fig. 9) is probably due to the reduction in the P_{O_2} of the blood causing the prebranchial blood to enter the steep portion of the oxygen dissociation curve, which results in a greater release of the oxygen combined with the respiratory pigment.

Cardiac output under normoxic conditions was about $5-7 \text{ ml min}^{-1}$ or $0.07-0.09 \text{ ml g}^{-1} \text{ min}^{-1}$ in *Carcinus* weighing 60–70 g. Unfortunately there are few reliable estimates of cardiac output in other decapods with which these values can be compared, but they would seem to be somewhat higher than the values obtained for other species, e.g. $0.029 \text{ ml g}^{-1} \text{ min}^{-1}$ in *Cancer magister* (Johansen *et al.* 1970) and $0.022-0.067$ in *Homarus* (Burger & Smythe, 1953). However, even higher values for cardiac output of $0.128 \text{ ml g}^{-1} \text{ min}^{-1}$ have been calculated for *Panulirus* (Belman, 1975) and of $0.141 \text{ ml g}^{-1} \text{ min}^{-1}$ for *Carcinus* (calculated by Belman (1975) using Blatchford's (1971) estimates of the stroke volume of large *Carcinus*).

Since the heart rate remains more or less constant over a range of oxygen tension, this suggests that the decreased cardiac output during hypoxia must be associated with a reduction in stroke volume. However, estimates of the capacity rate ratio at different oxygen tensions suggest that the increase in the amount of oxygen released by the respiratory pigment to the tissues, due to the prebranchial blood entering the steepest part of the dissociation curve, tends to compensate for the reduction in cardiac output, since the capacity rate ratio remains approximately constant under conditions of declining oxygen tension. The effectiveness of oxygen uptake by the blood remains high over a wide range of oxygen tension, since the postbranchial blood continues to be fully saturated down to quite low oxygen tensions. At the same time gaseous exchange is facilitated during hypoxia by an initial increase in the transfer factor for oxygen at the gills.

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