RESPIRATION OF CRABS IN AIR AND WATER

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Abstract—1. Oxygen consumption (VO2), ventilation volume (V) and O2 extraction (Ext) were measured for three species of crabs: the terrestrial Geocarcinus lateralis, the amphibious Cardisoma guanahumi, and the aquatic Callinectes sapidus. In air the VO2 of the crabs was ranked Geocarcinus > Cardisoma > Callinectes. In water the VO2 was Callinectes > Cardisoma > Geocarcinus.

2. When terrestrial Geocarcinus was submerged in water, VO2 fell to 1/1 of its aerial value because both V and Ext fell. When aquatic Callinectes was exposed to air, VO2 fell to 1/3 of its aquatic value because both V and Ext fell. Only the amphibious Cardisoma maintained VO2 constant in both media; in water V was increased to offset a fall in Ext.

3. All species behaved as VO2 conformers when they were exposed to short-term hypoxia; the effect was more pronounced in the aquatic environment.

4. Severe short-term hypercapnia caused no change in the aquatic environment; but it stimulated increased V and decreased Ext in air.

5. Such effects are consistent with vertebrate responses: O2 seems to be the most important regulatory factor of respiration in water and CO2 is the most important in air.

INTRODUCTION

Out of several million species living on earth, few can survive in both air and water. The crustaceans are members of this elite group, and they deserve particular attention for most rely on the same respiratory structure, the gill, in both media (Wolvenkamp and Waterman, 1960). Moreover, the gill chamber is ventilated in basically the same way in both water and air; the tiny respiratory appendage, the scaphognathite, beats water or air through the gill chamber, drawing the fluid in the edge of the carapace and expelling it out of openings near the mouth. Only in highly specialized air breathers does the lining of the gill chamber begin to take on the characteristics of a lung (Diaz and Rodriguez, 1977; Taylor and Greenway, 1979).

Respiration in water and air presents different problems. Oxygen uptake is considerably more expensive in water because of the medium’s density, viscosity and low capacitance for O2, demanding high ventilation requirements (Dejours, 1981). Carbon dioxide removal is accomplished more readily in water because of the gas’s high solubility in the medium. This results in a lower Pco2 in water breathers and a different strategy of acid–base balance than in air (Cameron, 1979; Dejours, 1978; Rahn, 1966). Respiratory control differs as well. Water breathers are sensitive to changes in ambient O2 while air breathers respond more readily to changes in CO2. These principles have emerged largely from investigation of vertebrates (Rahn and Howell, 1976). Studies on crustacean respiration tend to support their general application (see Cameron, 1981b and Taylor, 1982).

In this paper, we examine both the aquatic and aerial respiration of three crab species which vary in their degree of terrestrial adaptation. One species, the blue crab, Callinectes sapidus, is highly specialized for aquatic life. Another species, Geocarcinus lateralis, is highly terrestrial, returning to water only briefly for reproduction. The third species, Cardisoma guanahumi, is an amphibious crab existing in moist land burrows along the seashore and fresh water canals of the tropics. To improve understanding of the control of respiration in both media, the present study provides a direct comparison of the crab species to respiratory stress (hypoxia and hypercapnia). This presentation clearly highlights the respiratory limitations and adaptations of crustaceans in the water/air transition.

MATERIALS AND METHODS

Animals

Three species of decapod crustaceans were used as experimental animals: Callinectes sapidus, the marine blue crab (88–147 g); Cardisoma guanahumi, a semi-terrestrial crab (83–176 g) and Geocarcinus lateralis, a land crab (51–75 g). All animals were obtained from southern Florida.

The crabs were housed in aquaria at a temperature of 24–26°C and were fed a combination of raw clams, fish, dog food, egg shell and lettuce. The aquaria of the marine crab contained sea water at pH = 8 and specific gravity = 1.025 to 1.030 units, while the two more terrestrial species had access to a large pan of 50% sea water.

Respiratory experiments

Experiments in this paper were designed to measure O2 consumption (VO2), ventilation volume (V) and oxygen extraction (Ext) of crabs as they were exposed to different respiratory media (air vs water) during hypoxia and hypercapnia. In all tests we used a respiratory mask, impermeable to gas and water. It was sealed over the mouth with hot glue and wax and separated the inhalant respiratory current at the base of the legs from the exhalant current near the...
mouth (Herreid et al., 1979). The mask did not obstruct free movements of any appendages. Leaks in the respiratory mask were discovered by putting the animals into a tank of water and looking for streams of bubbles. When a leak was detected, the mask was resealed and tested again.

In the aquatic experiments, the water surface was aerated with gas mixtures containing a low concentration of CO2. During the hypercapnia studies, the CO2 content of the water was increased by bubbling with a gas mixture containing CO2. The gases were mixed in a National Appliance Controlled Environmental Flow Meter Mixer. The mixed gas from the exit tube of the mixer was divided into two streams by a two way stopcock, to two large balloons that functioned as miniature "Douglas Bags". The maximum volume a balloon could hold was approximately 2 4 ml. Later, another small balloon was used and fed into two flow meters (Lab Cost Century) which were attached to air stones in the experimental chamber and reservoir.

The O2 content and Pco2 were measured on inhalant and exhalant water samples drawn from the exhalant tube. A piece of styrofoam kept the animal submerged. As the crabs were submerged, air bubbles were seen leaving the gill chambers. This observation suggests that air retention in gill chambers was not a major problem. Large amounts of air could be retained in the branchial chambers of Cardisoma carica upon immersion, so that the crabs may not have been fully water-breathing for several hours (Cameron, 1981b). To ensure that our animals were breathing water, crabs were subjected to hyperoxia or hypercapnia only after a 3 hr rest period. Any oxygen trapped in air bubbles would be depleted well before the end of this period.

Experiments were 9 hr in duration. An inhalant and exhalant water sample was taken once an hour to determine the oxygen content of the water. The first 3 hr of the experiment were used to determine normal or baseline data. During the second 3 hr the gas concentration of the water was varied in a step-wise fashion by either decreasing the Pco2, or increasing the Pco2 of the incoming gas. At the end of the third hour of the experiment N2 or CO2 was turned on. It required less than 15 min for the water to become equilibrated with the gas mixture. At the end of the fourth hour, the N2 or CO2 was again increased. The final increase in N2 or CO2 took place at the end of the fifth hour of the experiment. At the end of the sixth hour of the experiment either N2 or CO2 was turned off and the gas content of the water returned to normal. Data from the last 3 hr of the experiment were used to determine if the animal had recovered from the experimental handling. Ventilation volumes were recorded continuously throughout the 9 hr experiment.

Throughout all experiments, the crabs rested quietly in their chambers except during the aquatic hypoxia tests when there were 2-3 min of sporadic struggling each time the O2 tension was lowered.

The sample sizes for the aquatic hypoxia tests were: Callinectes = 8, Cardisoma = 10 and Gecarcinus = 6. The volume of air bubbles released by the animals in the aquatic and aerial experiments could be readily observed by noting the movement of exhaled air or water. A reversal of production occurred an abrupt interruption of flow. No sustained periods of reversed ventilation occurred except in the cases mentioned. Infrequent and brief periods of reversed ventilation would not cause significant errors in measurement of V. Resistance to ventilation could not be completely eliminated, but every effort was made to reduce flow resistance. This included the use of short, large diameter tubing along with receptacles producing only small pressure gradients against ventilatory flow.

Aerial respiration. Aerial respiration experiments were similar to the aquatic tests except for the following modifications. A large (11.25 l) plexiglass respiratory chamber was used for aerial experiments on Callinectes and large specimens of Cardisoma. A smaller (3.25 l) chamber of similar design was used for Gecarcinus and small specimens of Cardisoma. Gas flowed through the large chamber at the rate of 825 ml/min. Gases introduced to the respirometer to be inhaled by a crab were first humidified by bubbling the gas through an Erylemeyer flask containing water.

Crabs exhaled through the respiratory mask. A short exhalant tube passed through the respiratory chamber wall and a two way stopcock, to two large balloons that functioned as miniature "Douglas Bags". The maximum volume a balloon could hold was approximately 10 l. The average volume of the balloon when emptied was 100 ml and therefore provided little resistance at ventilation. The tubing had an inner diameter of 7 mm to minimize ventilatory resistance. The balloons were periodically emptied. The time for filling noted and the volume of exhaled air was determined by water displacement. Exhalant gas samples were withdrawn by syringe via a piece of polyethylene tubing in the respiratory mask and measuring pH at each Pco2. The Pco2 of the water reservoir was determined by measuring pH and using the calibration curve. The O2 content of the water was used to determine Pco2. O2 tension fell from 150 to 35 torr.

Procedure. Two sets of experiments were carried out to examine the response of the crab's respiratory system in water. At the beginning of each experiment, a crab wearing a respiratory mask, its chelae closed with rubber bands, was placed in the experimental chamber and attached to the exhalant tube. A piece of styrofoam kept the animal submerged.
RESULTS

Aquatic vs aerial respiration

Figure 1 compares the resting aquatic and aerial \( V_{\text{O}_2} \), ventilation volume (\( V \)), and \( O_2 \) extraction (Ext) during normoxia for three species of crabs. No significant trends were found among the three hr baseline measurements, so the three hourly values were averaged to obtain resting data. In an aquatic environment the marine crab, Callinectes, had the greatest \( V_{\text{O}_2} \) baseline values while the most terrestrial species, Gecarcinus, had the lowest. Cardisoma, a semi-terrestrial crab, had intermediate \( V_{\text{O}_2} \) values. Student's t-tests of the baseline data confirm that statistical differences exist among the species \( (P < 0.05) \). Figure 1 clearly shows that Callinectes' high \( V_{\text{O}_2} \) was maintained by a high aquatic ventilation \( (V) \), and a moderate \( O_2 \) extraction \( (\text{Ext}_a) \). The low \( V_{\text{O}_2} \) of Gecarcinus in water was a result of both a low \( V_a \) and a low \( \text{Ext}_a \). Cardisoma had intermediate \( V_w \) and \( \text{Ext}_w \) values.

The respiration of crabs in normoxic air is shown in Fig 1. The terrestrial crab, Gecarcinus, had the highest \( V_{\text{O}_2} \), the semi-terrestrial crab, Cardisoma, had an intermediate rate, and the aquatic crab, Callinectes, had the lowest rate. All differences as judged by t-tests were significant at \( P < 0.05 \) whereas Gecarcinus showed no change in the two media. \( O_2 \) extraction was higher in water than air for both Cardisoma and Gecarcinus, whereas in Callinectes no difference occurred between environments.

Aquatic hypoxia

Figure 2(A)-(C) compare the aquatic \( V_{\text{O}_2} \), ventilation volume \( (V) \), and \( O_2 \) extraction \( (\text{Ext}) \) at various partial pressures of \( O_2 \) for three species of crabs. Linear regression analysis (method of least-squares) was applied to the \( V_{\text{O}_2} \) data. All regression slopes were significantly different from zero (Table 1). Therefore, the \( V_{\text{O}_2} \) of all the species decreased as the \( P_{\text{O}_2} \) of the water was reduced. Callinectes showed the fastest rate of decline in \( V_{\text{O}_2} \) with a decrease in \( P_{\text{O}_2} \) and Gecarcinus the smallest; the slopes of the regression lines of all three species were significantly different from one another (Table 1).

As the \( P_{\text{O}_2} \) of the aquatic medium was reduced, \( O_2 \) \( \text{Ext}_w \) fell slightly but consistently in all three species of crabs (Fig 2(C)), whereas the \( V_w \) was not altered significantly (Fig 2(B)). Recovery from hypoxia was rapid and apparently complete for all crabs: there were no statistical differences between the mean baseline values for \( V_{\text{O}_2} \), \( \text{Ext}_w \) or \( V_w \) and those
recorded for the first hour of recovery ($t$-test, $P > 0.05$).

**Aerial hypoxia**

Figures 2(D)-(F) show the results for aerial hypoxia. All three crab species showed some tendency to decrease $V_i$, at some point in hypoxia (Fig. 2(D)), yet the slopes of the least squares regression lines were not significantly different than zero (Table 1).

It should be noted that during the extreme hypoxia established in some experiments, it was impossible to measure $V_i$, especially in *Gecurcinus*. All the *Gecurcinus* used in the experiment regurgitated gastric fluid during the fifth hour of the experiment when $P_o$, fell below 25 torr. Because gastric fluid bubbles could be seen in the transparent exhalant tube, we noted that normal ventilation had stopped and a pattern of "oscillatory ventilation" began: a small volume of air (about 2 ml) was passed back and forth through the gill chamber. This could be detected by the slow back and forth movement of the entrained bubbles every 2 or 3 min. Some animals used this oscillatory ventilation for periods lasting more than 2 hr and even continued to ventilate in this manner after the $O_2$ tension returned to normoxia. All animals survived the experience and lived many weeks in the laboratory without abnormality.

In general, any lowered $V_o$ seen during aerial hypoxia for the crabs (Fig. 2(D)) can be accounted for by a lowering of the aerial $O_2$ extraction (Ext.) (Fig. 2(F)). However, *Callinectes* showed a significant drop in aerial ventilation ($V_i$) as well as $O_2$ Ext., (Fig. 1(E)). Recovery aerial hypoxia was relatively rapid and complete for all crabs: $t$-tests comparing initial $V_o$, $V_i$, and Ext., levels with the 1 hr recovery values showed no significant difference ($P > 0.05$).

**Aquatic hypercapnia**

Figs. 3(A)–(C) show the respiratory response of the three species of crabs to a progressive increase in $CO_2$ of the inhaled water. Figure 3(A) indicates that *Callinectes* and *Cardisoma* showed a modest but significant decrease in $V_i$, whereas *Gecurcinus* seemed unaffected. The regression equations for the three crabs are shown on Table 1. Only the slopes of *Callinectes* and *Cardisoma* are significantly different from zero (Table 1).

In summary, $CO_2$ did not have much effect on aquatic respiration even when the $P_o$ was drastically elevated in the experiments.

A comparison of the baseline measurements of the three species with those of the recovery period show that $V_o$, $V_i$, and Ext., values are not significantly different ($t$-test, $P > 0.05$) except for *Callinectes*.
At Pco2 of 30 torr or higher, the Ext, in these two coincident with the increased O2, mentioned earlier. Yet the slopes of the regression equations elevated O2 at a Pco2 = 40 torr which then drops at levels of sampling or if the crab does indeed have an whether the three species in air were similar to one another. As the Pco2 of the environment was raised, the V, of the crabs as they were exposed to increasing levels of CO2 in air. Figure 2(D) shows that the initial VO2 of the 4 to 14 crabs.

Aerial hypercapnia

Figures 3(D)-(F) show the respiratory response of the crabs as they were exposed to increasing levels of CO2 in air. Figure 2(D) shows that the initial VO2 of the three species in air were similar to one another. As the Pco2 of the environment was raised, the VO2 of Callinectes showed no general trend. It is not clear whether the Callinectes' response is due to the vagaries of sampling or if the crab does indeed have an elevated VO2 at a Pco2 = 40 torr which then drops at higher ambient Pco2 levels. On the other hand, Cardisoma and Gecarcinus both displayed an apparent increase in VO2, as the environmental Pco2 was increased. Yet the slopes of the regression equations were not different from zero (Table 1).

Examination of Figs 3(E) and 3(F) reveals the effect of increased aerial Pco2 levels on Vi and Ext. In general, ventilation volumes increased with el evated Pco2, however this effect was only significant at the lower Pco2 levels. After an ambient Pco2 of 40 torr was reached, Vi stayed relatively constant. Oxygen extraction (Fig. 3(F)) showed a general and significant tendency to fall as Pco2 levels increased. Gecarcinus and Cardisoma showed an abrupt drop in Ext, when Pco2 was increased above 20 torr. This was coincident with the increased Vi mentioned earlier. At Pco2 of 30 torr or higher, the Ext in these two species remained constant. Callinectes also displayed a general decrease in Ext, with an elevated ambient Pco2 except the largest drop appeared between 40 to 80 torr.

All crabs recovered within 1 hr once they were returned to room air; i.e. no significant differences existed between their baseline and recovery values (P > 0.05). None of the crabs showed any overt signs of stress during the experiments in spite of the high levels of CO2 tested.

**DISCUSSION**

Respiration in air and water

The blue crab, *Callinectes sapidus*, is primarily an aquatic species, but it can survive at least 24-48 hr in air (Pearse, 1936; O'Mahoney, 1977). Our data show that such an exposure is accompanied by a decrease in VO2 to about one-third of the aquatic value (Fig. 1). This decline occurs with a drop in ventilation volume. Batterton and Cameron (1978) estimated a 50% decrease in ventilation for the blue crab after 4 hr in air. It is not clear whether the fall in ventilation was the result of a decrease in scaphognathite frequency or stroke volume; both mechanisms are possible (Wilkens, 1981). A decrease in ventilation might result in an energy savings in air. However, the possible energetic reduction seems inadequate to explain the fall in VO2, since the cost of ventilation is estimated at only 1-20% of the standard VO2 (Batterton and Cameron, 1978; Standaert, 1970). The best explanation for the fall in VO2 may be that ventilation efficiency is reduced in air; the blue crabs' scaphognathite system may not be well designed for the air.

*Callinectes* did not compensate for the decrease in ventilation by increasing extraction (Fig. 1). Gill collapse probably was involved, since the gill lamellae of aquatic crabs are not rigid (Cameron, 1981a). Such collapse would sharply reduce the surface area for gas exchange. In the face of gill collapse, the extraction could only remain constant (Fig. 1) if, as we presume, circulatory adjustments were made.

The ineffectiveness of the *Callinectes* respiratory system in air did not cause death. This indicates *Callinectes* either decreased its total metabolic rate or the crabs switched to anaerobic metabolism. We lack the data to distinguish between the possibilities, but a few points are germane. *Callinectes* does have significant glycolytic capacity as it generates lactate readily during exercise (Booth et al., 1982). However, any prolonged anaerobic activity in this species may be limited by the acidic effects. O'Mahoney (1977) showed a decreased hemolymph pH in *Callinectes* from 7.87 (water) to 7.71 (air) after 48 hr of air exposure. Hemolymph Pco2 rose from 2.9 torr (water) to 8.05 torr (air) along with a corresponding increase in bicarbonate.

*Cardisoma guanhumi*, a semiterrestrial crab, shows a relatively constant VO2 in air and water (Fig. 1). This result is consistent with Standaert's (1970) unpublished observations. The amphibious behavior is not unexpected because this crab is found on both land and in water. Moreover, water is located in the bottom of the land burrows (Gifford, 1963; Herreid and Gifford, 1963; Bliss and Mantel, 1968). A constant VO2 in both air and water has also been reported for other crustaceans such as the shore crab *Carcinus maenas* and the freshwater crayfish *Austropotamobius*
pallipes (Taylor and Butler, 1973; Taylor and Wheatly, 1980).

To achieve a constant $V_O_2$ in both water and air, C. guanhumi manipulates both ventilation and $O_2$ extraction. In water, where $O_2$ concentrations are low and $O_2$ extraction falls dramatically, $V_e$ is increased correspondingly (Fig. 1). In air, where both $O_2$ content is high and $O_2$ extraction rises, the $V_e$ drops. The gills of Cardisoma are well supported with stiffened margins of small gill leaflets (Cameron, 1981a). The branchial lining which is reported to have extensive folds may act as a lung (Wood and Randall, 1981). These respiratory surfaces apparently function adequately in both water and air to provide a constant gas exchange.

Consistent with its amphibious nature, C. guanhumi maintains a constant hemolymph $pH$ in both media. Standaert (1970) noticed that submergence of the crab caused a transitory rise in $pH$ which may be due to the elevation of $V_e$ and a washout of $CO_2$, but that $pH$ returned to its original value within 4-6 hr. O’Mahoney (1977) measured a drop in blood $P_{CO_2}$, but saw no difference in $pH$ after 48 hr of submergence. Forced water-breathing of another species, Cardisoma carnifex, showed similar results: a hypocapnic alkalosis followed by a metabolic acidosis which restored $pH$ (Cameron, 1981b).

Geocarcinus lateralis, a terrestrial species, had an average aerial $V_O_2$ of 93 $\mu$L $O_2$/hr and a $V_e$ of 20 $mL$/min (Fig. 1). These values are comparable to rates reported by Cameron (1975) but are inexplicably higher than those observed by Taylor and Davies (1981). When $G. \ lateralis$ was submerged in water, where $O_2$ content is relatively low, the $O_2$ extraction plummeted to one-seventh of its aerial value (Fig. 1). There was no ventilatory compensation so $V_e$, dropped one-seventh of that in air.

$G. \ lateralis$ cannot survive prolonged submersion. O’Mahoney (1977) found only one individual of the four tested that could manage 18 hr exposure. The species appears specialized for land existence; its gill surface area is reduced to 60% of the area of Cardisoma and only 15% of that of Callinectes (Bliss and McMahon, 1980; McMahon, 1977). Its branchial lining has extensive finger-like projections between gill leaflets for support in air (Cameron, 1981a). Even though $G. \ lateralis$ can respire through its highly vascularized gill chamber lining (Diaz and Rodriguez, 1977), gas exchange by this route in water may be limited. The obvious conclusion seems that neither gills nor branchial lining allow the necessary $O_2$ exchange for survival.

Acid–base balance is profoundly affected in water. O’Mahoney (1977) submerged $G. \ lateralis$ for 12 hr and noticed hemolymph $pH$ increased significantly from 7.38 to 7.54, while $P_{CO_2}$ shifted from 8.3 to 6.4 torr. In three animals that survived 18 hr exposure, the $pH$ had dropped to 7.00 just before death. Such wild oscillations of acid–base balance may contribute to death.

**Control of respiration**

**Hypercapnia.** Theoretical arguments suggest that the control of respiration differs in air and water (see Dejours, 1981). Vertebrate air-breathers are most sensitive to environmental $CO_2$, regardless of the degree of terrestriality, while water-breathers do not respond to elevated $CO_2$ by an increased ventilation. Similar responses have reported for a number of crustaceans in water (Batterton and Cameron, 1978; Dejours and Beckenkamp, 1977) and air (Cameron, 1975, 1981b; Cameron and Mecklenburg, 1973). Yet, there are exceptions to this generalization among other crustaceans (e.g. Arudpragasam and Nayelor, 1964; Larzemer, 1961; Massabau et al., 1980). For example, $O_2$ appears to control ventilation rate in the terrestrial anomuran, Coenobita clypeatus (McMahon and Burggren, 1979). For crabs in water, all subject to the same experimental regime, we noted that even drastically elevated $CO_2$ levels did not trigger compensatory increases in ventilation (Fig. 3(C)), whereas in air they did (Fig. 3(E)).

Hypercapnia does not usually stimulate hyper-ventilation in water breathers, since blood $P_{CO_2}$ levels do not normally become significantly elevated. Because of the large ventilation requirement of water breathers and the medium’s high $CO_2$ capacitance the difference between inspired and expired $P_{CO_2}$ is usually small. Correspondingly, there are only small changes in arterial $P_{CO_2}$, with ventilation. So ventilation cannot serve as an effective method for controlling blood $P_{CO_2}$, or $pH$ (Rahn, 1966; Dejours, 1978). Instead, in crabs acid–base regulation during aquatic hypercapnia is mainly carried out by gill ion exchange (Cameron, 1978; DeFur et al., 1980; Truchot, 1979).

Hyperecapnia in air-breathing vertebrates often stimulates hyperventilation, which in turn minimizes increases in arterial $P_{CO_2}$ and $pH$ (Dejours, 1981). The situation seems similar in the three crab species depicted in Fig. 3(E) where aerial hypercapnia increased ventilation. Other authors report comparable results for $G. \ lateralis$, C. guanhumi, Holthuisiana transversa and the coconut crab, Birgus latro (Cameron, 1975, 1981b; Cameron and Mecklenburg, 1973; Greenway et al., 1983). However, Batterton and Cameron (1978) found no change in the ventilation of $C. \ sapidus$ in air; their results may differ from ours on the same species because we used higher levels of $CO_2$.

In summary, high $P_{CO_2}$ in air stimulates crustacean ventilation just as it does for vertebrates, even though crabs may use the shell carbonate as a buffer to compensate for acid–base problems as well (DeFur et al., 1980; Cameron, 1981b; Henry et al., 1981).

**Hypoxia.** A range of respiratory responses have been observed in crustaceans, as well as in other invertebrates during hypoxia (Herreid, 1980). At one extreme one finds oxygen regulation and at the other extreme oxygen conformity. The same individual may operate in either mode depending upon lab stress, time of day, temperature, salinity, activity, rate of hypoxic exposure, etc. (Herreid, 1980; McMahon et al., 1974; Taylor et al., 1977; Taylor and Butler, 1973). If a strategy of regulation is adopted in the face of declining $P_{O_2}$ then either ventilation must increase or extraction must remain constant. When the latter occurs in hypoxia, this means a greater percentage of $O_2$ must be removed ($%_{Ext}$) as $P_{O_2}$ is decreased. If a strategy of O$_2$ conformity is adopted, the animal must be able to tolerate the lowered $P_{O_2}$ by reducing its total energy expenditure or by shifting to anaerobic metabolism.
All the species of crabs we tested during aquatic hypoxia acted as almost ideal O₂ conformers (Fig. 2). When P₀₂ decreased to one-half its value, V₀₂ showed a similar decline. No compensation in V₀₂ occurred, and the fall in V₀₂ was accompanied by a progressive and proportional decline in O₂ extraction.

In contrast to these results, many authors report that crustaceans in water show a significant degree of O₂ regulation during hypoxia which is accomplished by an increase in V₀₂ (Batterson and Cameron, 1978; Butler et al., 1978; Childress, 1971; Dejours and Beeckenkamp, 1977; McMahan et al., 1974; Wheatly and Taylor, 1981). However, sometimes an adjustment on O₂ extraction can be evident also (McMahon and Wilkens, 1975; Taylor, 1976). These results re-emphasize the tremendous diversity in crustacean response to hypoxia both within and between species (Taylor, 1982). Unfortunately, the causes underlying this variability are unknown.

Crustacean responses to hypoxia in air are less variable than in water (Fig. 2); generally regulation prevails, although mechanisms vary. For example, the aerial V₀₂ of Cardisoma guanhumi showed no change except at very low P₀₂ (Fig. 2(D)). A similar response was reported for the same species by Herreid and Clifford (1963). Moreover, this response was reported for the same species by Cameron (1975).

Rather Gecarcinus adjusted to hypoxia by maintaining O₂ extraction fairly constant or even increasing it. Both these species respond to treadmill exercise in an analogous way: Cardisoma guanhumi compensates primarily by increasing ventilation while Gecarcinus lateralis adjusts primarily by extraction presumably via circulatory modifications (Herreid et al., 1979, 1983). Another difference in the species must be emphasized: Gecarcinus is less tolerant to hypoxia than Cardisoma. G. lateralis showed extreme stress at P₀₂ below 20 torr, regurgitating fluid and performing an oscillatory ventilation. Only two C. guanhumi showed oscillatory ventilation patterns and those appeared only at P₀₂ = 5 torr. Cardisoma guanhumi appears better adapted to hypoxic conditions than G. lateralis; both crabs are largely terrestrial but their burrow habitats differ. C. guanhumi lives in mud burrows with water in the living chamber that smells of H₂S (Herreid and Gifford, 1963). Moreover, this species retires below ground and plugs its burrow for several months. Conditions are surely relatively hypoxic. G. lateralis tends to exist in shallow dry burrows in open sandy soil with good air circulation. Reflecting such ecological differences between species: there are physiological differences as well; e.g. Cardisoma has a low hemolymph P₀₂ of 4.5 torr while Gecarcinus has a higher P₀₂ of 18 torr (Redmond, 1968; Taylor and Davies, 1981).

What of Callinectes sapidus? This aquatic species showed no special response to aerial hypoxia (Fig. 2). V₀₂ declined somewhat early in the experiment and then remained constant over a broad range of P₀₂, from 135 to 50 torr. Certainly no significant ventilatory compensation occurred at all. A similar comment might be made for the coconut crab Birgus; increased ventilation does not appear to be used until very low V₀₂ are reached (Cameron and Mecklenburg, 1973). In short, most crabs do not show undue dependency on P₀₂ in air, no doubt due to the large absolute amounts of O₂ present even at low P₀₂. Adjustments to a declining P₀₂ do not seem to be ventilatory except in the case of Cardisoma guanhumi. Most crustaceans that regulate in air do so by maintaining constant O₂ extraction, probably via circulatory adjustments.

In conclusion, this comparative study suggests that the short-term response of decapod crustaceans to respiratory stress (hypoxia and hypercapnia) depends on the medium, water vs air. In general oxygen sensitivity dominates in the aquatic environment, while CO₂ or pH sensitivity in air is the most important regulatory factor. This general principle of gas exchange developed from vertebrate studies has been supported for invertebrates. Further study of crustacean respiration can lend information on the evolutionary transition from water to land.

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