THE SHORT-TERM RESPIRATORY RESPONSES ON THREE CRABS EXPOSED TO WATER-AIR MEDIA

M. C. F. SANTOS and VALÉRIA I. COSTA

Departamento de Fisiologia Geral, Instituto de Biociências, Centro de Biologia Marinha, Universidade de São Paulo, São Paulo, Brasil

Abstract - l. The measurements of oxygen consumption (MO_2) in crabs following abrupt transference of media was found to be a useful tool for comparative studies. The results are of the same magnitude as the ones found in the literature. Careful handling permitted determinations on undisturbed animals, at the minimal level of activity.

2. The MO_2 was measured on three species of crabs, the semi-terrestrial *Goniopsis cruentata,* the amphibious *Ucides cordatus* and the aquatic *Callinectes danae.* There was a highly significant increase in the rates when they were suddenly transferred from water to air. This increase was highest in the blue crabs acclimated to the dilute salinity, but the salinity effect *per se* was negligible.

3. When *U. cordatus* was submerged, MO_2 fell to one-tenth of its aerial value and this effect was softened with the previous acclimation in water.

4. *G. cruentata* drowned after 210 min submerged in water. The females are more sensitive than the males, showing frequent occurrence and long duration of apnoeic periods in air, both sexes presenting behavioral depression.

INTRODUCTION

The respiratory system of amphibious crabs has been studied by several authors and important contributions have been made on such species as the intertidal *Carcinus maenas,* some land crabs belonging to the genus *Gecarcinus* and *Cardisoma* and the coconut crab *Birgus latro* (Taylor, 1976; Shah and Herreid, 1978; Cameron, 1975; McMahon and Burggren, 1988 reviews).

Usually there is no Opportunity for researchers to work with Species of distinct habits, from the same geographical area during one season, but is easier to achieve in a tropical country due to the biological diversity. The adaptive changes necessary for a terrestrial existence should have appeared often in tropical regions, where crabs face fluctuating environmental conditions, providing ideal situations for the gradual evolution of terrestriality. Crabs showing varied degrees of independence from water are interesting subjects for investigation, because of the lack of available literature and data. We investigated the estuarine blue crab *Callinectes danae,* the mangrove crab *Ucides cordatus* and the tree climbing mangrove crab *Goniopsis cruentata* because of the osmotic and ionic regulation studies, water loss studies and the effects of pollutant on them (Zanders and Martelo, 1984; Santos and Salomão, 1985; Santos *et al.,* 1987; Martinez, 1989; Carmo, 1991), whereas details about their respiratory system, at present are almost unknown (Young, 1973; Santos *et al.,* 1985). On the other hand, the crabs such as *Carcinus maenas* and *Callinectes sapidus* are portunids as well as *C. danae* and they have been extensively studied (see reviews: Cameron, 1989; Morris, 1991). So, the data from crabs belonging to the same family, but from diverse geographical distribution may also be of interest.

Callinectes danae occurs on the Occidental Atlantic coast from Florida to Argentina (MeIo, 1985). This species is common in Brazil, inhabiting muddy estuaries in mangroves and algae-covered broken shell bottoms, to beaches and open ocean depths of upto 75 m (Williams, 1984). *C. danae* survives for several hours when exposed to air and when kept in shallow sea water, it ventilates the branchial chamber with air, although highly adapted to an aquatic existence.

The mangrove crab *Ucides cordatus* is an abundant species on the Brazilian coast, living in water-filled bottom burrows among mangrove roots. They are exposed to both seasonal and semi-diurnal salinity changes. At low tide they perform terrestrial incursions for several hours in air, during activities of burrow cleaning and feeding behavior. This land crab survives more than 50 hr when submersed, possesses a highly vascularized branchial chamber walls and a reduced number of gills (Santos *et al.,* 1985; Santos and Salomão, 1985). Recently it was regarded as the largest of the Ocypodidae (Rodrigues, 1982; Hartnoll, 1988).

Goniopsis cruentata is a tree climbing grapsid crab, occurring on the Occidental Atlantic coast from Florida to Santa Catarina (Brazil). When pursued it climbs actively amongst the trees or leaps on the swamp floor. During the high tide they are seen at the top of the trees, but very often they wet their gills in the disposable water either in burrows of other species or in the re-entering angles of trees. According to Hartnoll (1988) this species is among the examples that live at or just above the high tide. *G. cruentata* and *U. cordatus* inhabit the same place in Brazilian mangrove, both exposed to the tidal cycle, the first one being more active and losing water faster than the second one (Santos *et al.,* 1986).

Therefore, the present study was designed to compare the rate of oxygen consumption of these three hyperhyposmotic regulator crabs under subtle environmental change as it occurs during air exposure (emersion, low tide) and the immersion (high tide). Also during a submersion period and under declining oxygen tension. The assumption was that short time exposure may help to understand the first respiratory changes, which could be correlated with a tidal cycle.

MATERIALS AND METHODS

Oxygen consumption measurements were performed on males of *Callinectes danae* and *Ucides cordatus* and both sexes of *Goniopsis cruentata.* The mangrove crabs were collected by hand, and the blue crabs by special traps, during spring season (September), from the North Coast of the State of São Paulo, Brazil (23º 44'S; 45º 54'S). Only intermoult animals were used. On alternate days *Callinectes* and *Goniopsis* were fed with pieces of shrimp and *Ucides* with lettuce, but they were starved for at least 24 hr prior to experiments. Five days elapsed between arrival of the animals and their use in experiments; the light-dark intervals followed the 12 hr:12 hr pattern. During this period the animals were maintained under specific acclimation conditions, followed by the oxygen consumption determinations (5 readings).

Submersed-submersed (s /5) situation

A group of *C. danae* and a group of *U. cordatus* were kept in 9 ppt sea water in two tanks (100 l) maintained under constant conditions of oxygenation provided by a continuous water circulation. These tanks had a substratum of sand and gravel. The blue crabs were held for 5 days whereas the mangrove crab was submersed for 24 hr. Another group of *C. danae* was held in the same conditions, but in 34 ppt sea water. On the day of the experiments the animal was placed for l0 min in a clean glass bottle (1.5 1) filled inside the tank, before the determinations.

Aerial-submersed (a /s) situation

U. cordatus and G. *cruentata* were maintained for 5 days in unleveled containers that had a layer of sand and gravel at one end and at the other, free access to 9 ppt sea water where the crab could submerge. Ten minutes before the measurement of oxygen consumption, the animals were placed in a bottle (1.5 1) immersed in a tank with 100 1 of 9 ppt sea water, care was taken to ensure that no air remained trapped in the branchial cavity.

Aerial-aerial (a/a) situation

U. cordatus and *G. cruentata* were kept for 5 days in unlevelled containers as described before,

with free access to 9 ppt sea water where submersion was permitted. The measurements of the oxygen consumption was carried out in a 1.5 1 glass bottle, after 10 min of the crab handling. The carbonic gas was absorbed with the use of ascarite pellets.

Submersed-aerial (s/a) situation

   G. cruentata were maintained under 9 ppt circulating sea water in a 100 1 tank, the males for 210 min and the females for 150 min, whereas *U. cordatas* were submersed for 24 hr and two groups of *C. danae* were held for 5 days in both salinities 9 ppt and 34 ppt, as described in the submersed-submersed situation. Then, they were transferred into the glass bottle inside the sea water. Ten minutes after water removal, the measurements were started.

   Respiratory rate was determined by measuring the oxygen concentration surrounding the crab in a closed system over a known period of time (1 hr) using an oxygen meter (model DMO-2 Digimed Ind. Brasil) attached to the bottle probe. When required the crabs were placed inside the respirometer, on a perforated platform under which the water was gently agitated to permit complete gas dispersion. At the end of each experiment the crab was dried of excess water and weighed. All the experiments were carried out at constant temperature ($19.01 \pm 0.55^{\circ}C$) and the measurements were made during the afternoon, to avoid effects of the 24 hr rhythms of activity. This was repeated for 28 specimens of *C. danae,* 25 of *U. cordatus* and 32 of *G. cruentata* (16 males, 16 females). When required the barometric pressure was recorded along with the analyzer scale reading, so that, the PO_2 of the air in the chamber could be calculated.

   The oxygen concentrations (mg/1) at each measurement interval were converted to weight-specific oxygen consumption rate (µM/kg/min). In all the experiments the oxygen consumption rate was measured at a standard situation, from 100 to 80% of oxygen available and in other series, it was also recorded when the oxygen availability in the water was lower than that level.

   Statistical treatments were performed according to Zar (1974). Means were compared and analyzed for differences using a ANOVA one-tailed and SNK tests, with a significance level of 0.05. Mean (X) values ± SE and *(N)* are reported.

RESULTS

   The oxygen consumption rates (MO_2) on *Callinectes danae* acclimated for 5 days in 9 and 34 ppt sea water were recorded and the values, in both salinities were considered similar as the difference was not statistically significant (53.88 ± 8.3 µM/kg/min; 45.25 ± 7.3 µM/kg/min; $P > 0.05$). When the blue crabs were transferred from those salinities to 1 hr air exposure, the mean MO_2 increased to 135.82 ± 21.3 µM/kg/min and to 115.25 ± 30.9 µM/kg/min respectively, in the crabs from diluted and 100% sea water. The highest rises in MO_2 during air exposure occurred in crabs from the diluted medium *(P <0.05)* as showed on Table 1 and Fig. l A and 1B. During these aerial measurements the blue crabs were quiescent throughout the experiments and when they returned into the sea water tanks, they showed vigorous and fast normal swimming.

   The mean MO_2 on the mangrove crab *Ucides cordatus* during 1 hr of air exposure was recorded following the aerial acclimation for 5 days. The data obtained were 48.0 ± 11.3 µM/kg/min, and they are shown in Table 1 and Fig. l C. Those values were significantly higher *(P <0.05)* than the ones determined for crabs transferred into 9 ppt sea water (4.63 ± 1.2 µM/kg/min) from the same previous aerial acclimation. When *U. cordatus* were acclimated to submersion for 24 hr into 9 ppt sea water and after they were transferred to aerial exposure, there was an abrupt increase of MO_2, from $17.14+1.8$ to 90.01 ± 16.1 µM/kg/min *(P <0.01)*.

   The values of MO_2 on *Goniopsis cruentata* obtained during the aerial-aerial experiment are given in Table 1 and Fig. 1 D,E. The effect of body weight range was evident between female and male; the females had a much higher and irregular rate. The respirometer chamber was large enough (1.5 1) to permit free locomotion, but both sexes were quiescent throughout the measurements and there was no difference in behavioral activity.

Table l. Oxygen consumption rate, availability of oxygen during tests and weight of crabs submitted to different experimental procedures, at 20° C

Species	Experimental situation	N	Oxygen consumption (µM/kg/min)	Oxygen available (%)	Body wt (8)
C.danae	0.9% x s/s	5	53.88	83.71	50.47
			8.30	2.88	1.57
	0.9% x s/a	6	135.82*	98.40	48.90
			21.27	0.49	5.32
	3.4% x s/s	4	45.25	81.46	62.57
			7.32	2.73	8.06
	3.4% x s/a	4	115.25*	97.83	60.60
			30.95	0.45	10.45
U.cordatus	a/a	5	48.03	97.00	186.10
			11.30	1.96	21.42
	a/s	6	4.63*	89.30	209.06
			1.20	4.47	6.78
	s/s	6	17.14	80.47	166.19
			1.84	2.52	8.24
	s/a	7	90.01**	96.51	150.50
			16.08	0.58	14.07
G. cruentata	Female a/a	6	107.03	97.18	42.16
			60.67	1.57	5.75
	Female a/s	5	39.73	88.62	46.79
			4.98	1.44	2.09
	Female s/a	4	20.90	98.54	39.21
			20.90	1.26	8.67
	Male a/a	5	16.55	99.34	74.80
			6.96	0.25	4.62
	Male a/s	6	31.19	87.60	75.68
			5.55	1.57	3.87
	Male s/a	4	70.76	95.62	63.78
			22.28	1.05	9.01

Values are expressed as mean ± SE. * = $P < 0.05$; ** = $P < 0.01$. Acclimation/test as in Materials and Methods: s/s = submersed/submersed; s/a = submersed/aerial; a/a = aerial/aerial; a/s = aerial/submersed.

In another set of experiments, *Goniopsis cruentata* were acclimated for 5 days in air and they were then transferred into 9 ppt sea water, for 1 hr. During this submersion period, the oxygen consumption was higher for small females than males but not significantly ($P > 0.05$), although the standard errors were similar (39.73 ± 5.0 µM/kg/min and 31.19 ± 5.5 µM/kg/min, respectively).

Due to the lack of literature data about the survival time of *Goniopsis cruentata* in submersion conditions, it was necessary to confine them in aerated recirculating tanks (100 1) and to record the death time. Male crabs submerged in 9 ppt sea water began to die after 4hr of total submersion. So the submersed-aerial experimentation was carried out 3.5 hr for the males and 2.5 hr for the females.

The body wt of the specimens (S/A) was statistically the same ($P > 0.05$). The males MO_2 values were constant (79.76 ± 22.3 µM/kg/min), whereas among the four females, only one had a measurable consumption (83.60 µM/kg/min). The rises of MO_2 in crabs when transferred to air

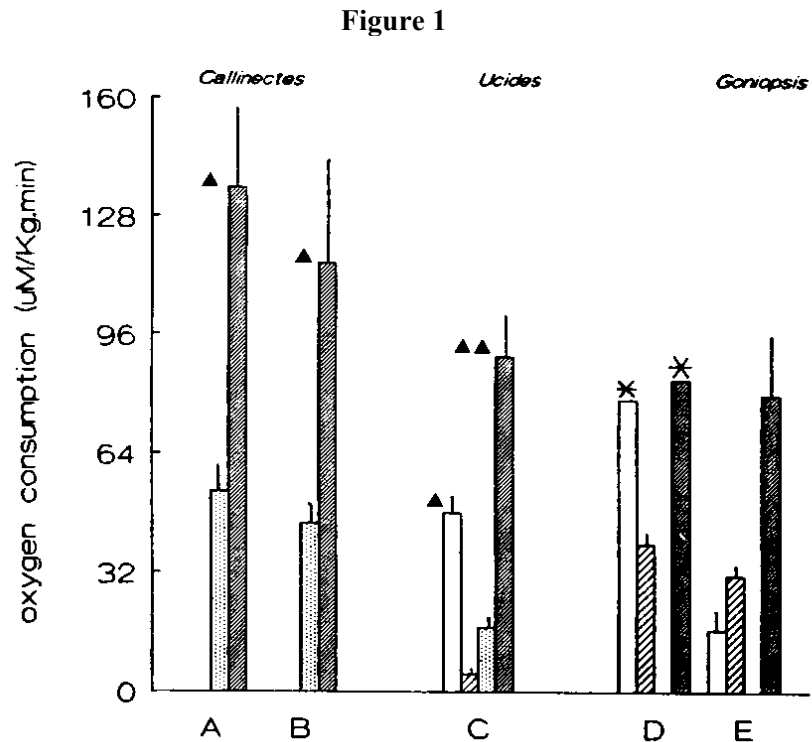**exposure after a submersion period was found for both sexes.**

Figure 1

Fig. 1. Oxygen consumption of crabs exposed for 1 hr, at 20°C, to different experimental procedures. □ a/a = aerial/aerial; ☒ a/s = aerial/submersed; ▦ s/s = submersed/submersed; ▨ s/a = submersed/aerial. A,B = C. *danae* in 9 and 34 ppt; C = U. *cordatus*, 9 ppt; D,E = G. *cruentata*, in 9 ppt, female and male. Height of bars represents mean ± SE ($N = 4$–7) except in *. ▲ = $P < 0.05$; ▲▲ = $P < 0.01$.

Figure 2 shows the rates of oxygen consumption for 1 hr on the three species of crabs submerged into 9 ppt sea water, in which the partial pressure was progressively lowered. The animals were previously acclimated to total submersion (S/S) in the same salinity water or to aerial exposure (A/S). *Callinectes danae* presented the higher rates, followed by *Goniopsis* and *Ucides*.
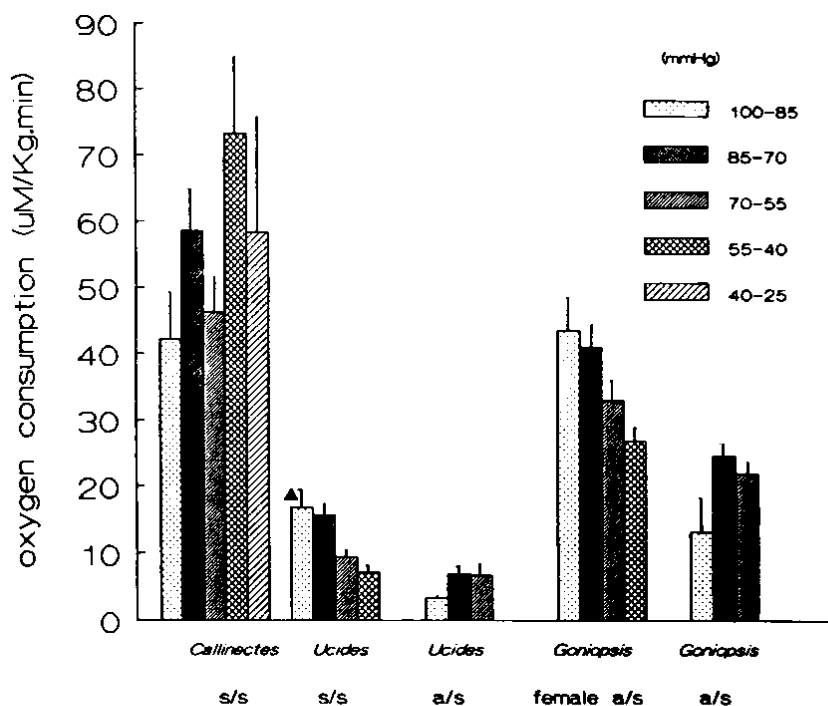
Figure 2

Fig. 2. Rates of oxygen consumption (MO$_2$) for 1 hr, on crabs from previous submersed or aerial acclimation, transferred into 9 ppt sea water with progressively lowered PO_2. Acclimation/test conditions as before. Height of bars represents mean $\pm$ SE ($N = 3$–11). ▲ $= P < 0.05$.

The blue crabs showed the general tendency to increase the MO$_2$ from 42.72 ± 22.94 to 58.35 ± 34.41 µM/kg/min, as the water partial pressure of oxygen decreased. The differences were not significant due to the individual variations. The movements of scaphognathite and buccal appendices increased too, the blue crabs did not move throughout the test.

The Oxygen consumption on submerged *Ucides cordatus* was significantly higher (P <0.05) at the beginning of the experiment, at 100 to 70 mm HgO$_2$: 16.76 ± 4.60 µM/kg/min, than at P O$_2$ 40 mmHg: 7.12 ± 2.21 µM/kg/min. The mangrove crabs stayed quiescent during the measurements.

The MO$_2$ for submerged *U. cordatus* which previously were acclimated to air exposure showed the lowest values, but they were statistically similar at the different levels of water PO$_2$ (3.35 ± 1.03 µM/kg/min, 6.95 ± 2.30 µM/kg/min and 6.69 ± 3.32 µM/kg/min). The animals remained static.

There was no significant difference between female and male MO$_2$ on *Goniopsis cruentata* when they were submitted to submersion in 9 ppt sea water, due to the large individual variations. The females during 1 hr of measurements consumed oxygen faster than the males, as the water P O$_2$ lowered to 40 mmHg. The general tendency, for both sexes was to decrease the MO$_2$ as the oxygen in the water decreased, the females from 43.64 ± 10.04 to 26.90 ± 3.34 µM/kg/min and the males from 31.19 ± 13.59 to 21.91 ± 5.51 µM/kg/min. There was no crab movement during the measurements.

DISCUSSION

Although the short-term measurements of oxygen consumption in crabs following different acclimation conditions include handling stress, they are a useful tool in comparative respiratory studies. The present results are similar to those presented by other authors. The oxygen consumption on the submersed *Callinectes danae,* in the range of 45-54 µM/kg/min, is similar to 46.2 µM/kg/min recorded by Batterton and Cameron (1976) on *Callinectes sapidus* at resting conditions, or to 59.2 µM/kg/min recorded by O'Mahoney and Full (1984), on the same species, resting in normoxic water and using the first 3 hr of a 9 hr experiment to determine baseline data. If we analyze the animal body mass, our results are lower than these, as we used 50-60 g *C. danae* and the previous authors used *C. sapidus* at 200 g and 88-147 g, respectively. *C. danae* showed a higher oxygen consumption than the other portunid species, *Carcinus maenas* with similar body mass, where the MO_2 recorded was around 20-30 µM/kg/min, after the crabs had been for 24 hr and overnight inside the respirometer (Taylor, 1976; Taylor *et al.,* 1977; Taylor and Butler, 1978) but the rates continued in both species, at the same level.

The respiratory response to lower salinity (9 ppt) in *Callinectes danae* was negligible, as it was for the same congeneric species *C. sapidus,* according to several author's data presented by Batterton and Cameron (1978). However, Taylor *et al.* (1977) reported that the rate of oxygen consumption of *Carcinus* increases when it is placed in a dilute medium depending on the temperature. At 18^0C, the summer temperature for this British crab, there was no significant increase in MO_2 on dilution, whereas it increased significantly with dilution at 10^0C. The water temperature in a Brazilian estuary during the summer is around 26^0C (Carmo, 1991) and *C. danae* oxygen consumption in a dilute medium, at 20^0C, was not different in 100% SW (53.9 and 45.3 µM/kg/min; $P > 0.05$). It appears that the inter-specific differences and individual variation could explain such response, in addition to the temperature effect.

The most interesting response showed on the three crabs presented here was a highly significant increase in MO_2 when the animals were transferred from submersion to air exposure. In the blue crabs, the MO_2 increase was higher in animals acclimated in the dilute salinity than in the ones from SW, probably as a result of payment of an initial debt acquired due to the osmoregulation cost. The good performance in air may be an indication that the gills were not clumping together, and the width of the individual lamellae were not altered, avoiding the limitation of gas exchange across the gill. According to DeFur *et al.* (1988) the gill chamber of small blue crabs may permit more effective retention of water, which in *C. danae,* is well aerated, as we observed air bubbles near to the exhalant openings when the animal was in shallow medium. The responses on portunids in air are not homogeneous. In *C. maenas* on emersion from hypoxic sea water there was an immediate and maintained tachycardia, with the heart rate increasing, accompanied by a marked increase in oxygen content of the blood (Taylor *et al.,* 1973). On this species, there was no bradychardia, and there were similar rates of VO_2 in air and in sea water (Taylor and Butler, 1978). In *C. sapidus* ventilation continued for at least 8 hr at room temperature and they were able to maintain oxygen consumption during exposure to air (Batterton and Cameron, 1978). On the other hand O'Mahoney and Full (1984) recorded a lower VO_2 in air than in water, although the ineffectiveness of *C. sapidus* respiratory system did not cause death in air. DeFur *et al.* (1988) demonstrated in large *C. sapidus* (>118 g) an increase and in small blue crabs (<70 g), a decrease in scaphognathite and cardiac rates over a 4 hr period of emersion. The limitation of gas exchange during emersion appears related to the crab size, besides humidity and temperature, suggested by Batterton and Cameron (1978) as factors in determining when a crab will come out of water and how long it will stay out. The meaning of such high MO_2 increases recorded here during -abrupt air exposure is not easy to understand, but for the mangrove crabs could be an oxygen debt payment as the submersion period during previous acclimation could have contributed to a hypoxic situation. These species are preferentially air breathing, although, *Ucides* is a bimodal breather, surviving more than 50 hr when completely submerged (Santos and Salomão, 1985), whereas *Goniopsis* drowned after 210 mm (present results). It will be interesting to study lactate measurements as the determinations in *Goniopsis* were often disturbed by behavioral depression, and three out of four females tested did not respond to air exposure, reemphasizing the diversity in crustaceans, both within and between species. Handling stress is also included in the values recorded when there was sudden water-air transference, but the females appear to be more

sensitive than the males, showing the frequent occurrence and long duration of the apnoeic periods. Even among undisturbed animals, acclimated for 5 days to aerial conditions, the MO_2 in air was irregular, three out of six females did not respond or presented values with high individual variation. Among the males, the responses were more homogeneous and *Goniopsis* males acclimated to air condition (5 days) showed an MO_2 in air comparable to the values recorded by Young (1973) in the same species, 16.55 and 11.99 µM/kg/min, respectively. However, the *Goniopsis* males presented an increase in MO_2 when suddenly transferred from air to water, from 16.55 to 31.19 µM/kg/min, probably due to the high activity in an air breather facing adjustments in ventilation, as observed in *Cardisoma guanhumi* by Burggren *et al.* (1985).

Aquatic respiration in the semiterrestrial *Ucides cordatus* depends on the previous acclimation condition. When the animal is transferred from air, the MO_2 decreased by about ten-fold, from 48.03 to 4.63 µM/kg/min, but when it was maintained for 24 hr in water before the measurements, the MO_2 is increased (17.14 µM/kg/min), although significantly lower than the MO_2 in air. The magnitude of values recorded in *Ucides* are comparable to the ones shown by O'Mahoney and Full (1984) in *Gecarcinus lateralis* and *Cardisoma guanhumi*. *Gecarcinus* cannot resist prolonged submersion, while *Cardisoma* is an amphibious crab which compensated for submergence by increased ventilation, without changing the oxygen consumption (around 33 µM/kg/min). They observed that submergence caused oxygen consumption in *Gecarcinus* to decline to one-sixth of the aerial value, from 63.37 to 9.99 µM/kg/min, due to a drop in O_2 extraction in water vs air. The results in *U. cordatus* seems at variance with the two aforementioned crabs as the gas exchange by its gilís appcars to be improved during prolonged submersion. This crab spends a proportion of its exposure to air like *Cardisoma,* nonetheless it had a higher MO_2 in air than water, similarly to *Gecarcinus* which is a true terrestrial crab. This response may be possibly due to the seven gill pairs which are active in water and, during air-breathing, gas exchange occurs also through its highly vascularized gill chamber lining in which the ventilation is aided by carapace movements (Santos *et al.,* 1985).

The responses of the three crabs for 1 hr, to stagnation (i.e. hypoxia plus hypercapnia) were measured and no clear pattern emerged from these data. The aquatic species *C. danae* had the greatest MO_2 values, while the tree climbing crab *Goniopsis* had intermediate and the semi-terrestrial *Ucides* the lowest MO_2 values. In *C. danae* the MO_2 values were quite irregular and due to the high individual variation, there was no statistical difference. In *Ucides,* the abrupt transference of media provoked the minimal MO_2 values recorded, which were maintained during exposure, and in this species after acclimation for 24 hr in water, the MO_2 decreased significantly as the PO_2 in the medium decreased too. In the tree climbing crabs, both female and male, the MO_2 values showed a tendency to conform with the $P O_2$ in the medium, but the regression slopes were not statistically different from zero. The short-time stagnation did not affect the MO_2 in the three crabs. According to O'Mahoney and Fuíl (1984) the VO_2 in *Cailinectes sapidus, Cardisoma guanhumi* and *Gecarcinus lateralis* decreased in hypoxic water; *C. sapidus* showed the fastest rate of decline and *Gecarcinus* the smallest. When submitted to hypercapnic water, *C. sapidus* and *Cardisoma* showed a significant decrease in VO_2, whereas *Gecarcinus* seemed unaffected. Batterton and Cameron (1978) observed that the VO_2 of *C. sapidus* showed a considerable degree of conformity to external $O2$ tensions and during hypercapnia its vcntilation was not employed to regulate PCO_2. From these results, *C. danae* could have showed a MO_2 decrease during stagnation either due to PO_2 decline or PCO_2 increase in the medium. But *C. danae* showed a tendency to high values independent of the ambient tensions. This should be achieved primary by an increase in ventilatory activity, we observed in inactive crabs an increase of movements of the buccal appendices and scaphognathite. An increase in ventilatory activity has been recorded in the other portunids *(Carcinus maenas)* and appears to be a common respiratory response to hypoxia in many species of Crustacea (Taylor, 1976). Under conditions of declining PO_2, inactive *Carcinus* were able to maintain their rate of respiration independent of the ambient oxygen tension. The tendency of MO_2 decrease during short stagnation was found in the two mangrove crabs. The ability to maintain effective oxygen uptake from an aquatic medium appears to have been affected especially in *Ucides* under abrupt medium transference. This effect is softened with previous acclimation in water. In both mangrove crabs, *Ucides* and *Goniopsis,* the failure of the respiratory system to meet the oxygen demand could be associated with a reduction of oxygen diffusion at the respiratory surfaces as suggested by Taylor and Davies (1982) in *Gecarcinus lateralis.* They also observed lactic

acid accumulation in *Gecarcinus* blood which would indicate an increase in anaerobic metabolism.

   The usual diversity present in crustaceans was shown in this study using short term respiratory response. The environment inhabited by the species is more important than the species to determine physiological responses. The three crabs studied here are facing the interface water-air, and they have acquired abilities which discriminate them from the really aquatic species. In some aspects, the *Callinectes danae* physiology is nearer to *Carcinus* than *Callinectes sapidus,* and *Ucides* is nearer to *G. lateralis* than *C. guanhumi,* whereas *Goniopsis* maybe, is half-way between *Ucides* and *Gecarcinus,* towards the terrestrial life.

REFERENCES

Batterton C. V. and Cameron J. N. (1978) Characteristics of resting ventilation and response to hypoxia, hypercapnia, and emersion in the blue crab *Callinectes sapidus* (Rathbun). J. *exp. Zool.* 203, 403-418.

Burggren W. W., Pinder A., McMahon B., Wheatly M. and Doyle M. (1985) Ventilation, circulation and their interactions in the land crab, *Cardisoma guanhumi. J. exp. Biol.* 117, 133-154.

Cameron J. N. (1975) Aerial gas exchange in the terrestrial brachyura *Gecarcinus lateralis* and *Cardisoma guanhumi. Comp. Biochem. Physiol.* 52A, 129-134.

Cameron J. N. (1989) Case study: the blue crab. In *The Respiratory Physiology of Animals* (Edited by Cameron J. N.), pp. 189-208. Oxford University Press, New York.

Carmo T. M. S. (1991) Regulação osmoiônica no siri *Callinectes danae* Smith, 1869 (Decapoda, Brachyura). Efeitos do inseticida organofosforado malation. *Tese de Doutoramento, Universidade de São Paulo,* São Paulo, Brasil.

DeFur P. L., Pearse A., Siebelink A. and Elfers S. (1988) Respiratory responses of blue crabs, *Callinectes sapidus,* to emersion. *Comp. Biochem. Physiol.* 89A, 97-101.

Hartnoll R. G. (1988) Evolution, systematics, and geographical distribution. In *Biology of Land Crabs* (Edited by Burggren W. W. and McMahon B.), pp. 6-54, Cambridge University Press, New York.

Martinez C. B. R. (1989) Regulação osmojônica no caranguejo de mangue *Ucides cordatus* (Linnaeus, 1763), em presença de benzeno, *Dissertação de Mestrado, Universidade de São Paulo,* São Paulo, Brasil.

McMahon B. and Burggren W. W. (1988) Respiration. In *Biology of Land Crabs* (Edited by Burggren W. W. and McMahon B.), pp. 249-297. Cambridge University Press, New York.

MeIo G. A. S. (1985) Taxonomia e padrôes distribucionais e ecológicos dos Brachyura (Crustacea: Decapoda) do litoral sudeste do Brasil. *Tese de Doutoramento, Universidade de São Paulo,* São Paulo, Brasil.

Morris S. (1991) Respiratory gas exchange and transport in crustaceans: ecological determinants. *Mem. Oueensland Mus.* 31, 241-161.

O'Mahoney P. M. and Full R. J. (1984) Respiration of crabs in air and water. *Comp. Biochem. Physiol.* 79A, 275-282.

Rodrigues M. D. (1982) Desenvolvimento pós-embrionário de *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Decapoda, Gecarcinidae). *Dissertação de Mestrado,* UNESP-Rio Claro, Rio Claro, São Paulo, Brasil.

Santos M. C. F. and Salomão L. C. (1985) Hemolymph osmotie and ionic concentrations in the gecarcinid crab *Ucides cordatus. Comp. Biochem. Physiol.* 81A, 581-583.

Santos M. C. F., Engelftein M. and Gabrielli M. A. (1985) Relationships concerning respiratory devices in crabs from different habitats. *Comp. Biochem. Physiol.* 81A, 567-570.

Santos M. C. F., Suadicani S. O., Martinez C. B. R. and Lobo E. (1986) Rates of water loss in four crabs from different habitats. *Comp. Biochem. Physiol.* 85A, 309-312.

Santos M. C. F., Martinez C. B. R., Suadicani S. O. and Lobo E. (1987) Hemolymph osmo-jonic concentrations in terrestrial crabs following desiccation. *Comp. Biochem. Physiol.* 88Â, 83-87.

Shah G. M. and Herreid II C. E. (1978) Heart rate of the land crab, *Cardisoma guanhumi* (Latreilie), during aquatic and aerial respiration. *Comp. Biochem. Physiol.* 60Â, 335-341.

Taylor A. C. (1976) The respiratory responses of *Carcinus maenas* to declining oxygen tension. J. *exp. Biol.* 65, 309~322.

Taylor A. C. and Davies P. S. (1982) Aquatic respiration in the land crab *Gecarcinus lateralis* (Fréminville). *Comp. Biochem. Physiol.* 72A, 683~688.

Taylor E. W. and Butler P. J. (1978) Aquatic and aerial respiration in the shore crab, *Carcinus maenas* acclimated to 15°C. *J. comp. Physiol.* 127, 315-323.

Taylor E. W., Butler P. J. and A1-Wassia A. (1977) The effect of a decrease in salinity on respiration, osmoregulation and activity in the short crab, *Carcinus maenas* (L.) at different acclimation temperatures*. J.* c*omp. Physiol* 119, 155-170.

Taylor E. W., Butler P. J. and Sherlock P. J. (1973) The respiratory and cardiovascular changes associated with the emersion response of *Carcinus maenas* (L.) during environmental hypoxia, at three different temperatures. *J. comp. Physiol.* 86, 95-115.

Williams A. B. (1984) *Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine lo Florida.* Smithsonian Institution Press, Washington.

Young R. E. (1973) Responses to respiratory stress in relation to blood pigment affinity in *Goniopsis cruentata* (Latreille) and (to a lesser extent) in *Cardisoma guanhumi* Latreille. *J. exp. mar. bioil. Ecol.* 11, 91-102.

Zanders P. I. and Martelo M. J. (1984) The influence of acclimation temperature on magnesium and sulphate regulation in two mangrove crabs. *Comp. Biochem. Physiol.* 78A, 487-492.

Zar H. H. (1974) *Biostatistical Analysis.* Prentice-Hall, Englewood Cliffs, NJ.