Respiratory responses of *Clibanarius taeniatus* (Kraus, 1843) and *Clibanarius virescens* (Milne-Edwards, 1848) (Decapoda: Diogenidae) to changes in ambient water temperature

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Abstract

The tropical marine hermit crabs, *Clibanarius taeniatus* (Kraus, 1843) and *Clibanarius virescens* (Milne-Edwards, 1848), were compared for their respiratory responses in a range of temperatures representative of environmental exposure and their vertical distribution on the shores at three locations along Keppel Bay, Queensland, Australia. Results show that oxygen consumption in *C. taeniatus* was unaffected by acute exposure to different water temperatures over the entire range tested, while temperature changes significantly affected *C. virescens*. Values of Q_{10} for *C. taeniatus* were at unity, whereas those for *C. virescens* ranged from 1.3 – 1.9. The ability to maintain respiratory homeostasis during rapid changes in temperature may be of adaptive significance for *C. taeniatus*, since this species is more likely to encounter greater temperature fluctuations in the high shore zone where it is abundant, than is *C. virescens* at low shore.
Key words: *Clibanarius*; hermit crabs; oxygen consumption; tropical; distribution.

Introduction

Rocky intertidal habitats have long been recognized as uniquely dynamic environments in which there are rapid and sometimes very large fluctuations in temperature and salinity. Although intertidal organisms on temperate shores are frequently exposed to rapid changes in temperature and salinity (Meadows and Campbell, 1972; Morris and Taylor, 1983; Metaxas and Scheibling, 1993), organisms in tropical regions sometimes face a wider range of these conditions on a daily, as opposed to seasonal, basis (Moore, 1972; Morton and Harper, 1995). However, most work concerning rocky shore communities and the effects of temperature on community structure, as well as physiological responses to temperature, have been concerned with temperate regions (Barnes, 1969; Ulbricht and Pritchard, 1972; Metaxas and Scheibling, 1993). On rocky shores, temperature stress is well recognized as a critical factor in the structuring of communities (Morris and Taylor, 1983; Little and Kitching, 1996; Bertness *et al.*, 1999). Of all physico-chemical factors encountered, the influence of temperature on the respiratory rate of some intertidal organisms has been well documented (Scholander *et al.*, 1953; Newell, 1969; Vernberg and Vernberg, 1972; Vernberg *et al.*, 1981). For example, Scholander *et al.* (1953) found that the metabolic rates of tropical crustaceans was approximately five to six times higher than that of arctic species. Their data further demonstrated that, within relative temperature ranges, the highest Q_{10} values for oxygen consumption generally occurred when crustaceans were exposed to mid and low temperatures. Bayne and Scullard (1978) reported oxygen consumption in the

temperate intertidal mollusc, *Thais lapillus* (Linnaeus, 1758), higher in summer than in winter. However, they suggested that these rates were influenced by the feeding regimes in summer versus winter. Stillman and Somero (1996) found that oxygen consumption increased as temperature increased for the temperate, low shore porcelain crab, *Petrolisthes eriomerus* (Stimpson, 1871) and its high shore relative, *Petrolisthes cinctipes* (Randall, 1839). Although there were no differences in oxygen consumption rates between species for large sized crabs, rates were different for small crabs, with the low shore species having a higher rate than the high shore species.

Despite the wealth of information on the effects of physico-chemical factors on intertidal organisms, few data regarding the respiratory metabolism of hermit crabs in relation to environmental factors have been reported, with even fewer studies published for tropical species. Scholander *et al.* (1953) found the metabolic rates of the arctic hermit crabs, *Pagurus splendescens* (Owen, 1839) and *Pagurus trigonocheirus* (Stimpson, 1858), to be significantly lower than the tropical species, *Clibanarius antillensis* Stimpson, 1862, as measured by oxygen consumption. In work with *Diogenes bicristimanus*, Sarojini and Nagabhushanam (1968) reported that when oxygen consumption was measured at 20°, 27°, 34° and 38°C, respiratory rate decreased at both low and high temperatures. In measurements of metabolic rates for *Clibanarius vittatus* (Bosc, 1802), in 35 ‰, Wernick (1982) reported no significant differences in oxygen consumption values for temperatures between 20° and 30°C in relation to the acclimation temperature (20°C).

This paper examines the respiratory responses of the hermit crabs, *C. taeniatus* and *C. virescens* in relation to a range of temperatures representative of tropical intertidal environments in Queensland throughout the year. Furthermore, this investigation deals with the metabolic responses of these species in relation to their vertical distribution on the shore. The comparison of closely related species occupying similar habitats may provide a meaningful demonstration of the adaptive significance of temperature insensitive metabolism in intertidal organisms and further our understanding of physiological responses in relation to ecogeographical distribution.

Materials and Methods

Specimens of *C. taeniatus* and *C. virescens* were collected from the rocky intertidal region of Keppel Bay, Queensland, Australia (23°08.5'S; 150°45.7'E) throughout June, 1998 – May, 1999. Hermit crabs were brought back to the laboratory at Central Queensland University and allowed to acclimate in continuously aerated aquaria at 25 ± 2°C under a 12 h light : 12 h dark regime for at least 7 days before exposure to experimental treatments. For acclimation aquaria and for all experiments, I collected seawater from a nearby tidal creek. Measurements of inshore water along the Keppel coast over the period from April, 1989 – March, 2001 indicated that salinity averaged approximately 36 ‰ (Coates, 1992; Dunbar, 2001) and temperatures ranged from 10.5° - 33°C (Dunbar, *et al.*, 2003). Therefore, acclimation tank salinity was adjusted to 36 ± 1 ‰ every 2 – 3 days. Crabs were fed frozen fish once a week and at the same time supplied with algae by the addition of algae-covered rocks into the aquaria.

Work on *Hemigrapsus nudus* (Dana, 1851) and *Hemigrapsus oregonensis* (Dana, 1851) by Todd and Dehnel (1960), *Carcinus maenus* (Linnaeus, 1758) by Siebers (1972), *Pagurus longicarpus* Say, 1817, by Biggs and McDermott (1973), and *Callinectes sapidus* Rathbun, 1896 by Findley (1978) have indicated no effect of gender on physiological response. Thus, animals were not sexed for oxygen consumption experiments.

Oxygen Consumption

To avoid lowering oxygen availability and increasing concentrations of waste products during treatments, a flow-through re-circulating water apparatus was made of three 250 ml Perspex chambers connected in series by inflow and outflow rubber tubing to measure oxygen consumption. Oxygen electrode probes connected to two TPS 90D Dissolved Oxygen (DO_2) meters and independently fitted to the incurrent and excurrent chambers, measured differences in percent saturation of oxygen every 300 s. Treatment temperatures were kept constant ($\pm$ 1.0°C) by having the three chambers of the apparatus submersed in a constant temperature water bath. For the 25° and 35°C treatments, two Thermoline, Mini Unistat immersion circulators were used to maintain temperature. For 15°C treatments, temperature was maintained by two Thermoline Mini Unistat heater-stirrers in combination with a Tecam unregulated coil dip cooler. I controlled flow of water through the system by using a Medos Univol 1100 variable-speed peristaltic pump, with an average flow rate of 239.36 ml.h^{-1}.

Individual hermit crabs were selected within the total weight (including shell) range of 1.00 – 2.50 g. Shell-free wet weights were calculated using the formula:

$$W_{SF} = W_{tb} - W_s \qquad (1)$$

where W_{tb} is the total weight (including shell) before treatment and W_s is the weight of the shell.

Groups of four hermit crabs of the same species were acutely exposed to one of three temperatures (15°, 25° and 35°C) in 36 ‰ water for 6 h, a period comparable to mean tidal exposure time in the field. Shell-free wet weight for each group of four individuals ranged from 0.51 g – 1.28 g for *C. taeniatus*, and from 0.49 g – 1.20 g for *C. virescens*. Upon completion of treatments, each shell was cracked open in a small, metal vise and the occupants removed, dabbed dry and weighed to determine wet tissue weight for calculations of weight-specific oxygen consumption. Weight-specific oxygen consumption was calculated from percent oxygen saturation readings taken after oxygen saturation levels had stabilized (3 – 5 h into the experiment) using the formula:

$$MO_{2WS} = S_i - S_e (C'_{ts}) (F) \bullet W^{-1} \qquad (2)$$

where S_i and S_e are the measured percent saturation of oxygen in the incurrent and excurrent treatment water, respectively; C'_{ts} is the calculated value for oxygen solubility at a given temperature and salinity in mlO_2/l SW; F is the average flow rate per hour; W is the total wet weight of tissue for samples in the treatment. Values of oxygen solubility in water with up to 20 ‰ chlorinity given by Kennish (1989) were converted to salinity by multiplying by the conversion constant, 1.80655. After conversion, values were calculated by linear regression for treatment temperatures (15°, 20°, 25°, 30°and 35°C).

Controls with seawater only were performed to determine oxygen consumption by water borne microbes and algae. Groups of four empty shells from which hermit crabs had been removed were also tested over the same treatment time at all temperatures. Since the aim of this control test was to see if shell epibionts significantly affected oxygen consumption rates measured for crabs with shells, test shells were not scrubbed clean of epibionts. All treatment and control experiments were replicated four times (n = 4).

Data were analyzed by Model I, two-way ANOVA for "Species" and "Temperature" followed by post-hoc Tukey pairwise comparisons.

Tidepool Temperature and Distribution on the Shore

In order to investigate if tidepool temperatures varied with height on the shore, sites were divided into three transects of approximately equal width (depending on shore width) and parallel to the water's edge. I defined Low Shore as the area between Mean Low Water Springs and Mean Low Water Neaps, Mid Shore as between Mean Low Water Neaps and Mean Sea Level, and High Shore between Mean Sea Level and Mean High Water Springs. A TPS WP 84 Salinity/Temperature meter was used to collect temperature data from tidepools at each level of the shore between March and April, 2001. Twenty readings for each shore height were taken at S. Cooee Bay, 35 at Emu Point and 30 at Fisherman's Beach.

Surveys for *C. taeniatus* and *C. virescens* took place between November, 1997 and June, 1999 at three rocky intertidal sites along Keppel Bay. The same transect system described above was used to randomly select 10 tidepools at each shore height. I then recorded a total of 15 animals from within or around (i.e. within roughly one metre) each pool. Only hermit crabs that were readily visible were included. Data for each shore height from three separate surveys were combined and relative abundances calculated to give a profile of the distribution of both species at each site.

Results

Oxygen Consumption

The effects of temperature on oxygen consumption in *C. taeniatus* and *C. virescens* exposed to temperatures between 15° and 35°C are shown in Figure 1. Although significant differences in oxygen consumption did not occur between species at 15° and 25°C, the metabolic rate of *C. virescens* differed significantly from *C. taeniatus* at the highest temperature tested (*C. virescens*: 305.0 $mlO_2.h^{-1}.g^{-1}$; *C. taeniatus*: 191.1 $mlO_2.h^{-1}.g^{-1}$; one way ANOVA, $F_{1,7}=17.55$, P<0.01).

I found that for *C. virescens*, while increases in oxygen consumption between 15° and 25°C (15°C: 122.1 ± 29 $mlO_2.h^{-1}.g^{-1}$; 25°C: 237.5 ± 27 $mlO_2.h^{-1}.g^{-1}$; P<0.05) and between 15° and 35°C (35°C: 305.0 ± 22; P<0.05) were significant, the increase between 25° and 35°C was not. In contrast, there was no significant increase in the oxygen consumption of *C. taeniatus* when exposed to temperatures 10°C above or below the acclimation temperature of 25°C. In order to further investigate the similarity in oxygen consumption of *C. taeniatus* over the range of treatment temperatures, I ran additional oxygen consumption tests on this species at the intermediate temperatures of 20° and 30°C, using the same methods as previously described. As shown in Table I, no significant differences in oxygen consumption occurred between any of the five temperatures tested from 15° to 35°C in 36 ‰ for *C. taeniatus* (one way ANOVA, $F_{4,15}=0.383$, P>0.05).

When temperature coefficients (Q_{10}) were calculated and compared between species and among temperatures, coefficients for both species were relatively low. For *C. virescens*, Q_{10} values ranged from 1.3 to 1.9, with the lowest value representing the change in oxygen consumption between the acclimation temperature (25°C) and 35°C and the highest value between 15° and 25°C (Table II). When Q_{10} values for *C. taeniatus* were compared, they were virtually identical over all temperatures tested, ranging from unity to only 1.1 (Table II).

Tidepool Temperature and Distribution on the Shore

Tidepool temperatures at S. Cooee Bay did not differ significantly between tidepools at the three heights on the shore over the period sampled (Figure 2A). There was also no difference in temperature between pools at low and mid shore at either Emu Point or Fisherman's beach (Figure 2A and C). In contrast however, water temperatures at high shore were significantly warmer (one way ANOVA, Emu Point: $F_{2,104} = 7.468$, P<0.01; Fisherman's Beach: $F_{2,89} = 12.141$, P<0.001) than pools at mid and low shore at both Emu Point and Fisherman's (Figure 2B and C).

Figures 3A, B and C show measurements for the relative abundances of *C. taeniatus* and *C. virescens* at three shore heights along South Cooee Bay, Emu Point and Fisherman's Beach, respectively. At all three sites, *C. taeniatus* is not only more abundant, but also has a greater relative abundance at all three heights along the shore than does *C. virescens*. Although *C. virescens* can be found on some shores at all three levels (Figure 3A and B), they occur in very low numbers when compared with *C. taeniatus*, particularly at high shore.
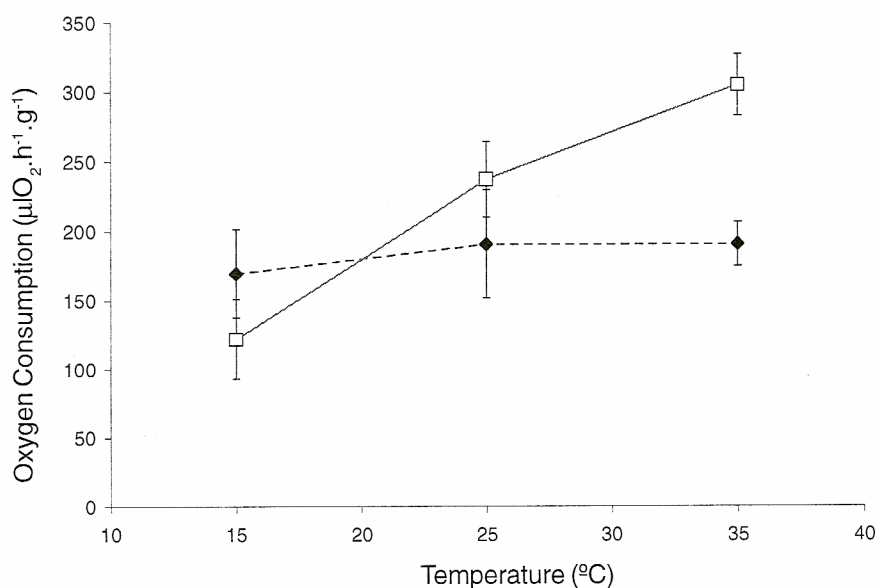

Figure 1: Comparison of mean oxygen consumption for *C. taeniatus* (◆) and *C. virescens* (□) at 15°, 25° and 35°C in 36 ‰. For each point, n = 4. Vertical bars represent ± S.E.M.

Table I: Results of Tukey comparisons of oxygen consumption ($\mu LO_2.h^{-1}.g^{-1}$) for *C. taeniatus* in intermediate treatment temperatures (20° and 30°C) to confirm no difference (at P= 0.05) in oxygen consumption between temperatures at the acclimation salinity of 36 ‰ seawater. Oxygen consumption is presented as mean ± 1 standard error. For each temperature n = 4. NS : P > 0.05.

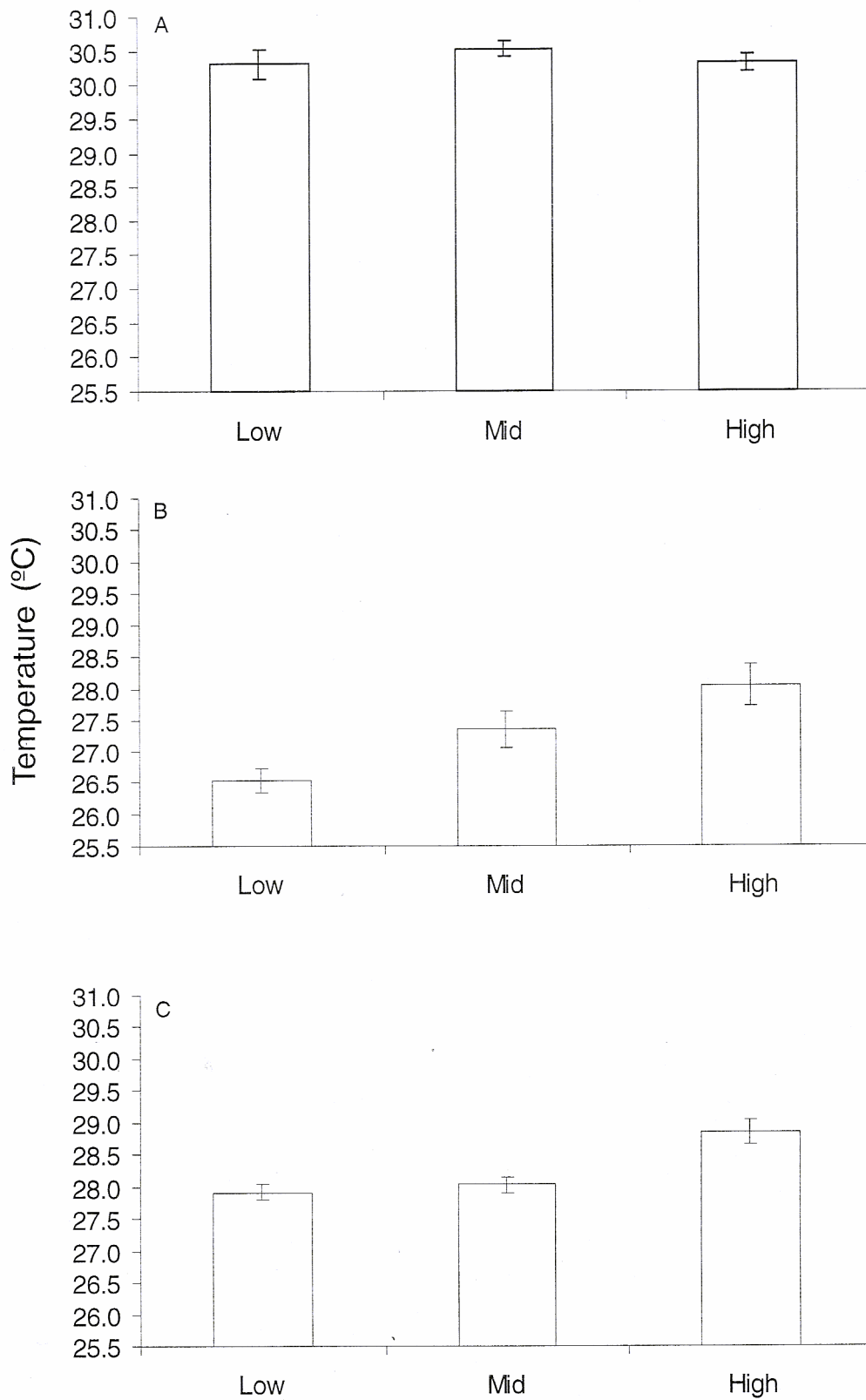| Oxygen consumption | | Temperature ± 1°C | | | | |
		(Oxygen consumption $\mu O_2.h^{-1}.g^{-1}$)				
at 36 ‰ ($\mu IO_2.h^{-1}.g^{-1}$)		15	20	25	30	35
		(169.9 ± 32)	(153.3 ± 21)	(190.9 ± 39)	(188.9 ± 9.8)	(191.1 ± 16)
15	169.9 ± 32	---	NS	NS	NS	NS
20	155.3 ± 21		---	NS	NS	NS
25	190.9 ± 39			---	NS	NS
30	188.9 ± 9.8				---	NS
35	191.1 ± 16					---

Figure 2: Differences in mean tidepool temperatures at three shore heights at **A**: S. Cooee Bay; n = 20 for each shore height, **B**: Emu Point; n = 35 for each shore height, and **C**: Fisherman's Beach; n = 30 for each shore height, during March and April, 2001. Vertical lines on each bar represent ±S.E.M.
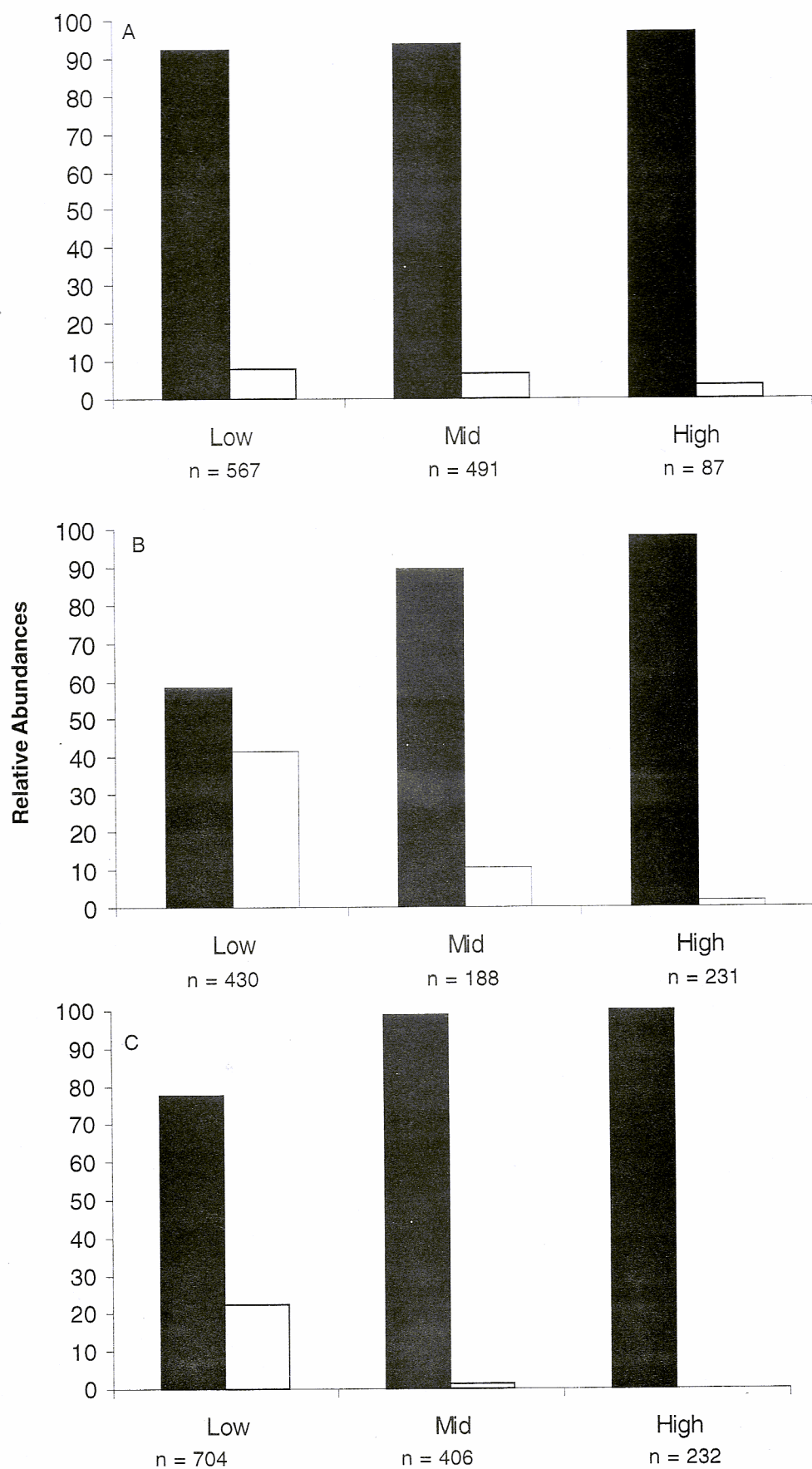
Figure 3: Relative abundances (%) of *C. taeniatus* (■) and *C. virescens* (□) along transects at three shore heights (low shore, mid shore and high shore) at **A**: S. Cooee Bay, **B**: Emu Point and **C**: Fisherman's Beach.

Table II: Comparison of Q_{10} values for oxygen consumption of *C. taeniatus* (*C.t.*) and *C. virescens* (*C.v.*) between the three experimental temperatures in 36 ‰.

	Temperature (°C)		
	15 - 25	25 - 35	15 - 35
C. t.	1.1	1.0	1.1
C. v.	1.9	1.3	1.6

Discussion

Oxygen Consumption

Measurements of standard oxygen consumption in the intertidal hermit crabs, *C. taeniatus* and *C. virescens* suggested that these species exhibit different physiological responses when exposed to acute changes in ambient water temperature at a constant salinity (36 ‰). While there was a significant effect of temperature on the oxygen consumption of *C. virescens*, respiration in *C. taeniatus* was unaffected when exposed to temperatures higher or lower than the acclimation temperature.

The high Q_{10} value for *C. virescens* between 15° and 25°C is consistent with results for other tropical decapods tested at temperatures below that of the habitat (Scholander *et al.*, 1953; Kutty *et al.*, 1971; Vernberg and Vernberg, 1972; Wernick, 1982). While not strictly a subtidal species, *C. virescens* is characteristically found at the lowest level of the intertidal shore as well as in the shallow subtidal. High Q_{10} values may not, necessarily, be a disadvantage for hermit crabs living among the low shore/shallow subtidal habitat, where acute changes in temperature are less likely to occur than on the exposed, upper intertidal, especially over long time periods.

In contrast, standard oxygen consumption in *C. taeniatus* was unaffected by changes in temperature throughout the entire range of temperatures tested (15° - 35°C) and is reflected in Q_{10} values of unity for this species. These results are in agreement with the few studies reporting Q_{10} values approaching unity for oxygen consumption in anomurans in response to changes in temperature (Scholander *et al.*, 1953; Burggren and McMahon, 1981; Wernick, 1982; McMahon and Burggren, 1988). For example, in measurements of standard oxygen consumption in hermit crabs from subtidal, intertidal and supratidal habitats in relation to rapid, stepwise increases in temperature ranges of 20°C, Burggren and McMahon (1981) found a clear correlation between habitat and lability of respiration. They showed that oxygen consumption for intertidal hermit crabs was lowest, subtidal crabs higher and supratidal crabs highest. Q_{10} values for oxygen consumption were significantly lower for intertidal hermit crabs than for supratidal and subtidal species in the same family or even the same genus. Nevertheless, the Q_{10} values for acutely determined oxygen consumption over a 15°C temperature range were significantly different from 1.0 in all species tested (Burggren and McMahon, 1981). Results of studies by Wernick (1982) showed that oxygen consumption in the tropical, intertidal hermit crab, *Clibanarius vittatus* is relatively insensitive to temperature changes between 20° and 30°C, with corresponding Q_{10} values of 0.84 (20° - 25°C) and 0.98 (25° - 30°C). However, Wernick also reported temperature zones at which Q_{10} values were low (10°-15°C, Q_{10}=1.15), and zones where values were high (30°-35°C, Q_{10}=3.60). Wernick suggested that low Q_{10} values in *C. vittatus* at 15°C likely reflected depressed metabolic rates due to a state of cold torpor, while high Q_{10} values at

35°C may have resulted from increases in activity she observed. In the present study, cold torpor may explain the low level of oxygen consumption during exposure to 15°C, as well as the large Q_{10} value seen between 15° and 25°C for *C. virescens*. However, activity does not appear to explain the high respiratory response of this species to 35°C, since an increase in activity was never observed during treatment. For *C. taeniatus* neither cold torpor nor level of activity explain the consistent level of respiration observed at all temperatures.

Burggren and McMahon (1981) suggest that high Q_{10} values for oxygen consumption in intertidal hermit crabs may be inappropriate, especially if the capacity for anaerobic metabolism is limited. In sudden aerial exposure during winter, this could leave the animal in a state of semi-torpor and unable to forage or escape predation, while in summer, frequent exposure to hot intertidal conditions could result in high rates of aerobic metabolism that could exhaust energy reserves (Burggren and McMahon, 1981). Although Scholander et al. (1953) hypothesised that a low Q_{10} could be of adaptive importance and would therefore be of advantage in offsetting the effects of changes in temperature, they also suggested that they had found no cases in which the effects of temperature fluctuations had been compensated for by low respiratory Q_{10}. However, Newell (1969) subsequently reviewed studies on a number of intact intertidal invertebrates whose standard metabolism did not vary greatly with fluctuations in temperature, and therefore had low Q_{10} values for respiration. He suggested that such responses were part of a complex sequence of changes in the activity and metabolism of intertidal organisms that may compensate for the rapid diurnal and semi-diurnal fluxes in temperature that are likely to occur in intertidal environments.

There is little doubt that mechanisms controlling respiratory responses may be highly influenced by genetic controls (Hazel and Prosser, 1974; Hochachka and Somero, 1984; Hawkins *et al.*, 1986, 1987; Koehn and Bayne, 1989; Hawkins, 1995) and more recently, the study of multi-locus heterozygosity has advanced our understanding of how genotype may affect the physiological function of some invertebrates (Hawkins *et al.*, 1986; Hawkins, 1995). An important point here is that if metabolic homeostasis is genetically controlled, and multi-locus heterozygosity increases with increasing height on the shore, as has been shown by Koehn *et al.* (1973) apud Hawkins, 1995) and Lavie and Nevo (1986), this physiological response to temperature fluctuations will be subject to natural selection.

Distribution

Both *C. taeniatus* and *C. virescens* can be found on the rocky shores of Queensland, Australia where they occupy tidepools and crevices and are frequently exposed to air during low tide. Surveys of three sites along the Capricorn Coast, suggest that there is a difference in the vertical distribution of these species on rocky shores of Cooee Bay, with *C. taeniatus* occurring from low to high shore, while *C. virescens* is mainly found at the water's edge. Data collected for tidepool temperatures at low shore, mid shore and high shore showed water temperatures in high shore pools to be significantly different from mid and low shore pools at two of the three beaches studied, with temperatures during Fall ranging from 27.9° - 32.8°C (Dunbar, 2001). These data are in agreement with other studies that have demonstrated increasing tidepool temperatures with increasing height on sub-tropical and tropical shores (Rao and Sundaram, 1974; Huggett and Griffiths, 1986; Morton and Harper, 1995; Raffaelli and Hawkins, 1996). It should also be re-emphasized that extreme fluxes in temperature over periods of 2 - 8 h are very characteristic of the intertidal zone.

For *C. virescens*, distribution along the low intertidal and shallow sub-tidal zones is likely to result in relatively limited exposure to the kinds of rapid and extreme temperature regimes that

characterize the mid and upper regions of the shore. Since *C. taeniatus* inhabits all levels of the intertidal zone, low, stable respiration over a wide range of fluctuating temperatures may be of adaptive significance. Other than the present study, I am unaware of any other data for acutely determined oxygen consumption in anomuran decapods that suggest metabolic homeostasis over such a wide range of temperature.

The current comparative study of the respiratory responses of *C. taeniatus* and *C. virescens* in relation to their vertical distribution on the shore provides further evidence of respiratory adaptation in intertidal organisms. The importance of such comparative studies is that we gain further insights into the abilities of intertidal animals to maintain a positive energy balance and to compete successfully under the dynamic conditions of the intertidal zone.

Acknowledgements

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