

OXYGEN UPTAKE DURING ENVIRONMENTAL TEMPERATURE CHANGE IN HERMIT CRABS: ADAPTATION TO SUBTIDAL, INTERTIDAL, AND SUPRATIDAL HABITATS¹

WARREN W. BURGGREN AND BRIAN R. McMAHON

Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003;

Department of Biology, University of Calgary, Calgary, Alberta, T2V 1N5, Canada

(Accepted 12/23/80)

Changes in oxygen uptake in response to stepwise changes in environmental temperature have been measured in anomuran decapod Crustacea inhabiting a subtidal habitat (*Paguristes turgidus*, *Elassochirus tenuimanus*), an intertidal habitat (*Pagurus granusimanus*, *Pagurus hirsutisculus*) and a supratidal habitat (*Coenobita clypeatus*, *Coenobita rugosus*). Individuals of each species were housed in respirometers and subjected to three rapid, progressive 5 °C increases above their initial acclimation temperature, with $\dot{M}O_2$ ($\mu M O_2/g/h$) measured during a 2–3-h pause at each temperature increment. The Q_{10} for $\dot{M}O_2$ is correlated with habitat, with intertidal species having a Q_{10} of 1.4–1.6, which is significantly lower ($P < .05$) when compared with Q_{10} values of 2.1–2.4 for subtidal species and 2.6–2.7 for the supratidal forms. Intertidal hermit crabs also showed a smaller $\dot{M}O_2$ overshoot and a more rapid $\dot{M}O_2$ acclimation to abrupt temperature change compared with the other anomurans. Intertidal anomuran Crustacea are apparently adapted to maintain a comparatively stable oxygen uptake in a habitat subject to considerable variability in temperature.

INTRODUCTION

The relationship between temperature and metabolism has received considerable attention in intertidal crustaceans, particularly Decapoda (see Vernberg 1969; Newell 1969, 1976; Vernberg and Vernberg 1970 for reviews). Much of this interest arises because these animals may face large and abrupt changes in environmental temperatures as they are alternatively exposed and submerged as the tide fluctuates. Environmental temperatures in the immediate vicinity of sessile intertidal invertebrates may change up to 20 °C within hours or even minutes as seawater levels rise and fall (Broekhuysen 1940; South-

word 1958; Lewis 1963; Johnson 1965; Jansson 1967; Green and Hobson 1970; Pollock and Hammon 1971; Edwards and Huebner 1977; among many others). More mobile intertidal fauna, such as the decapod Crustacea, can often attenuate body temperature changes by moving into crevices or underneath vegetation at low tide or, of course, retreating down the littoral zone as the tide recedes. However, as Reese (1969) argues, the exposed intertidal zone is one of often intense foraging activity by many decapods, particularly anomurans. The advantages of remaining exposed to feed apparently must counteract any disadvantages of the resulting fluctuations in body temperature.

In any event, metabolic rate in response to acute temperature change varies little over a wide portion of the physiological temperature range in intertidal invertebrates, including decapods (see Vernberg 1969; Newell and Pye 1971). The possible adaptive significance of a reduced metabolic temperature lability in intertidal organisms has been discussed by

¹The authors would like to thank Margaret Burggren for assistance in making oxygen consumption measurements, and Mary Chamberlain, Chuck Daxboeck, Tony Farrell, and Jeff Dunn for the thankless task of midnight intertidal collecting in a Vancouver winter rain.

Physiol. Zool. 54(3):325–333, 1981.

© 1981 by The University of Chicago. 0031-935X/81/5403-8019\$02.00

many authors (Roberts 1957; Newell 1969; Vernberg 1969; Mangum 1973; among others). However, such adaptive significance could be more meaningfully demonstrated and interpreted if very closely related species native to the bordering subtidal and supratidal habitats could also be examined. No such study that we are aware of has specifically addressed this problem in decapod Crustacea, although offshore and intertidal onuphid polychaetes, for example, have been examined together in this context (Mangum 1973).

The present study, therefore, investigates a range of phylogenetically similar decapod Crustacea to determine their acute responses of oxygen uptake to temperature changes resembling those commonly occurring in many intertidal habitats. Anomurans were selected for this study because the hermit crabs have been particularly successful in exploiting the supratidal and intertidal as well as the subtidal environments (see Reese 1969; De Wilde 1973), and numerous genera and hundreds of species abound in temperate to tropical regions.

MATERIAL AND METHODS

Six species of anomuran decapods from four genera were used in this study (table 1). *Paguristes turgidus* and *Elassochirus tenuimanus*, both strictly subtidal hermit crabs, were collected in water 2–20 m deep on the west coast of Vancouver Island and in the straits of Georgia, British Columbia, during the winter of 1978. The intertidal anomurans, *Pagurus hirsutissimus* and *Pagurus granosimanus*, were collected above water level at low tide in Stanley Park and Deep Cove, Vancouver, British Columbia, in the spring of 1978. The distinctly supratidal *Coenobita clypeatus* were provided by animal suppliers in the winter of 1977–1978, having been collected in the Florida Keys and Bahamas. *Coenobita rugosus* was collected in the Palau Islands group, Western Caroline Islands, during an expedition of R. V. Alpha Helix in August of 1979. (No exclusively supratidal temper-

ate zone anomuran occurs; hence the study of these tropical species.)

Hermit crabs were maintained in aquaria under constant light conditions for at least 2 wk prior to experimentation and were thereafter assumed to retain only insignificant tidal rhythms. The animals were kept at the acclimation temperatures indicated in table 1 except where other temperatures are indicated. The north-eastern Pacific subtidal and intertidal crabs were kept in air-saturated sea water at 5 C, but the intertidal animals were also provided with rocks upon which they could emerge from the water into humid air maintained at 5–10 C. The terrestrial hermit crabs were acclimated in humid terraria at 20 C, with free access for drinking to both fresh and salt water. All animal populations were fed ad libitum with fresh vegetable material and shredded fish.

Respirometers were constructed from glass jars with airtight lids (volume 50–460 ml). The jars were wrapped in translucent plastic sheeting to visually shield the occupants from movements by the investigators. The lid of each jar was perforated by two stopcocks, one for an incoming flow of water or air, the other serving as an exit. All respirometers were suspended in a thermostatted water bath. All contained sterilized fine gravel spread over the floor to a depth of 5 mm, into which the crabs often partially settled.

Individual crabs were placed in a respirometer, the volume of which was large enough to allow unimpaired movement of the crab within, yet sufficiently small so that a 10–30-min period of respiration by the crab in the closed respirometer would cause a water PO_2 decrease of 5–15 mmHg, or an air PO_2 decrease of 3–5 mmHg. A constant flow of aerated sea water (subtidal, intertidal crabs) or air (supratidal crabs) through the respirometer was then begun. These flow rates were sufficient to insure a complete turnover of medium in the respirometer, yet not so large as to cause any apparent disturbance to the crabs. Crabs were then allowed at least 24 h without disturbance

acclimate to the respirometers, before the first MO₂ measurement was made. Most crabs exhibited some locomotor activity immediately after introduction into the respirometers, but had stopped moving and settled down within 2–4 h, after which only very infrequent movements were evident.

After this acclimation period, the flow of water or air through the respirometer was gently shut off, without vibrating or otherwise disturbing the crabs. A 150- μ l sample of the respiratory medium was then immediately taken and analyzed for PO₂ in either a Radiometer PHM 71 or an Instrumentation Laboratory μ 13 blood gas analyzer. To avoid potential disturbance of the crabs from pressure transients produced by sampling, a 150- μ l volume of either air or water was drawn in through one stopcock as the sample to be analyzed was drawn out the other. Given the comparatively large volume of the respirometer and the spatial separation of the stopcocks, it was assumed that no significant contamination of the analyzed sample, or change in the respirometer PO₂, had occurred. Each crab was then left undisturbed as it began to deplete the O₂ from the closed respirometer. After a time period constant for all experiments on any one individual, water or air was sampled a second time from the respirometer, as previously described. Reductions in PO₂ of 3–15 mmHg (and any increases in metabolic products) were assumed to have unimportant physiological effects. Water in the respirometer was not mechanically stirred during these periods, to avoid disturbing the crabs. Water or air currents generated from the exhalent canals were apparently sufficient to achieve mixing in the respirometer, as revealed by initial experiments with and without mechanical stirring. Following sampling, a flow of air or air-saturated water was resumed for 30 min before the respirometer was again closed for a second determination of O₂ uptake. Four such sequential measurements were made for each animal at each temperature (see below). The mean of these four measurements was then used

in further calculations. Movements of taps associated with sampling were carried out slowly and very gently to minimize disturbance to the animals. In fact, the four measurements within each set were very similar, indicating that little progressive disturbance had occurred.

Measurements were made initially on undisturbed, inactive hermit crabs at the acclimation temperature given in table 1, which for each species was toward the lower end of its tolerable temperature range. These values represented the routine, acclimated level of O₂ consumption. When the four determinations at that temperature were completed, the temperature of the entire apparatus was raised by 5.0 C over the course of 15 min. Four determinations at this new temperature were then made immediately, requiring approximately 2½–3 h. After these measurements were made, another 5.0 C increase in temperature was produced, the amount of O₂ depletion from the respirometer measured four times as before, and so on. In almost all instances, therefore, measurements were made in 5° increments over a total temperature range of 20 C, which for every species bracketed its preferred temperature. We assume that the comparatively brief period of time spent at each measurement temperature (less than 3 h) provided for little or no temperature acclimation (see Results and fig. 2), so in effect the values for oxygen depletion from the respirometer could be interpreted as very similar to those which would have resulted from a single stepwise increase in temperature from the initial acclimation level. Moreover, the considerable care taken to avoid disturbance during sampling or flushing of the respirometer probably prevented any cumulative stress effects during the course of the experiment.

After all experiments on a particular crab were completed, it was removed from the respirometer and induced to leave its molluscan shell. Weight and volume of both shell and crab were measured, and these volumes were subtracted from the empty respirometer volume to determine

the exact amount of respiratory medium available to the crab during each experiment. Oxygen uptake in $\mu\text{M O}_2/\text{g wet w/h}$ ($\dot{\text{M}}\text{O}_2$) was then calculated from these data and the calculated decline in O_2 concentration from the respirometer during the measurement period.

In a separate series of experiments, $\dot{\text{M}}\text{O}_2$ was measured hourly in acclimated crabs for 2 h before and for at least 8 h after a stepwise 10 C increase in temperature. Constant, gentle renewal of air-saturated seawater or air was provided between measurement periods.

Experiments were also carried out on subtidal and intertidal crabs in which, after a period of measurements of $\dot{\text{M}}\text{O}_2$ in water at acclimation temperature, the water was gently drained from the respirometers and replaced with water-saturated air at acclimation temperature. The $\dot{\text{M}}\text{O}_2$ in air-exposed animals was then measured at 1–2-h intervals for 7 h.

STATISTICAL ANALYSIS

Differences between means for oxygen uptake measured at acclimation temperature were compared according to Student's *t*-test.

For each species, Q_{10} for oxygen uptake over the 15° temperature range specified in table 1 was tested for significance against the null hypothesis that $Q_{10} = 1.0$. A test statistic assumed to follow the distribution for the *t*-statistic, and modified specifically for use with Q_{10} data, was used. Details of the test, developed by Van Winkle, are given in Coyer and Mangum (1973).

The significance of interspecific differences in Q_{10} values determined over the same temperature intervals was tested by a similar procedure, also described by Coyer and Mangum (1973).

A significance level of .05 was adopted in all instances.

RESULTS

The resting oxygen uptake of each species at its acclimation temperature, as well as Q_{10} values for acutely measured $\dot{\text{M}}\text{O}_2$ over the indicated temperature range,

are presented in table 1. No correlation of acclimated levels of $\dot{\text{M}}\text{O}_2$ with habitat appeared to exist since, with the exception of *Paguristes turgidus*, there were no significant interspecific differences ($P > .10$) in the acclimated levels of $\dot{\text{M}}\text{O}_2$.

The Q_{10} values for acutely determined $\dot{\text{M}}\text{O}_2$, measured over a physiological 15 C temperature range (table 1), were significantly different from 1.0 ($P < .05$) in all six species. That is, regardless of habitat or species, $\dot{\text{M}}\text{O}_2$ was correlated with ambient temperature.

No significant difference ($P > .10$) in Q_{10} for acutely determined $\dot{\text{M}}\text{O}_2$ existed between the two species within any one habitat group, e.g., *Paguristes turgidus* compared with *Elassochirus tenuimanus* (intertidal group), or *Coenobita clypeatus* compared with *C. rugosus* (supratidal group). In addition, there were no significant differences ($P > .10$) in the Q_{10} for $\dot{\text{M}}\text{O}_2$ when either of the subtidal species were compared with either of the supratidal species. Importantly, however, the Q_{10} values for both intertidal species were always lower (not significantly lower in the case of *P. turgidus*) than either the subtidal or supratidal habitat group. The general Q_{10} relationships can thus be summarized by:

$$\text{intertidal } Q_{10} < \text{supratidal } Q_{10} = \text{subtidal } Q_{10}.$$

The relationship between temperature and the acutely determined $\dot{\text{M}}\text{O}_2$ is revealed in more detail in figure 1. In order to minimize the effects of interspecific differences in $\dot{\text{M}}\text{O}_2$ (table 1), all data have been normalized. Thus, $\dot{\text{M}}\text{O}_2$ for each species is expressed as a function of $\dot{\text{M}}\text{O}_2$ at the measurement temperature (T_m) divided by $\dot{\text{M}}\text{O}_2$ at the acclimation temperature (T_a). These data indicate that, over a 15 C rise in temperature range, mean $\dot{\text{M}}\text{O}_2$ increases over four times in the terrestrial anomurans, approximately three times in the subtidal species, but only twice in the intertidal hermit crabs. Locomotor activity was not quantified during the experi-

TABLE 1
HABITAT, OXYGEN CONSUMPTION, AND Q_{10} FOR OXYGEN CONSUMPTION IN ANOMURAN CRUSTACEA

Species	Habitat	Acclimation Temperature (°C)	No	Body Mass (g)	$\dot{M}O_2$ at Acclimation Temperature ($\mu\text{m O}_2/\text{g/h}$)	Q_{10} for $\dot{M}O_2$
<i>Paguristes turgidus</i>	Subtidal, often deeper than 3 m, southern British Columbia to southern California	5	5	20.13 ± 4.44	4.74 ± 2.18	2.12 ± .55 (5°-20°)
<i>Elassochirus tenuimanus</i>	Subtidal, shallow water, southern British Columbia to California	5	8	1.48 ± .51	1.88 ± .75	2.37 ± .61 (5°-20°)
<i>Pagurus hirsutisculus</i>	Intertidal, very abundant, Alaska to southern California	5	5	2.37 ± .87	2.60 ± .30	1.64 ± .23 (5°-20°)
<i>Pagurus granusimanus</i>	Intertidal, Alaska to southern California	5	10	.61 ± .20	2.86 ± 1.43	1.44 ± .11 (5°-20°)
<i>Coenobita clypeatus</i>	Supratidal, tropical shores of western Atlantic, very terrestrial, prefers semiarid habitat	20	7	22.93 ± 5.97	1.24 ± .34	2.67 ± .35 (20°-35°)
<i>Coenobita rugosus</i>	Supratidal, tropical shores of western Pacific, very terrestrial, prefers humid habitat	20	7	1.01 ± .79	1.39 ± .71	2.56 ± .44 (20°-30°)

NOTE.—Mean values ± 1 standard deviation are given

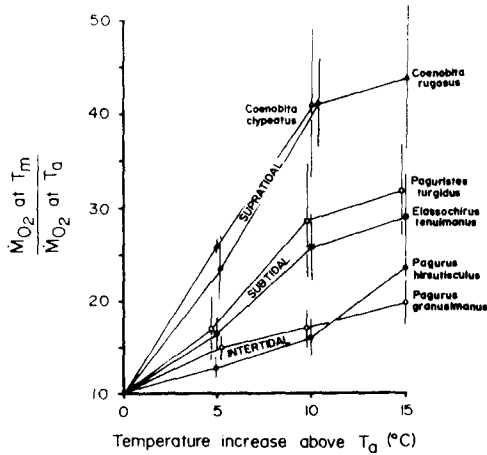


FIG. 1.—Relationship between oxygen consumption at acclimation temperature (T_a) and at other measurement temperatures (T_m) in subtidal, intertidal, and supratidal hermit crabs. Mean values ± 1 SD are presented. (For number of animals and body weights, see table 1. (Note that the staggering of points at each temperature is only for clarity of data presentation.)

ments, but visual observation revealed that the sharp 5° rises in temperature did not usually cause onset of locomotor activity, with most crabs remaining partially or completely withdrawn into their shells. The changes in $\dot{M}O_2$ presented in figure 1 are thus considered to represent resting or routine values.

It should be noted that the rate of increase in $\dot{M}O_2$ with increasing temperature varied to some extent, depending upon how far T_m was above T_a . For example, in *C. rugosus*, *Paguristes turgidus*, and *E. tenuimanus*, the highest 5° temperature interval was characterized by a lower rate of increase in $\dot{M}O_2$ than had occurred over lower temperature ranges. *Pagurus granusimanus* exhibited a constant rate of $\dot{M}O_2$ increase between 5° and 20° , while in *Pagurus hirsutisculus* the $\dot{M}O_2$ increase was greatest over the highest final temperature increment. To avoid introducing bias by calculating Q_{10} on specific 5° temperature intervals, the Q_{10} values presented in table 1, and discussed earlier, were calculated from $\dot{M}O_2$ values over the entire 15° temperature interval.

To investigate possible differences between species in patterns of temperature acclimation, the longer term effects of a $10^\circ C$ stepwise increase in temperature on $\dot{M}O_2$ were examined (fig. 2). *Paguristes hirsutisculus*, the intertidal species, showed an increase in $\dot{M}O_2$ of approximately 100% immediately upon a $10^\circ C$ increase in temperature, but $\dot{M}O_2$ immediately began to fall back toward control levels. In fact, within 2 h of an increase to $20^\circ C$, $\dot{M}O_2$ had apparently stabilized at a level of 30%–50% above that evident at $10^\circ C$. The subtidal species (*Paguristes turgidus*) and especially the supratidal species (*C. clypeatus*) also developed an immediate increase in $\dot{M}O_2$ when temperature was increased from 10° to 20° , but in these animals $\dot{M}O_2$ did not decline as rapidly as in *Pagurus hirsutisculus*, remaining more than 70% elevated even after 22 h at $20^\circ C$.

The effect of air exposure upon $\dot{M}O_2$ was tested in an intertidal species (*Pagurus hirsutisculus*) and subtidal species (*Pagu-*

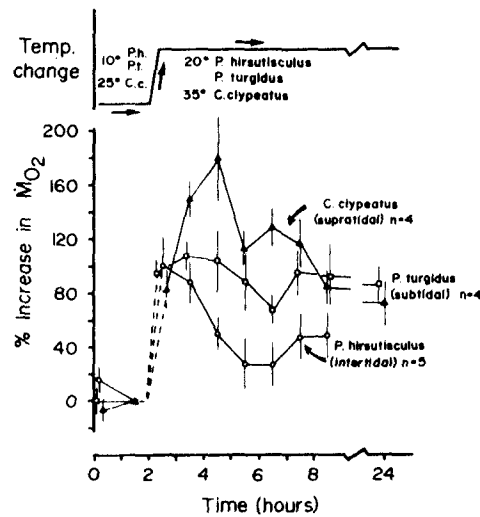


FIG. 2.—Percent increase in O_2 uptake in three species of hermit crabs following a sustained $10^\circ C$ increase above acclimation levels. Mean values ± 1 SD are presented. The dashed lines indicate the period during which the stepwise rise in temperature occurred and during which data were not collected. (Note that acclimation temperatures are $5^\circ C$ above those used for previous experiments.)

turgidus). A very clear difference in the response occurs between hermit crabs from these two habitats (fig. 3). *Paguristes turgidus* experienced a marked fall in $\dot{M}O_2$, with no recovery to pre-exposure levels occurring within at least 7 h. These subtidal crabs remained inactive and withdrawn into their shell throughout air exposure. In contrast, *Pagurus hirsutisculus* was able to elevate oxygen consumption by threefold immediately following air exposure and still showed elevated levels after 4 h. Some of this increase in $\dot{M}O_2$ in *Pagurus hirsutisculus* was due to the onset of locomotor activity concurrent with air exposure.

DISCUSSION

A clear correlation of habitat and lability of oxygen uptake in the face of abrupt temperature changes has emerged from an examination of subtidal, intertidal, and supratidal anomuran decapods. Over normal environmental ranges of body temperature, Q_{10} values for $\dot{M}O_2$ determined for the intertidal hermit crabs were significantly lower than those for subtidal or supratidal species in the same family or even the same genus, and were generally lower than in many ectotherms from strictly terrestrial or aquatic envi-

ronments (see Vernberg and Vernberg 1970; Prosser 1973). We are unaware of any other data on Q_{10} for acutely determined $\dot{M}O_2$ in anomuran decapods, but similarly low values are evident in the intertidal brachyurans *Uca pugilator* (Vernberg 1969) and *Carcinus maenas* (Wallace 1972), and the intertidal macruran *Palaemonetes vulgaris* (McFarland and Pickens 1965). The $\dot{M}O_2$ of the intertidal invertebrates other than crustaceans is also largely insensitive to body temperature change (Halcrow and Boyd 1967; Newell and Northcroft 1967; Siefken and Armitage 1968; Barnes and Barnes 1969; among others).

For intertidal hermit crabs a high Q_{10} for oxygen uptake comparable to the supratidal and subtidal anomurans examined may be inappropriate, particularly if the animal's capacity for anaerobic metabolism is limited. It could in winter, for example, result in a rate of oxygen consumption during abrupt intertidal exposure to cold air which might suddenly leave the organism semitorpid and thus unable to forage, to avoid predators, or to seek out more favorable microhabitats. During the summer months, twice daily exposure to a hot intertidal environment in tidal pools or on a bare substrate could result in a high aerobic metabolism that could deplete the animal's energy reserves. Thus, a comparatively stable $\dot{M}O_2$ over that range of temperature fluctuation encountered on a daily basis is of significant value to these intertidal organisms. On the other hand, a high Q_{10} for acutely determined $\dot{M}O_2$ is not particularly disadvantageous for the supratidal forms examined, where environmental temperature changes may be much more gradual and attenuated. In the supratidal habitat of *C. rugosus*, normal daily and even seasonal fluctuations in air temperature rarely exceed 5°–10° (McMahon and Burggren, in preparation). Temperature variations in the detritus of the jungle floor where *C. rugosus* were collected may be even less. Selection pressures for a low Q_{10} for $\dot{M}O_2$ probably have not been great for this

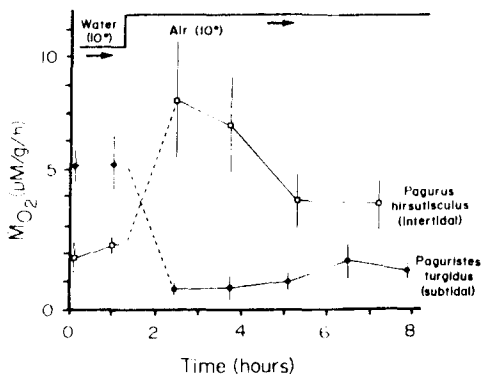


FIG. 3.—Effect of air exposure on the oxygen consumption of a subtidal and intertidal species of hermit crab. Mean values \pm 1 SD are presented. No. = 5 for both species. The dashed lines indicate the period during which air immersion occurred and during which data were not collected.

tropical, supratidal hermit crab, nor for subtidal forms inhabiting a comparatively thermally stable environment. *Coenobita clypeatus* inhabits a geographic region with a slightly greater temperature variation, but through behavioral thermoregulation involving choices between microhabitats of varying temperatures, this species normally experiences only small temperature fluctuations (De Wilde 1973), similar to those encountered by *C. rugosus*.

The intertidal hermit crabs of the present study not only showed the lowest Q_{10} for oxygen consumption but also showed the most rapid initial stabilization of oxygen uptake after an abrupt change to a higher temperature level (fig. 2). Whether a further decrease in metabolic rate would occur after several more hours or days at this temperature requires further investigation. However, it must be emphasized that extreme temperature regimes lasting perhaps only 1–6 h are highly characteristic of the intertidal zone (see references in Introduction). Within this time frame, the intertidal anomurans, through their more rapid recovery from a metabolic overshoot, again show evidence of adaptation to ameliorate the effects on oxygen uptake of an abrupt temperature change.

Aerial exposure during low tide also results in the loss of seawater as a respiratory medium. Intertidal anomurans, particularly those which venture well away from tidal pools, must be able to respire in air if oxidative metabolism is to be

maintained. Such aerial respiration is clearly possible in *Pagurus hirsutisculus* (fig. 3), where $\dot{M}O_2$ may actually increase manifold as locomotor activity begins to develop. This can be contrasted with the subtidal *Paguristes turgidus*, which showed a sharply diminished $\dot{M}O_2$ and a noticeable absence of any sustained locomotor movements when exposed to air. Both anatomical and physiological adaptations for aerial respiration have been described for intertidal anomuran and brachyuran crabs (Harms 1932; Edney 1961; Bliss 1968; Taylor and Butler 1978).

A correlation between a low Q_{10} for $\dot{M}O_2$ and a large temperature fluctuation in the normal habitat has been revealed within a single family of decapod Crustacea, which are close phylogenetically but morphologically adapted to three diverse habitats. What has yet to be investigated in these species, however, is the contribution of glycolytic pathways to total metabolism. Many intertidal invertebrates, particularly bivalves, are "facultative anaerobes," capable of surviving long periods of hypoxia or anoxia (Hamman 1969; Saz 1971). Such anaerobic pathways in intertidal hermit crabs could sustain tissue metabolism in the face of large imbalances in O_2 transport and O_2 demand resulting from environmental temperature variation. Anaerobic metabolic pathways as well as a low Q_{10} for oxidative metabolism could serve concurrently as adaptations to the intertidal environment.

LITERATURE CITED

- BARNES, H., and M. BARNES. 1969. Seasonal changes in the acutely determined oxygen consumption and effect of temperature for three common cirripedes, *Balanus balanoides* (L.), *B. balanus* (L.) and *Chthamalus stellatus* (Poli). J. Exp. Marine Biol. Ecol. **4**:35–50.
- BLISS, D. E. 1968. Transition from water to land in decapod crustaceans. Amer. Zool. **8**:355–392.
- BROEKHUYSEN, C. J. 1940. A preliminary investigation of the importance of desiccation, temperature and salinity as factors controlling the vertical distribution of certain marine gastropods in False Bay, South Africa. Trans. Roy. Soc. South Africa **28**:255–292.
- COVER, P. E., and C. P. MANGUM. 1973. Effect of temperature on active and resting metabolism in Polychaetes. Pages 173–180 in W. WIESER, ed. Effects of temperature on ectothermic organisms. Springer-Verlag, New York.
- DE WILDE, P. A. W. J. 1973. On the ecology of *Coenobita clypeatus* in Curacao, with reference to reproduction, water economy and osmoregulation.

- tion in terrestrial hermit crabs. Pages 3-138 in *Studies on the fauna of Curacao and other Caribbean islands*. Vol. 44. Nyhoff, The Hague.
- EDNEY, E. B. 1961. Terrestrial adaptations. Pages 367-393 in T. WATERMAN, ed. *The physiology of crustacea*. Vol. 1.
- EDWARDS, D. C., and J. D. HUEBNER. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology* 58:1218-1236.
- GREEN, R. H., and K. D. HOBSON. 1970. Spatial and temporal structure in a temperate intertidal community, with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). *Ecology* 51:999-1011.
- HALCROW, H., and C. M. BOYD. 1967. The oxygen consumption and swimming activity of the amphipod *Gammarus oceanicus* at different temperatures. *Comp. Biochem. Physiol.* 23:233-242.
- HAMMAN, C. S. 1969. Metabolism of the oyster, *Crassostrea virginica*. *Amer. Zool.* 9:309-318.
- HARMS, J. W. 1932. Die Realisation von Genen und die consecutive Adaptation. II. *Birgus latro* L. als Landkrebs und seine Beziehungen zu den Coenobiten. *Z. Wiss. Zool.* 140:167-290.
- JANSSON, B. O. 1967. Diurnal and annual variations in temperature and salinity of interstitial water in sandy beaches. *Ophelia* 4:173-201.
- JOHNSON, R. G. 1965. Temperature variation in the infaunal environment of a sand flat. *Limnology Oceanogr.* 10:114-120.
- LEWIS, J. B. 1963. Environmental and tissue temperature of some tropical intertidal marine animals. *Biol. Bull.* 124:277-284.
- McFARLAND, W. M., and P. E. PICKENS. 1965. The effects of season, temperature and salinity on standard and active oxygen consumption of the grass shrimp *Palaemonetes vulgaris* (Say). *Can. J. Zool.* 43:571-585.
- McMAHON, B. R., and W. W. BURGGREN. In press. Acid-base balance following temperature acclimation in land crabs. *J. Exp. Zool.*
- MANGUM, C. P. 1973. Temperature sensitivity of metabolism in offshore and intertidal onuphid polychaetes. *Marine Biol.* 17:108-114.
- NEWELL, R. C. 1969. Effect of fluctuations in temperature on the metabolism of intertidal invertebrates. *Amer. Zool.* 9:293-307.
- NEWELL, R. C., and H. R. NORTHCROFT. 1967. A reinterpretation of the effect of temperature on the metabolism of certain marine invertebrates. *J. Zool.* 151:177-198.
- NEWELL, R. C., and V. I. PYE. 1971. The influence of thermal acclimation on the relation between oxygen consumption and temperature in *Littorina littorea* (L.) and *Mytilus edulis* L. *Comp. Biochem. Physiol.* 34:385-397.
- POLLOCK, L. W., and W. HAMMON. 1971. Cyclic changes in interstitial water content, exposure and temperature in a marine beach. *Limnology Oceanogr.* 16:522-535.
- PROSSER, C. L. 1973. *Comparative animal physiology*. 3d ed. Saunders, Philadelphia.
- REESE, E. S. 1969. Behavioral adaptations of intertidal hermit crabs. *Amer. Zool.* 9:343-355.
- ROBERTS, J. L. 1957. Thermal acclimation of metabolism in the crab *Pachygrapsus crassipes*. II. Mechanisms and the influence of season and latitude. *Physiol. Zool.* 30:242-253.
- SAZ, H. J. 1971. Facultative anaerobiosis in the invertebrates: pathways and control systems. *Amer. Zool.* 11:125-135.
- SIEFKEN, M., and K. B. ARMITAGE. 1968. Seasonal variations in metabolism and organic nutrients in *Diaptomus* (Oustacea: Copepoda). *Comp. Biochem. Physiol.* 24:591-609.
- SOUTHWORD, A. J. 1958. Note on the temperature tolerance of some intertidal animals in relation to environmental temperatures and geographic distribution. *J. Marine Biol. Ass. U.K.* 37:49-66.
- TAYLOR, E. W., and P. J. BUTLER. 1978. Aquatic and aerial respiration in the shore crab, *Carcinus maenas* (L.), acclimated to 15°C. *J. Comp. Physiol.* 127:315-323.
- VERNBERG, F. J. 1969. Acclimation of intertidal crabs. *Amer. Zool.* 9:333-341.
- VERNBERG, F. J., and W. B. VERNBERG. 1970. *The animal and the environment*. Holt, Rinehart & Winston, New York.
- WALLACE, J. C. 1972. Activity and metabolic rate in the shore crab *Carcinus maenas*. *Comp. Biochem. Physiol.* 41A:523-533.