

# Oxygen Uptake During Repeated Exposure to Temperature Change: Physiological Divergence in Panamanian Cognate Pairs and Latitudinally Distant Populations of Decapod Crustacea

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With 8 figures

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**Abstract.** The emergence of the Isthmus of Panama subdivided the amphi-American biota. In the present study, Pacific and Atlantic populations of four cognate pairs of crabs were used to discern whether exposure to different thermal regimes in habitats, in the putative absence of gene flow, has resulted in physiological divergence. Populations that potentially form a common genetic pool were also used; these were populations of the Atlantic Panama cognate that occur in Belize and Florida. Decreases in water temperature occur periodically in Pacific Panama and Florida, but not in Atlantic Panama or Belize. In this study, physiological divergence in oxygen uptake was assessed in response to repeated exposure to either control and decreased temperature or control and increased temperature. Results indicate that, in only some of the genera tested, exposure to decreases in habitat temperature has resulted in divergence. Partial support is found for the corollary that adaptation to an environment with periods of decreased temperature results in reduced compensation during exposure to elevated temperature.

## Problem

Two hypotheses are addressed in the present study. (1) Since their geologically recent separation, physiological divergence has occurred between Panamanian cognate species of crabs, relative to exposure to different temperature regimes and (2) among geographically distant populations physiological divergence has

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occurred, intraspecifically, relative to exposure to the different temperature regimes of respective habitats. These hypotheses are based on the following considerations.

The Isthmus of Panama emerged as a land bridge about 3 million years ago (KEIGWIN, 1982), separating the Eastern Pacific from the Western Atlantic. It thus subdivided the amphi-American biota and set the stage for allopatric speciation. In about 45% of the decapod crustaceans examined, slight morphological changes have occurred resulting in presently recognized species pairs, termed geminate or cognate species (ABELE, 1972, 1976). Marine cognate species spanning multiple phyla form the basis for study of various evolutionary processes (*e.g.*, RUBINOFF & RUBINOFF, 1971; GRAHAM, 1971, 1972; LESSIOS & CUNNINGHAM, 1990; BERMINGHAM & LESSIOS, 1993; KNOWLTON *et al.*, 1993). In the present study, four pairs of cognate brachyurans were used to assess physiological divergence in response to a specific environmental variable and in the putative absence of gene flow.

The Atlantic cognate of each of the species pairs chosen also occurs at Carrie Bow Cay, Belize, Central America and the Indian River region of Florida. This allowed intraspecific population comparisons using populations that potentially form a common genetic pool.

The coasts of Pacific Panama and Atlantic Panama differ with respect to seawater temperatures (GLYNN, 1972). During the dry season, Pacific seawater temperatures are lower and more variable (due to upwelling) than in the Atlantic. During the wet season, seawater temperatures on both coasts are similar. Atlantic Panama is characterized by stable, narrow-range water temperatures year round. Belize is thermally stable (FERRARIS, 1981; RÜTZLER & FERRARIS, 1982) and has seawater temperatures similar to Atlantic Panama. Florida, relative to other sites, is cold and thermally unstable (WILCOX & GILMORE, 1972-1975). Thus, Florida-Atlantic Panama comparisons approximate Pacific-Atlantic cognate comparisons but are intraspecific. In all cases, comparisons involved populations that are either subject to constant or to fluctuating thermal environments.

## Material and Methods

### 1. Collection and maintenance of animals

Individuals were found and collected, most frequently, from the following habitats: *Uca* in mud burrows in high mangrove swamps, *Panopeus* in mud under intertidal rocks among mangrove roots, *Pachygrapsus* on intertidal rocks and *Cataleptodius* in sand under coral rubble in the low intertidal. *Uca galapagensis herradurensis* BOTT, *Panopeus purpureus* LOCKINGTON, *Pachygrapsus transversus* (GIBBES) and *Cataleptodius taboganus* RATHBUN were collected on the Pacific coast of Panama (9°N) at Diablo Heights and Boy Scout Beach, Naos Island. *Uca rapax rapax* (SMITH), *Panopeus lacustris* DESBONNE, *Pachygrapsus transversus* (GIBBES) and *Cataleptodius floridanus* (GIBBES) were collected on the Atlantic coast of Panama (9°N) at Galeta and Minas Beach, in Belize (17°N) at Carrie Bow Cay, South Water Cay and Twin Cays, and on the east coast of Florida (27°N) at Fort Pierce Inlet, Sebastian Inlet and Bessie's Cove. The identity of each species from each location was verified from type collections at the National Museum of Natural History (B. F. KENSLEY, NMNH; A. B. WILLIAMS, National Marine Fisheries Service).

Following collection, crabs were maintained under natural photoperiod conditions on running-seawater tables at the Naos Island Laboratory of the Smithsonian Tropical Research Institute (Panama), the Carrie Bow Cay field station of the Smithsonian National Museum of Natural History (Belize) or the Smithsonian Marine Station at Link Port (Fort Pierce, Florida). Due to fluctuating salinity conditions at the Panama laboratory, all Panamanian crabs were transported for experimentation to Belize where

salinity and temperature conditions were constant. Crabs were fed Tetra-Marin Marine Staple Food *ad libitum* and allowed to acclimatize to new surroundings for at least two weeks prior to use in experiments. During experiments, crabs were kept in incubators in individual plastic containers; containers were partially filled with coral rubble and were perforated to allow water flow. Crabs were thus free to emerge from the water.

## 2. Experimental protocol

Crabs were subjected to acute temperature changes consisting of four 24 h periods of control or experimental temperature at constant salinity. Thus, crabs acclimated to control conditions were subjected to decreased or increased temperature for 24 h, returned to control temperature for 24 h and the cycle repeated. Control temperatures were 28 °C for Panama and Belize crabs and 21 °C for Florida crabs. (Control temperatures were those that prevailed during collection periods and to which crabs were acclimated). Experimentally decreased temperatures (21 °C, Panama and Belize; 14 °C, Florida) were 7 °C lower than the respective control temperature. Experimentally increased temperatures (35 °C, Panama and Belize; 21 °C, Florida) were 7 °C higher than the respective control temperature. Salinity was 35‰ ( $1080 \pm 1.64 \text{ mOsm} \cdot \text{kg}^{-1} \text{ H}_2\text{O}$ ;  $528.0 \pm 2.14 \text{ Na}^+$ ;  $10.22 \pm 0.086 \text{ K}^+$ ;  $585.0 \pm 2.01 \text{ Cl}^- \text{ mEq} \cdot \text{l}^{-1}$ ; mean  $\pm$  SE) under all circumstances.

Feeding was terminated 96 h before measurement of oxygen uptake to ensure a post-absorptive nutritional state. The influence of diel rhythms was eliminated by examining individuals of a given genus at the same time of day. To avoid the potential effects of seasonal acclimatization, all studies were performed 2 months after the end of the dry season at each locale. Members of a cognate pair (Panama) were examined simultaneously, whereas Belize and Florida populations were tested individually. All crabs were in intermolt, adult-sized and non-ovigerous.

The oxygen uptake rates of six crabs were measured simultaneously using specially designed aquaria as previously described (FERRARIS *et al.*, 1994). Briefly, aquarium design allowed individual chambers to be either sealed and isolated or interconnected with each other and with the surrounding water bath. Aquarium design allowed a complete water change without handling the crabs. Initial ( $\approx 5.5$ – $6.5 \text{ mg O}_2 \cdot \text{l}^{-1}$ ) and final ( $\approx 3.5$ – $4.5 \text{ mg O}_2 \cdot \text{l}^{-1}$ ) oxygen concentrations were measured by inserting a shielded self-stirring oxygen probe (YSI 5720; YSI Temperature/Salinity Compensated Dissolved Oxygen Meter 58) through a sealed port in the top of each chamber; values were corrected for background ( $\approx 0.1 \text{ mg O}_2 \cdot \text{l}^{-1} \cdot \text{h}^{-1}$ ). Measurements were made at the beginning and end of the first hour and at the beginning and end of the 24th hour of each 24 h cycle of experimental temperature manipulation. At the end of the 4-day experimental period, crabs were killed following destruction of the thoracic ganglion, dried at 60 °C, frozen and transported to Mt. Desert Island Biological Laboratory (MDIBL). There, each crab was dried (60 °C) to constant weight (Cahn Automatic Electrobalance TA 450; 0.1 mg), ashed (510 °C, 4 h) and the dry weight corrected for ash content (FERRARIS, 1981). The ash-free dry weight (= afdw; mean  $\pm$  SE) of each population of crabs tested ( $n = 6$ /population) is reported with the results obtained for that population (see Results). The crabs within a given population did not differ sufficiently in weight to allow determination of the relationship between metabolic rate and size. Weight specific oxygen uptake rate [ $\text{mg O}_2 \cdot \text{g}(\text{afdw})^{-1} \cdot \text{h}^{-1}$ ] was determined at each temperature.  $Q_{10}$  was estimated for each temperature change, *i.e.*, 0–1, 24–25, 48–49 and 72–73 h.

Data were compared using analyses of variance for separation of significant means. Only when differences were found to be statistically significant at least at the 0.05 level are they referred to as significant.

## Results

### 1. Repeated exposure to control and decreased temperature

#### a. *Uca galapagensis herradurensis* and *U. rapax rapax*

The rate of oxygen uptake ( $\dot{M}\text{O}_2$ ) of Pacific *Uca galapagensis herradurensis* [mass =  $0.2844 \pm 0.0346 \text{ g}(\text{afdw})$ ] did not decrease significantly below control levels

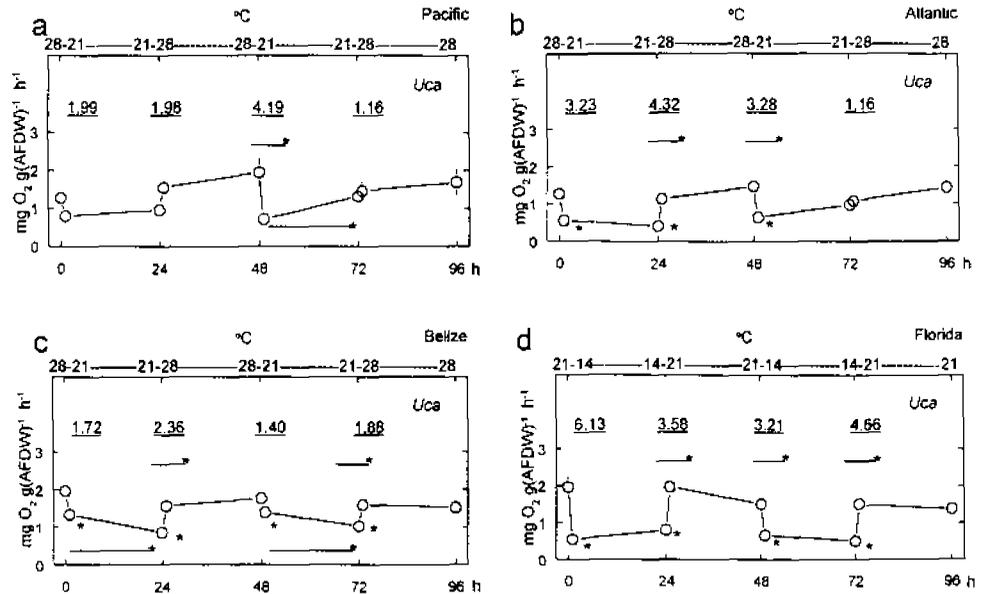


Fig. 1. Oxygen consumption [ $\text{mg O}_2 \cdot \text{g (afdw)}^{-1} \cdot \text{h}^{-1}$ ; mean  $\pm$  SE] in *Uca galapagensis herradurensis* and *Uca rapax rapax* ( $n = 6$ ) during repeated exposure to control and decreased temperature at constant salinity. Experimental temperature profile appears on the upper scale. All populations were acclimated to control temperature (28°C, Pacific, Atlantic, Belize; 21°C, Florida) and salinity (35‰). a, *U. galapagensis herradurensis*, Pacific Panama; b, *U. rapax rapax*, Atlantic Panama; c, *U. rapax rapax*, Belize; d, *U. rapax rapax*, Florida.  $Q_{10}$  values are indicated for each temperature change. Where an SE bar is not visible, the data point symbol is larger than the SE bar. Significant difference ( $P < 0.05$ ) between any point and the oxygen uptake rate at 0 h is indicated by \* next to the point. Significant difference between any other two points is indicated by an \* plus a bar extending from the first point to the second.

(0 h) when exposed to reduced temperature, whereas that of Atlantic *U. rapax rapax* [mass =  $0.5232 \pm 0.1067$  g (afdw)] did (Fig. 1a, b). The amount of increase in oxygen uptake for a 7°C increase in temperature ( $Q_{10}$ ) measured in Atlantic *U. rapax rapax* at 24–25 h was greater than that in Pacific *U. galapagensis herradurensis*. The Pacific *Uca* population demonstrated significant compensation in oxygen uptake during the exposure to decreased temperature, which produced a  $Q_{10}$  value (72–73 h) close to unity. During the same exposure, the Atlantic *Uca* population increased oxygen uptake only slightly (ns); upon subsequent return to control temperature this population did not initially respond. These events also produced a  $Q_{10}$  value at 72–73 h that was close to unity even though the Atlantic population did not demonstrate significant compensation in  $\dot{M}\text{O}_2$  during the second exposure to reduced temperature.

*U. rapax rapax* from both Belize [mass =  $0.3491 \pm 0.0463$  g (afdw)] and Florida [mass =  $0.2370 \pm 0.0170$  g (afdw)], like the Atlantic Panama population, decreased  $\dot{M}\text{O}_2$  significantly below control levels upon each exposure to reduced temperature (Fig. 1c, d). Additionally,  $\dot{M}\text{O}_2$  of *U. rapax rapax* from Belize continued to decrease significantly while the crabs were in low temperature seawater (1–24; 49–72 h). There was no evidence for compensation of  $\dot{M}\text{O}_2$  at low temperature in *U. rapax rapax* from either Belize or Florida. Hence, for the Belize and particularly for the

Florida population,  $Q_{10}$  measured for the final temperature transition (72–73 h) was greater than that measured for either Panamanian population at that time.

When the mean  $O_2$  uptake rate at 21°C was calculated for each population ( $n = 24$  or 30), in order of increasing rate, the populations were ranked Atlantic Panama, Pacific Panama, Belize and Florida. The Florida population had a greater rate of oxygen uptake ( $P < 0.001$ ) than the Belize, Pacific Panama or Atlantic Panama populations; the mass of the Florida population was not different from that of the Pacific Panama population but was less than that of the Belize and the Atlantic Panama populations ( $P < 0.05$ ). The Belize population had a greater rate of oxygen uptake ( $P < 0.02$ ) but did not differ significantly in mass from the Atlantic Panama population.

### b. *Pachygrapsus transversus*

Overall, *P. transversus* populations from the Pacific [mass =  $0.1677 \pm 0.0222$  g (afdwt)] and Atlantic [mass =  $0.0672 \pm 0.0077$  g (afdwt)] coasts of Panama responded similarly to exposure to decreased temperature (Fig. 2a, b). Except for the first change to reduced temperature (0–1 h), both populations changed significantly in oxygen uptake with each change in temperature, regardless of the direction of the temperature change. At the final return to control temperature (72–73 h),  $Q_{10}$  in the Atlantic population was higher than that of the Pacific population. This was

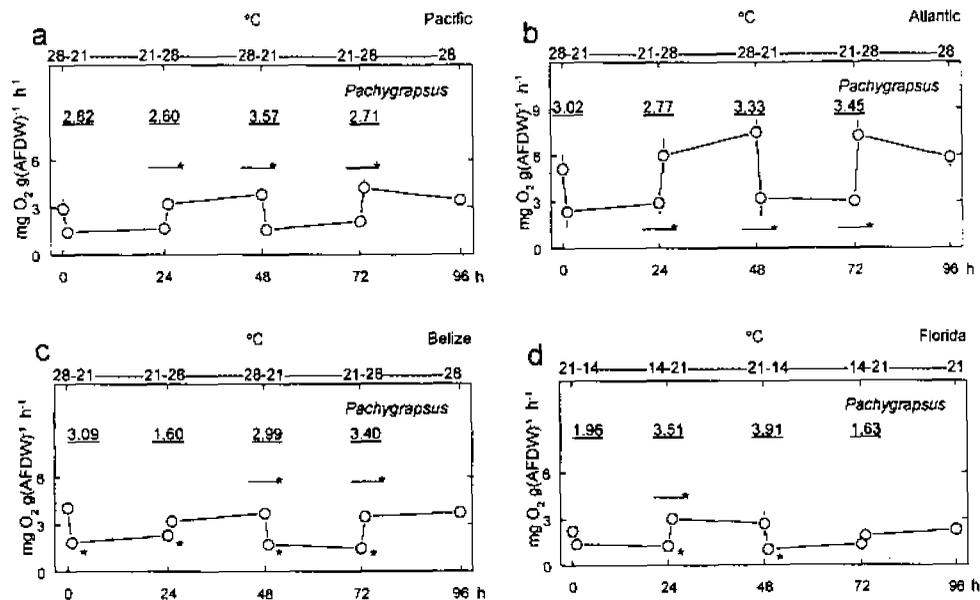


Fig. 2. Oxygen consumption [ $\text{mg O}_2 \text{ g (afdwt)}^{-1} \text{ h}^{-1}$ ; mean  $\pm$  SE] in *Pachygrapsus transversus* ( $n = 6$ ) during repeated exposure to control and decreased temperature at constant salinity. Experimental temperature profile appears on the upper scale. All populations were acclimated to control temperature (28°C, Pacific, Atlantic, Belize; 21°C, Florida) and salinity (35‰). a, Pacific Panama; b, Atlantic Panama; c, Belize; d, Florida. For further explanation of symbols, see Fig. 1.

due to some compensation (ns) in Pacific, but not Atlantic, *P. transversus* during the second exposure to decreased temperature.

Oxygen uptake in *P. transversus* from Belize [mass =  $0.1513 \pm 0.0076$  g (afdwt)] decreased significantly below control levels (0 h) during each exposure to low temperature; like populations from Pacific and Atlantic Panama, oxygen uptake increased when temperature was returned to the control value (Fig. 2c). At the final return to control temperature,  $Q_{10}$  for Belize *P. transversus* equalled that for the Atlantic Panama population, but was higher than that for the Pacific population. *P. transversus* from Belize were thus similar to those from Atlantic Panama, i.e., the Belize population did not tend to compensate in  $MO_2$  during the second exposure to reduced temperature.

*P. transversus* from Florida [mass =  $0.1609 \pm 0.0149$  g (afdwt)] (Fig. 2d) initially were as sensitive to temperature variation as other populations. However,  $Q_{10}$  for final return to control temperature (72–73 h), was lower than that of the other populations. This was due to both a tendency to compensate during the second exposure to decreased temperature and to an insignificant increase in oxygen consumption upon final return to control temperature.

When the mean  $O_2$  uptake rate at 21 °C was calculated for each *P. transversus* population ( $n = 24$  or 30), in order of increasing rate, the populations were ranked Pacific Panama, Belize, Florida and Atlantic Panama. The Atlantic Panama population had a greater oxygen uptake rate ( $P < 0.05$  compared with Belize and Pacific Panama) but also a smaller mass ( $P < 0.001$ ) than all of the other populations. Florida *P. transversus* had a greater oxygen uptake rate than either the Belize ( $P < 0.05$ ) or Pacific Panama ( $P < 0.01$ ) populations; the three populations did not differ significantly in mass.

### c. *Panopeus purpureus* and *P. lacustris*

Pacific *Panopeus purpureus* [mass =  $0.1623 \pm 0.0356$  g (afdwt)] and Atlantic Panama *P. lacustris* [mass =  $0.1483 \pm 0.0252$  g (afdwt)] showed no significant change in oxygen uptake during repeated exposure to decreased temperature (Fig. 3a, b).  $Q_{10}$  for the Pacific population at 0–1 h was close to unity and was lower than that of all other populations. Uptake in *P. lacustris* from Belize [mass =  $0.3568 \pm 0.0294$  g (afdwt)] decreased significantly below control levels (0 h) with each exposure to low temperature (Fig. 3c). All three populations tended to return to control levels of oxygen uptake during the second exposure to decreased temperature. *P. lacustris* from Florida [mass =  $1.2665 \pm 0.1304$  g (afdwt)] also decreased below control levels with each exposure to reduced temperature (Fig. 3d), but did not show evidence of compensation. Thus, at 72–73 h, when crabs were returned to control temperature,  $Q_{10}$  for the Florida *P. lacustris* was higher than that for other populations.

When the mean  $O_2$  uptake rate at 21 °C was calculated for each population ( $n = 24$  or 30), in order of increasing rate, the populations were ranked Florida, Belize, Pacific Panama and Atlantic Panama. The populations from Pacific and Atlantic Panama had greater oxygen uptake rates ( $P < 0.05$ ) but were also smaller in mass ( $P < 0.01$ ) than the Belize or Florida populations.

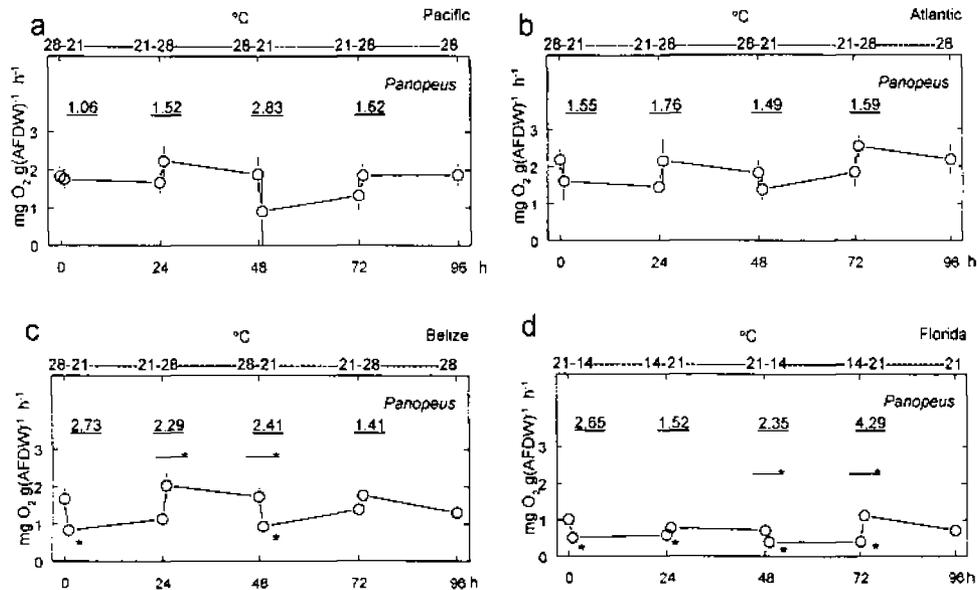


Fig. 3. Oxygen consumption [ $\text{mg O}_2 \text{g(afdw)}^{-1} \text{h}^{-1}$ ; mean  $\pm$  SE] in *Panopeus purpureus* and *P. lacustris* ( $n = 6$ ) during repeated exposure to control and decreased temperature at constant salinity. Experimental temperature profile appears on the upper scale. All populations were acclimated to control temperature (28 °C. Pacific, Atlantic, Belize; 21 °C. Florida) and salinity (35‰). a. *P. purpureus*, Pacific Panama; b. *P. lacustris*, Atlantic Panama; c. *P. lacustris*, Belize; d. *P. lacustris*, Florida. For further explanation of symbols, see Fig. 1.

#### d. *Cataleptodius taboganus* and *C. floridanus*

With each exposure to decreased temperature, oxygen uptake in both Pacific Panama *Cataleptodius taboganus* [mass =  $0.3496 \pm 0.0321$  g (afdwt)] and Atlantic Panama *C. floridanus* [mass =  $0.2023 \pm 0.0343$  g (afdwt)] decreased below control levels (Fig. 4a, b). Both populations increased  $\text{MO}_2$  during the second exposure to decreased temperature; this compensation was significant only in the Pacific population. Oxygen uptake increased significantly, in both populations, with each return to control temperature. However, the  $Q_{10}$  values at each return were higher for the Atlantic Panama population than those for the Pacific population because Atlantic Panama *C. floridanus* exceeded control levels of oxygen uptake at each return.

*C. floridanus* from Belize [mass =  $0.4309 \pm 0.0133$  g (afdwt)], like the other populations, decreased in oxygen uptake at low temperature (Fig. 4c). Their overall response pattern, however, was unusual in that they compensated toward control levels during first exposure to low temperature, but subsequently lost this capacity. Oxygen uptake decreased during the first return to control temperature (25–48 h) and continued to decrease through the second exposure to low temperature. Oxygen uptake increased significantly upon final return to control temperature. *C. floridanus* from Florida were not examined.

When the mean  $\text{O}_2$  uptake rate at 21 °C was calculated for each *Cataleptodius* population ( $n = 24$ ), in order of increasing rate, the populations were ranked

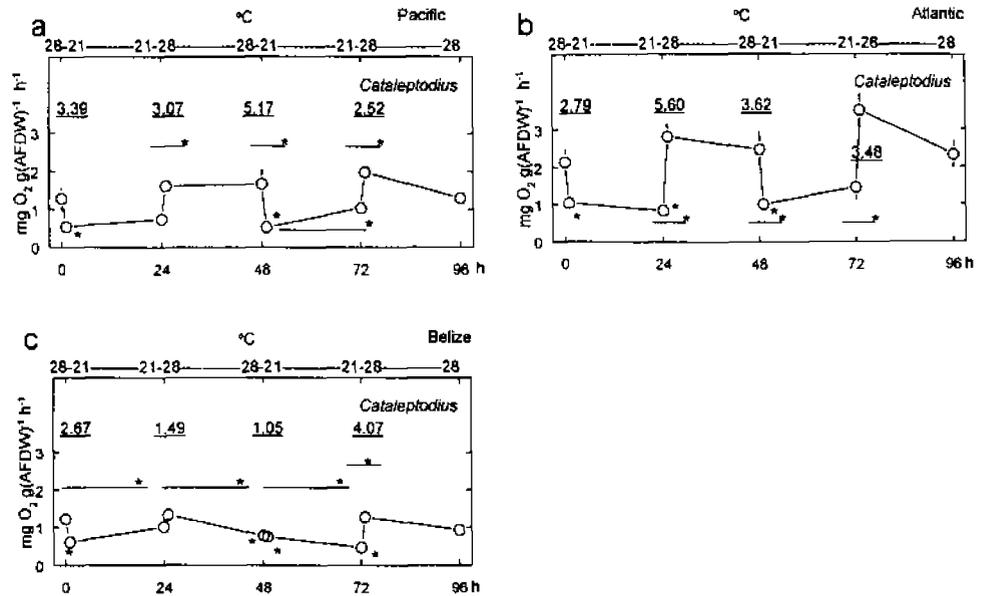


Fig. 4. Oxygen consumption [ $\text{mg O}_2 \text{ g(afdw)}^{-1} \text{ h}^{-1}$ ; mean  $\pm$  SE] in *Cataleptodius taboganus* and *C. floridanus* ( $n = 6$ ) during repeated exposure to control and decreased temperature at constant salinity. Experimental temperature profile appears on the upper scale. All populations were acclimated to control temperature ( $28^\circ\text{C}$ ) and salinity (35‰). a, *C. taboganus*, Pacific Panama; b, *C. floridanus*, Atlantic Panama; c, *C. floridanus*, Belize. For further explanation of symbols, see Fig. 1.

Pacific Panama, Belize and Atlantic Panama. The Atlantic Panama population had a greater oxygen uptake rate ( $P < 0.001$ ) but was also smaller in mass ( $P < 0.01$  and  $0.02$ ) than the other two.

## 2. Repeated exposure to control and increased temperature

### a. *Uca galapagensis herradurensis* and *U. rapax rapax*

Oxygen uptake in *U. galapagensis herradurensis* from Pacific Panama [mass =  $0.2296 \pm 0.0371$  g (afdwt)] increased significantly above control levels (0 h) during each exposure to elevated temperature (Fig. 5a). This population responded rapidly to the first exposure, but response was delayed as well as reduced at the second. With each return to control temperature,  $\text{MO}_2$  of the Pacific Panama population initially decreased and thereby returned to control levels. However, these decreases were transient; oxygen consumption had increased by the next measurement period. This response, plus the delayed increase in oxygen uptake at the second exposure to high temperature resulted in a  $Q_{10}$  at 48–49 h that was close to unity.

In Atlantic Panama *U. rapax rapax* [mass =  $0.2930 \pm 0.0594$  g (afdwt)] oxygen uptake also increased significantly above control levels during the first exposure to increased temperature (Fig. 5b). As in the Pacific population, oxygen consumption

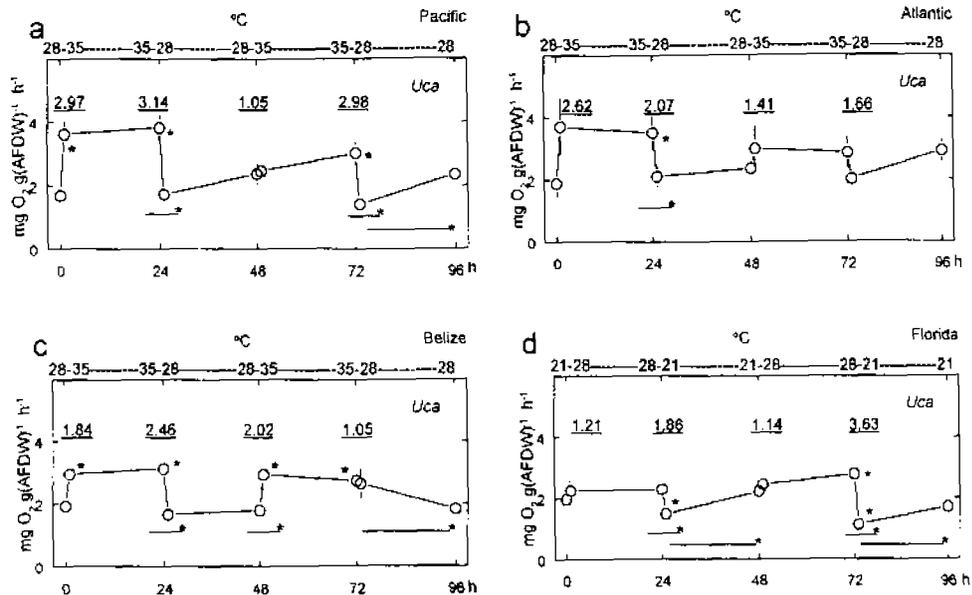


Fig. 5. Oxygen consumption [ $\text{mg O}_2 \cdot \text{g (afdwt)}^{-1} \cdot \text{h}^{-1}$ ; mean  $\pm$  SE] in *Uca galapagensis herradurensis* and *Uca rapax rapax* ( $n = 6$ ) during repeated exposure to control and increased temperature at constant salinity. Experimental temperature profile appears on the upper scale. All populations were acclimated to control temperature (28°C, Pacific, Atlantic, Belize; 21°C, Florida) and salinity (35‰). a. *U. galapagensis herradurensis*, Pacific Panama; b. *U. rapax rapax*, Atlantic Panama; c. *U. rapax rapax*, Belize; d. *U. rapax rapax*, Florida. For further explanation of symbols, see Fig. 1.

returned to control levels upon the first return to control temperature. Thereafter, the Atlantic differed from the Pacific Panama population, *i.e.*, the continuing response was essentially square wave but without significant change in the oxygen uptake rate regardless of experimental temperature.

Like the Atlantic population, *U. rapax rapax* from Belize [mass =  $0.2486 \pm 0.0244$  g (afdwt)] showed a square wave response pattern through the second exposure to increased temperature (Fig. 5c). The oxygen uptake rate increased above control levels with each exposure and returned to control  $\dot{\text{M}}\text{O}_2$  with each return to control temperature.

In contrast with other populations, *U. rapax rapax* from Florida [mass =  $0.2880 \pm 0.0294$  g (afdwt)] appeared to be relatively insensitive to elevated temperature; oxygen uptake did not increase significantly above control levels until the end of the second exposure (Fig. 5d). Correspondingly,  $Q_{10}$  at 0–1 h was lowest for Florida *U. rapax rapax*. However,  $\dot{\text{M}}\text{O}_2$  decreased below control levels with each return to control temperature. In both instances the decrease was transient and was followed by return to control levels. Florida *U. rapax rapax* was markedly similar in overall response pattern to Pacific Panama *U. galapagensis herradurensis*, but with oxygen uptake rate shifted below rather than above control levels.

The mean O<sub>2</sub> uptake rate at 28°C for each population ( $n = 24$  or 30) yielded, in order of increasing rate, the ranking: Pacific Panama, Belize, Atlantic Panama and Florida. The Florida population had a greater rate of oxygen uptake ( $P < 0.001$ ) than the Belize or the Pacific Panama population but was not significantly different in mass.

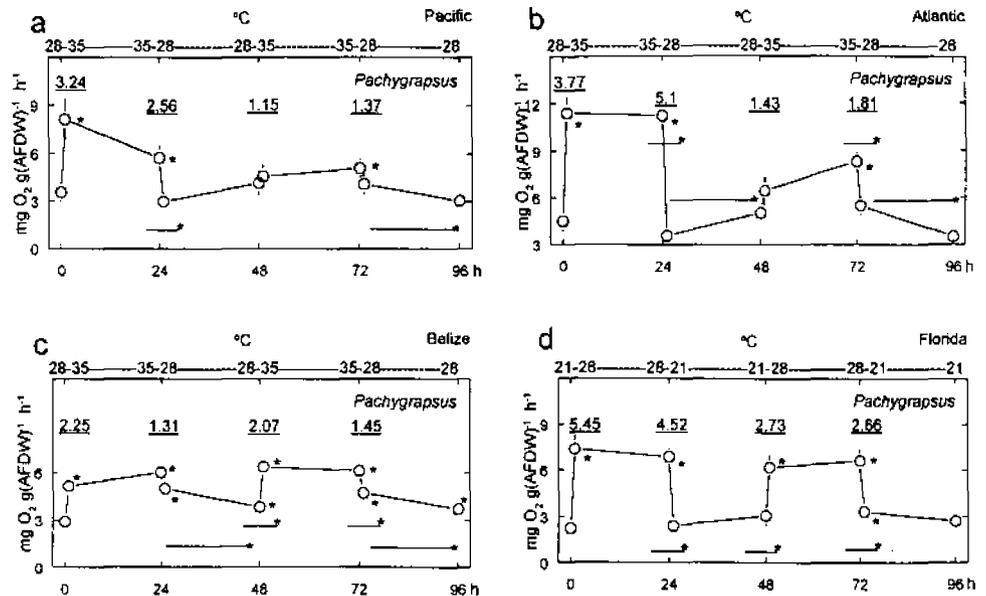


Fig. 6. Oxygen consumption [ $\text{mg O}_2 \cdot \text{g (afdw)}^{-1} \cdot \text{h}^{-1}$ ; mean  $\pm$  SE] in *Pachygrapsus transversus* ( $n = 6$ ) during repeated exposure to control and increased temperature at constant salinity. Experimental temperature profile appears on the upper scale. All populations were acclimated to control temperature ( $28^\circ\text{C}$ , Pacific, Atlantic, Belize;  $21^\circ\text{C}$ , Florida) and salinity (35‰). a, Pacific Panama; b, Atlantic Panama; c, Belize; d, Florida. For further explanation of symbols, see Fig. 1.

#### b. *Pachygrapsus transversus*

The Pacific [mass =  $0.1189 \pm 0.0254$  g (afdw)] and Atlantic [mass =  $0.0500 \pm 0.0038$  g (afdw)] Panama populations of *Pachygrapsus transversus* were similar in overall response pattern (Fig. 6a, b). However, the Atlantic Panama population responded more strongly to temperature change. Regardless of the direction of the temperature change,  $Q_{10}$  values were greater in the Atlantic versus the Pacific population. With first exposure to elevated temperature, oxygen uptake rate in both increased significantly; their response to the second exposure to increased temperature was delayed as well as decreased compared to the first exposure. In Pacific *P. transversus* this compensation was significant. Both populations decreased significantly in  $\text{MO}_2$  with each return to control temperature.

The oxygen consumption of Belize *P. transversus* [mass =  $0.1146 \pm 0.0059$  g (afdw)] increased to the same degree above control levels at the first and second exposure to high temperature, indicating a lack of compensation (Fig. 6c). As in the Panamanian populations, oxygen uptake in Belize *P. transversus* also decreased with return to control temperature, yet it remained significantly higher than control levels throughout the experiment.

Florida *P. transversus* [mass =  $0.1475 \pm 0.0203$  g (afdw)] responded similarly to the Belize population but did not remain at an elevated oxygen consumption level upon return to control temperature (Fig. 6d). As in the Belize population, there was no evidence of compensation.  $Q_{10}$  values at 0–1 and 48–49 h were greater than in the other populations.

Calculating the mean  $O_2$  uptake rate at 28 °C for each *P. transversus* population ( $n = 24$  or 30) revealed, in order of increasing rate, the ranking: Belize, Pacific Panama, Atlantic Panama and Florida. The Florida population had a greater oxygen uptake rate ( $P < 0.001$ ) than all other populations. Populations did not differ significantly in mass (exception: Atlantic Panama was smaller than all others;  $P < 0.001$ ).

### c. *Panopeus purpureus* and *P. lacustris*

*Panopeus purpureus* from Pacific Panama [mass =  $0.3177 \pm 0.0503$  g (afdwt)] increased in  $\dot{M}O_2$  above control levels with each exposure to increased temperature (Fig. 7a). During the first exposure, oxygen uptake rate decreased toward control levels indicating compensation. This trend, plus a delayed response to return to control temperature, resulted in a  $Q_{10}$  at 24–25 h close to unity and no significant change in oxygen uptake rate. Renewed exposure, however, resulted in no evidence of compensation; there was also a significant decrease upon subsequent return to control temperature.

*P. lacustris* from Atlantic Panama [mass =  $0.2134 \pm 0.0201$  g (afdwt)] appeared to increase oxygen uptake rate at the first exposure to increased temperature, although the change in oxygen consumption was not significant (Fig. 7b). This population also showed no subsequent significant response to temperature vari-

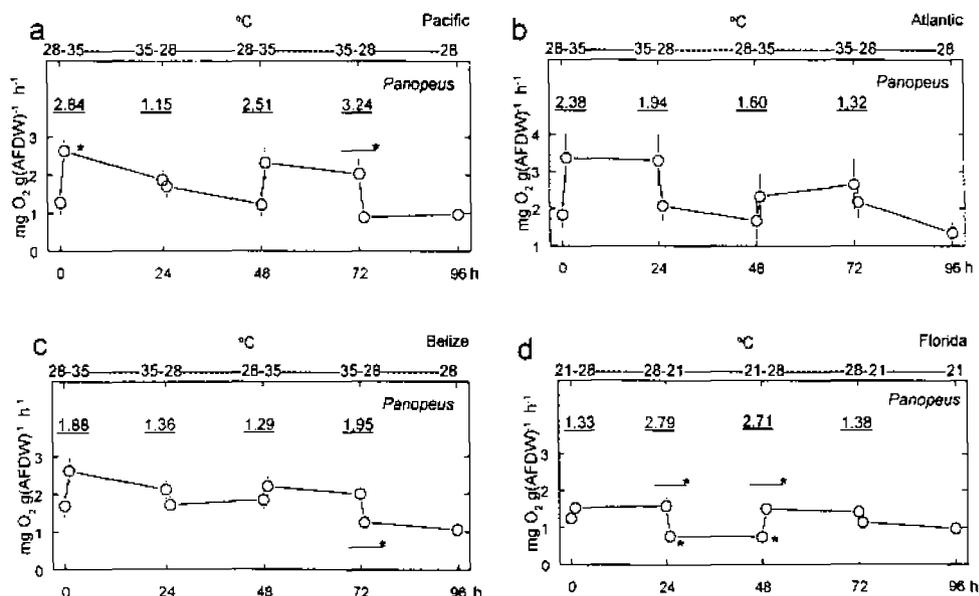


Fig. 7. Oxygen consumption [ $\text{mg O}_2 \cdot \text{g (afdwt)}^{-1} \cdot \text{h}^{-1}$ ; mean  $\pm$  SE] in *Panopeus purpureus* and *P. lacustris* ( $n = 6$ ) during repeated exposure to control and increased temperature at constant salinity. Experimental temperature profile appears on the upper scale. All populations were acclimated to control temperature (28 °C, Pacific, Atlantic, Belize; 21 °C, Florida) and salinity (35‰). a. *P. purpureus*, Pacific Panama; b. *P. lacustris*, Atlantic Panama; c. *P. lacustris*, Belize; d. *P. lacustris*, Florida.  $Q_{10}$  values are indicated for each temperature change. For further explanation of symbols, see Fig. 1.

ation. In comparison with the Pacific Panama *P. purpureus*, this cognate generally had lower  $Q_{10}$  values.

*P. lacustris* from Belize [mass =  $0.5126 \pm 0.1691$  g (afdwt)], like the Atlantic Panama population, did not increase oxygen uptake significantly above control levels with exposure to increased temperature (Fig. 7c). Consequently,  $Q_{10}$  values at elevated temperature were lower than in the Pacific Panama population. In contrast to the first return to control temperature, at the second, Belize *P. lacustris* significantly decreased oxygen uptake.

*P. lacustris* from Florida [mass =  $0.9081 \pm 0.2038$  g (afdwt)] appeared to be less sensitive to increased temperature since  $Q_{10}$  at 0–1 h was less than in any other population (Fig. 7d). At the first return to control temperature, however, oxygen consumption dropped significantly below control levels and remained at that level until transfer to increased temperature seawater. Upon second transfer to elevated temperature,  $Q_{10}$  was higher than that of other populations.

The mean  $O_2$  uptake rate at 28°C for each population ( $n = 24$  or 30) yielded the ranking, in order of increasing rate, of: Pacific Panama, Florida, Belize and Atlantic Panama. The Atlantic Panama population had a greater oxygen uptake rate ( $P < 0.02$ ) than the Pacific Panama population. The former was smaller than all others and significantly different from the Florida population ( $P < 0.02$ ).

#### d. *Cataleptodius taboganus* and *C. floridanus*

Pacific Panama *Cataleptodius taboganus* [mass =  $0.2978 \pm 0.0228$  g (afdwt)], Atlantic Panama *C. floridanus* [mass =  $0.1280 \pm 0.0139$  g (afdwt)] and Belize *C. floridanus* [mass =  $0.4087 \pm 0.0397$  g (afdwt)] demonstrated a similar response pattern to repeated exposure to increased temperature (Fig. 8a–c). All three increased oxygen uptake above control levels at elevated temperature and decreased to control levels upon return to control temperature. Only Atlantic Panama *C. floridanus* responded at lower amplitude to the second exposure. However,  $Q_{10}$  values for the Atlantic Panama population at 0–1 h were higher than those for the other populations; they were also higher than those for Belize *C. floridanus* at 48–49 h. These data indicate greater relative increase in oxygen uptake at elevated temperature in the Atlantic Panama population. *C. floridanus* from Florida were not examined.

The ranking of the mean  $O_2$  uptake rate at 28°C for each *Cataleptodius* population ( $n = 30$ ), in order of increasing rate, was: Belize, Pacific Panama and Atlantic Panama (Atlantic Panama > Pacific Panama population,  $P < 0.01$ , or Belize,  $P < 0.001$ ). The mass of the Atlantic Panama population was significantly smaller than the other two populations ( $P < 0.001$ ).

## Discussion

In Crustacea, temperature affects oxygen consumption in various ways and can differentially affect both standard and active metabolism (HALCROW & BOYD, 1967). Oxygen uptake rate usually varies directly with temperature, but some species are thermally insensitive. For example, in some *Uca* spp., no change in oxygen uptake rate occurs over the temperature range in which they are active

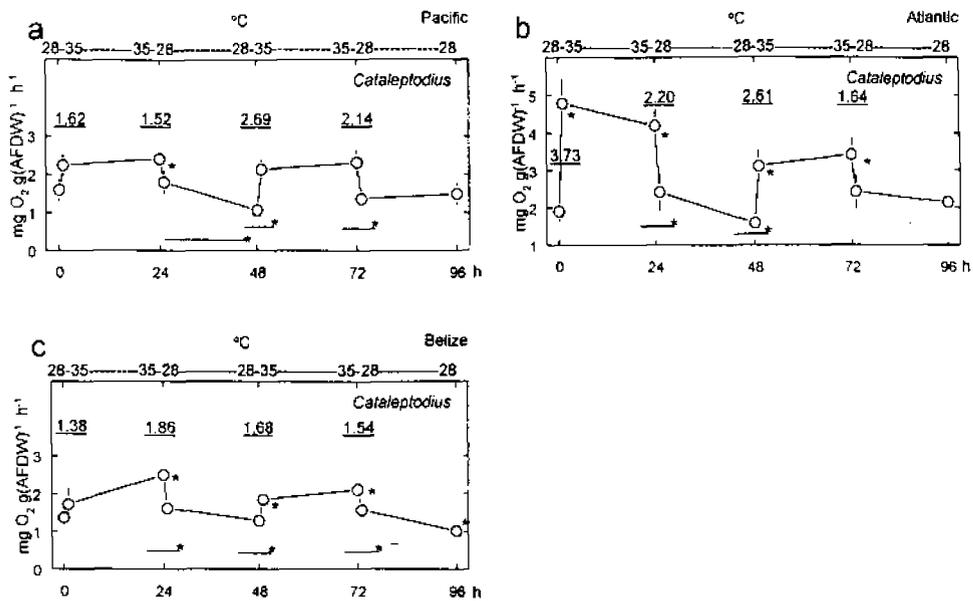


Fig. 8. Oxygen consumption [ $\text{mg O}_2 \cdot \text{g (afdw)}^{-1} \cdot \text{h}^{-1}$ ; mean  $\pm$  SE] in *Cataleptodius taboganus* and *C. floridanus* ( $n = 6$ ) during repeated exposure to control and increased temperature at constant salinity. Experimental temperature profile appears on the upper scale. All populations were acclimated to control temperature ( $28^\circ\text{C}$ ) and salinity (35‰). a. *C. taboganus*, Pacific Panama; b. *C. floridanus*, Atlantic Panama; c. *C. floridanus*, Belize. For further explanation of symbols, see Fig. 1.

(VERNBERG, 1983). Acclimation state also affects response to temperature. Both *Panopeus herbstii* and *U. pugilator* have lower oxygen consumption rates when acclimated to cyclic versus constant thermal regimes (DAME & VERNBERG, 1978). As with thermal insensitivity, such reduced oxygen consumption also occurs at temperatures corresponding to the annual thermal range over which the populations are most active. As a result, the authors suggested that *Panopeus herbstii* and *U. pugilator* use energy more efficiently during natural cyclic temperature fluctuation than during exposure to constant temperature. Although strict comparison with the present study is not possible, it should be noted that similar correlation was not observed here. In the present study, the Florida and Pacific Panama populations experience substantial temperature variation in natural habitats. In both *Uca* and *Pachygrapsus*, however, the Florida populations had the highest oxygen uptake rates, rather than the lowest, at both 21 and  $28^\circ\text{C}$ . The Pacific Panama populations did not demonstrate any distinguishable correlation. Evidence is frequently found for compensatory acclimation or, more commonly, correlation of direct physiological response with distribution, based on environmental factors (GRAHAM, 1971; SHICK, 1972; BURTON *et al.*, 1981; FERRARIS, 1981; VERNBERG, 1983). VERNBERG and VERNBERG demonstrated metabolic adaptation in temperate versus tropical zone congeners of *Uca*, particularly with respect to low temperatures (reviews: F. J. VERNBERG, 1983, 1984). Their results generally support the theory that, at a given temperature, a cold-adapted form will show a higher metabolic rate than a warm-adapted form. ROBERTS (1957), working with *Pachygrapsus crassipes* populations collected from sites ranging from southern

California to Oregon, also reported similar results. Different acclimation and experimental conditions prevent direct comparison with the present study.

### 1. *Uca galapagensis herradurensis* and *U. rapax rapax*

When *U. galapagensis herradurensis* and *U. rapax rapax* were repeatedly exposed to decreased temperature, the Panamanian cognates were similar in overall response pattern. Applying the same overall response criterion, the Belize and Florida populations appeared to respond more similarly to each other than to either of the Panamanian populations. The most obvious difference was that Belize and Florida populations showed no compensatory increase during the second exposure. However, only the Pacific population actually showed significant compensation (the Atlantic population achieved the control oxygen consumption level only after being returned to control temperature, and then only after 24 h). The Belize population appeared to be somewhat less sensitive than the Atlantic population; initially, with each exposure they did not decrease oxygen uptake as much. The difference between the Atlantic and Belize populations was, however, primarily a function of time rather than degree of response. These data, taken alone, suggest that populations such as those in Atlantic Panama and Belize, which are not naturally subject to temperature drops in surrounding seawaters, do not develop the ability to compensate when faced with repeated exposure to lower temperature. Conversely, populations such as those found in Pacific Panama and Florida should exhibit greater compensatory ability. The response in oxygen consumption of the Pacific Panama population minimally supports this hypothesis, whereas that of the Florida population does not.

Response to repeated exposure to increased temperature was also examined for *U. galapagensis herradurensis* and *U. rapax rapax* populations. In these experiments, the Pacific and Florida populations showed a similar overall response pattern, as did the Atlantic Panama and Belize populations. There is evidence that the Pacific Panama population was more sensitive to increased temperature than the Atlantic Panama population since the latter's oxygen uptake did not change significantly after the first return to control temperature. The Florida population could be interpreted as the least sensitive to increased temperature based on  $Q_{10}$  values that were close to unity with each transfer to elevated temperature. However, this would be erroneous since increased temperature affected the Florida population significantly; *i.e.*, after exposure to elevated temperature, oxygen uptake decreased progressively further below control levels (0 h) with each return to control temperature. This effect produced the similarity of overall response pattern between Florida and Pacific Panama populations.

While response in oxygen consumption is important, it is not the only physiological parameter affected by temperature. Thus, the same *Uca* populations were also examined for whole body water and ion regulation during repeated exposure to either decreased or increased temperatures (FERRARIS & NORENBURG, 1997). With regard to ion regulation, the *Uca* populations also fall into two groups during repeated exposure to decreased temperature. The result: maintained, elevated  $\text{Na}^+$  and  $\text{Cl}^-$  concentrations in Pacific Panama and Florida populations but not in Atlantic or Belize populations. During repeated exposure to increased temperature,

Pacific Panama *Uca* were more sensitive than Atlantic Panama and Belize populations, that is, the Pacific population maintained the least stable water and ion content (FERRARIS & NORENBURG, 1997). Under the same conditions, the Florida population showed a quite variable response although solute content did not change significantly (FERRARIS & NORENBURG, 1997). A number of these results resemble those observed for other genera in two ways. First, Pacific Panama and Florida, but not Atlantic Panama and Belize, populations show evidence of adaptation to reduced habitat temperature. Second, adaptation to decreases in temperature may have reduced the capacity of Pacific Panama and Florida populations to compensate at elevated temperature. Overall, in *Uca*, the correlation between habitat temperature and physiological divergence was greater with regard to water and ion regulation than to oxygen uptake.

Since *U. galapagensis herradurensis* and *U. rapax rapax* are semi-terrestrial, differences in air temperature among habitats should also be considered. Thus, the population subject to the lowest water or air temperature, *i.e.*, Florida, demonstrates the highest mean oxygen uptake rate at a given temperature (21 and 28 °C). These results, like others found for *U. rapax* (VERNBERG, 1959), support the theory that at a given temperature, a cold-adapted form will show a higher metabolic rate than a warm-adapted form.

## 2. *Pachygrapsus transversus*

*Pachygrapsus transversus* populations appeared to respond similarly to repeated exposure to decreased temperature, but demonstrated certain differences that may relate to natural exposure to temperature reduction in habitats. Specifically, Atlantic Panama and Belize *P. transversus* showed no evidence for compensation during second exposure to decreased temperature, while Pacific Panama and Florida populations did. This resulted in lower  $Q_{10}$  values for Pacific Panama and, particularly, Florida populations during subsequent return to control temperature. This indicates that Pacific Panama and Florida populations may have developed mechanisms that are adaptive in an environment characterized by periodic temperature drops. Taken alone, the oxygen uptake response in these populations would support this hypothesis, but only weakly.

The present study, also revealed that the *P. transversus* population that experiences the coldest water or air temperatures (Florida) demonstrated the highest mean oxygen uptake at a given temperature. This parallels the findings for the *Uca* populations, which are also semi-terrestrial in habit.

In contrast, the response patterns of the various *P. transversus* populations to repeated exposure to elevated temperature were not correlated with habitat temperature. Under these conditions there was similarity in overall response pattern between the Pacific and Atlantic Panama populations but not the other two populations. In addition, although both the Atlantic and the Pacific Panama population demonstrated evidence of compensation, the Atlantic population was more sensitive to exposure to increased temperature. Since Belize and Florida populations did not compensate, they may be more sensitive than either of the Panama populations. These populations also showed sensitivity in that the oxygen uptake rate of Belize *P. transversus* was significantly higher than control levels (0 h) throughout

the experiment, while the Florida population demonstrated the more extreme  $Q_{10}$  values. These results do not correlate with the temperature characteristics of their habitats and are in contrast with volume regulatory response during repeated exposure to temperature change (FERRARIS & NORENBURG, 1997). These complementary studies indicate that the Pacific Panama and Florida *P. transversus* populations have adapted to the low water temperatures that periodically occur in their respective habitats. Thus, during repeated exposure to decreased temperature, these populations of *P. transversus* maintained stable water and solute contents, whereas Atlantic Panama and Belize populations did not. During repeated exposure to increased temperature, the converse was found; that is, Atlantic Panama and Belize, but not Pacific Panama and Florida, *P. transversus* maintained stable water and ion content. These results led to the hypothesis that, in Pacific Panama and Florida populations, adaptation to decreases in habitat temperatures has reduced volume regulatory ability during exposure to temperature increases.

Overall, in *P. transversus*, both volume regulation and oxygen uptake correlate with habitat temperature, but oxygen uptake rate is only correlated with exposure to decreased temperature.

### 3. *Panopeus purpureus* and *P. lacustris*

The Pacific Panama population of *Panopeus purpureus* was initially insensitive to decreased temperature. Subsequently, however, its overall response pattern was similar to that of *P. lacustris* from Atlantic Panama and Belize. The response pattern of *P. lacustris* from Florida differed from that of other populations primarily because it showed no evidence of compensation. There was little difference in sensitivity between Pacific and Atlantic Panama populations. The Belize population was more sensitive than either of the Panamanian populations, and the Florida population appeared the most sensitive. These results do not correlate with relative exposure to habitat temperature drops. This contrasts with results obtained by exposing *Panopeus* populations to increased temperature.

During repeated exposure to increased temperature, the overall response pattern in *P. lacustris* was similar in the Atlantic Panama and Belize populations. Overall, *Panopeus* from Pacific Panama and Florida differed from the other populations. Based on  $Q_{10}$  values, Pacific Panama crabs were more sensitive to increased temperature than either the Atlantic Panama or the Belize population. The Florida *Panopeus* population initially appeared to be insensitive to high temperature. However, as in *Uca*, exposure to increased temperature produced a significant decrease below control oxygen uptake levels (0 h) upon return to control temperature.

Overall, these results indicate that Pacific Panama and Florida populations of *Panopeus*, which experience the greatest habitat temperature drops, were the most sensitive to elevated temperature. While there are no comparative data on relative volume regulatory abilities for other *Panopeus* populations, the Florida population can regulate volume efficiently during repeated exposure to reduced temperature (FERRARIS, unpubl.). Other than a transient increase in whole body water,  $\text{Na}^+$  and  $\text{Cl}^-$  contents upon initial exposure to reduced temperature (1 h), these crabs maintained stable water and solute contents as well as osmolality and inorganic

ion concentrations throughout experimental manipulation. In contrast, when the Florida *Panopeus* population was subjected to elevated temperature, whole body water,  $\text{Na}^+$  and  $\text{Cl}^-$  contents increased above control values and remained significantly elevated until the end of return to control temperature. These data are in accord with volume regulatory data found for other genera (FERRARIS & NORENBURG, 1997) which indicate that populations that have adapted to periodically decreased temperatures are less able to compensate when exposed to increased temperature.

Overall, in *Panopeus* populations, response in oxygen uptake rate to increased, but not decreased temperature, can be correlated with natural exposure to decreases in habitat temperature. As far as data are available, volume regulatory response to both increased and decreased temperature can be correlated with habitat temperatures.

#### 4. *Cataleptodius taboganus* and *C. floridanus*

The Pacific Panama population of *Cataleptodius taboganus* compensated significantly at decreased temperature, whereas Atlantic Panama *C. floridanus* did not. The latter was also more sensitive than the Pacific Panama population at return to control temperatures. The Belize population showed an unusual oxygen uptake pattern, primarily due to its response during the first return to control temperature. This population had initially appeared able to compensate better than either of the Panamanian populations. Subsequently, however, it became evident that Belize *C. floridanus* were as sensitive to repeated temperature drops as the Atlantic population.

During repeated exposure to increased temperature, response of the *Cataleptodius* populations did not appear correlated with habitat temperature regimes. As in *Pachygrapsus*, Atlantic Panama *Cataleptodius* were more sensitive to increased temperature than the Pacific population; however, they also appeared to be more sensitive than the Belize population.

When *Cataleptodius* were exposed to the same experimental temperature conditions, Pacific Panama, but not Atlantic Panama or Belize, populations regulated water and solute contents efficiently with repeated exposure to decreased temperature (FERRARIS & NORENBURG, 1997). These data are consistent with the hypothesis that Pacific populations have adapted to habitat temperature drops.

Consistent with the hypothesis that adaptation to habitat temperature decreases had reduced volume regulatory ability during exposure to increased temperature, the Pacific Panama *Cataleptodius* population regulated volume less efficiently than the Atlantic Panama or Belize populations at increased temperature (FERRARIS & NORENBURG, 1997). Overall, in *Cataleptodius*, correlation between habitat temperature and physiological adaptation is found in oxygen uptake rate during exposure to decreased temperature and volume regulatory ability, regardless of the direction of the temperature change.

If the differences seen among populations of the various genera in the present study did not persist following acclimation it would indicate the occurrence of environmentally induced phenotypic variation as opposed to genotypic variation (VERNBERG, 1983). SCHNEIDER (1967 cited in VERNBERG, 1983) found an interesting

example of this. In his study, many of the differences found in metabolic-temperature curves among field-collected populations of *Rhithropanopeus harrisii* from Maine, North Carolina, and Florida did not persist when crabs from the three populations were laboratory-reared. Field-collected populations of Panamanian cognate fish species, *Apogon*, also exhibit differences in oxygen consumption that correlate with trans-isthmian temperature differences (GRAHAM, 1971). In *Apogon*, however, these differences in temperature sensitivities, determined as a direct response, persist after acclimation, indicating that genetic capacity differs (GRAHAM, 1971). To our knowledge, GRAHAM's is the only study that has examined physiological divergence in response to environmental parameters in trans-isthmian cognate species. His study provided another interesting finding. Reflecting potentially different physico-chemical regimes among habitats, trans-isthmian cognate fishes in the high littoral (*Bathygobius ramaosus* and *B. saporator*) differ less in temperature sensitivity than do *Apogon dovii* and *A. maculatus* (low littoral to sublittoral) (GRAHAM, 1971, 1972). Thus, the low temperatures characteristic of Pacific Panama, but not Atlantic Panama, may affect low intertidal animals more than high intertidal species. This follows if one recognizes that, while water temperatures differ across the isthmus, air temperatures do not.

It should be recognized that many studies demonstrate no correlation between oxygen uptake rates and habitat temperature. For example, in subtidal *Hyalinoecia* (Polychaeta), oxygen uptake is independent of temperature over a wide range, even though the animal lives in a thermally stable environment (MANGUM, 1972). Temperature insensitivity is more common in organisms that experience regular fluctuation in habitat temperature (review: NEWELL, 1973), but exceptions certainly exist, e.g., *Alpheus viridari* (Decapoda) (FERRARIS *et al.*, 1994).

### Summary

(1) *Pachygrapsus* and *Cataleptodius*, Pacific Panama and Florida populations, where examined, were less sensitive to decreased temperature than were Atlantic Panama or Belize populations. To a degree, the same was observed in Pacific *Uca* but not in *Panopeus*, indicating that, in only some of the genera tested, exposure to habitat temperature decreases has resulted in divergence. (2) Correlation between higher mean O<sub>2</sub> uptake rates and populations that experience the lowest habitat temperatures was detected in *Uca* and *Pachygrapsus*; no conclusion could be drawn from experiments with *Cataleptodius* or *Panopeus* because results were not independent of crab mass. (3) During exposure to elevated temperature, there is evidence that Pacific and Florida populations of *Uca* and *Panopeus* are more sensitive to increased temperature than Atlantic Panama or Belize populations. These results support the hypothesis that adaptation to an environment in which decreased temperatures occur results in reduced compensation during exposure to elevated temperature, but the evidence is not strong. (4) *Pachygrapsus* and *Cataleptodius*, Pacific and Florida populations were not more sensitive to increased temperatures than Atlantic and Belize populations, which would not support the hypothesis stated in (3).

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