

Causes and Consequences of Thermal Tolerance Limits in Rocky Intertidal Porcelain Crabs, Genus *Petrolisthes*¹

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SYNOPSIS. Vertical zonation of intertidal organisms, from the shallow subtidal to the supralittoral zones, is a ubiquitous feature of temperate and tropical rocky shores. Organisms that live higher on the shore experience larger daily and seasonal fluctuations in microhabitat conditions, due to their greater exposure to terrestrial conditions during emersion. Comparative analyses of the adaptive linkage between physiological tolerance limits and vertical distribution are the most powerful when the study species are closely related and occur in discrete vertical zones throughout the intertidal range. Here, I summarize work on the physiological tolerance limits of rocky intertidal zone porcelain crab species of the genus *Petrolisthes* to emersion-related heat stress. In the eastern Pacific, *Petrolisthes* species live throughout temperate and tropical regions, and are found in discrete vertical intertidal zones in each region. Whole organism thermal tolerance limits of *Petrolisthes* species, and thermal limits of heart and nerve function reflect microhabitat conditions. Species living higher in the intertidal zone are more eurythermal than low-intertidal congeners, tropical species have the highest thermal limits, and the differences in thermal tolerance between low- and high-intertidal species is greatest for temperate crabs. Acclimation of thermal limits of high-intertidal species is restricted as compared to low-intertidal species. Thus, because thermal limits of high-intertidal species are near current habitat temperature maxima, global warming could most strongly impact intertidal species.

INTRODUCTION

The marine intertidal zone is formed within the transition from land to sea, and accordingly organisms that live within this zone are exposed to marine conditions during high tide and terrestrial conditions during low tide. Organisms living in the intertidal zone experience a suite of physical stresses, including fluctuations in temperature, aerial exposure, salinity, and hydrodynamic forces (Vernberg and Vernberg, 1972; Newell, 1979; Denny, 1988). The local tidal conditions and the vertical position of an organism on the seashore together determine the frequency and duration of emersion during low tide. The organisms inhabiting the intertidal zones of rocky shores are often distributed in sharp vertical bands over the entire spring tide range. Many studies have shown that the upper vertical limits of species distributions are correlated with the physiological limits of those species to terrestrial conditions (e.g., for crustaceans Wethey, 1983; Pellegrino, 1984; Jensen and Armstrong, 1991; Lohrer *et al.*, 2000; Stillman and Somero, 2000; Flores and Paula, 2001). The lower limits of a species vertical distribution range may be set by biotic factors such as competition or predation (Connell, 1961; Paine, 1974), or may be set by tolerance to or preference of abiotic factors such as substratum type (Jensen and Armstrong, 1991). In general, these studies imply that species living higher in the intertidal zone have evolved specific adaptations that allow them to withstand the environmental stresses associated with the increasing exposure to terrestrial conditions, and thus to explore new ecological niches.

Understanding these adaptations requires the incorporation of the comparative method, as described below.

ENVIRONMENTAL PHYSIOLOGY: GENERAL CONSIDERATIONS

Adaptation of ectothermic organisms to environmental temperature stress has been intensively studied during the past 50 yr (reviews in Johnston and Bennett, 1996; Somero, 1996; Feder and Hofmann, 1999). Studies conducted within an explicit evolutionary framework, as defined by modern usage of the comparative method, have been made most frequently on lizards (e.g., Huey and Bennett, 1987; Garland *et al.*, 1991) and insects (e.g., Kimura, 1988; Gilchrist *et al.*, 1997). Incorporation of the evolutionary history into any analysis follows from the “unarguable premise that species are not independent biological units that are devoid of history and genealogical affinities” (Huey, 1987). Methods of data transformation, such as phylogenetic independent contrasts, have been created to control for the effects of evolutionary history, by combining phylogenetic information with biological data to create a new, independent, set of data (Felsenstein, 1985; Harvey and Pagel, 1991; Miles and Dunham, 1993). From a methodological standpoint, appropriate study species for comparative analyses must be selected because they possess the specific organismal or environmental diversity that is of interest (Huey, 1987), and for which phylogenetic analyses are available.

From the above guidelines, an ideal group of species with which to conduct studies of evolutionary responses to the environmental stresses associated with life in the intertidal zone would possess the following characteristics. The group of study species would be one that was comprised of a large group of closely related

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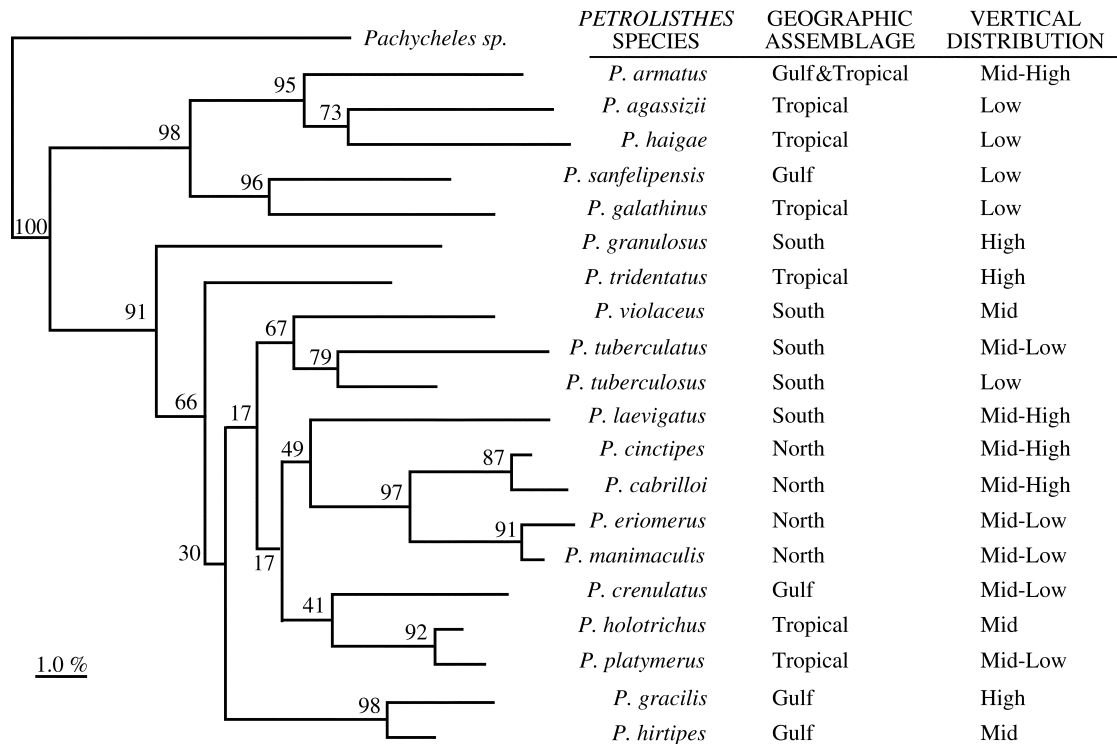


FIG. 1. Phylogeny and distribution of eastern Pacific porcelain crabs in the genus *Petrolisthes* for which thermal tolerance data have been collected. The phylogenetic tree was constructed by neighbor-joining based on a distance matrix from ~450 bp of the 16sRNA gene sequence with bootstrap values given for each node (for details see Stillman and Somero (2000) and Stillman and Reeb (2001)). Geographic assemblages are as follows: North = north Temperate (California to Alaska); Gulf = northern Gulf of California (Guaymas to Puerto Peñasco); Tropical = southern Gulf of California to Ecuador, South = south Temperate (Peru and Chile). Vertical distributions in the intertidal zone are as follows: High = above the low high water mark, Mid = mean water mark, Low = at or below the low low water mark, Mid-High and Mid-Low are intermediate designations. Distribution data are from Haig (1960), Caravacho (1980), and Stillman (1998).

species that occur in discrete vertical zones. The group of species would be comprised of multiple smaller groups of closely related species, each small group possessing members that live over the complete range of microhabitat conditions observed in all species. The organisms would be abundant, easy to collect, and tractable for study. Lastly, the group of species would possess members with a wide range of physiological responses to their particular microhabitat conditions. Not very many groups of organisms meet the above criteria, and as lamented by Huey (1987), practical considerations have unfortunately made such broad comparative studies rare.

STUDY SYSTEM: PORCELAIN CRABS

A group of intertidal organisms that meets many of the above criteria for selection of a study system is the porcelain crabs, genus *Petrolisthes* (Crustacea: Decapoda: Anomura: Porcellanidae). There are over 100 species of *Petrolisthes* worldwide, with 46 species found in the Eastern Pacific Ocean (Haig, 1960). Porcelain crabs are among the most common, abundant, and diverse groups of crustaceans found in wave-sheltered cobble or boulder intertidal habitats (Villalobos Hiriart *et al.*, 1992), and densities of *P. cincitipes* have been estimated at nearly 4,000 individuals m^{-2} in beds of the mussel *Mytilus californianus* (Jensen, 1990). A

molecular phylogenetic analysis of eastern Pacific porcelain crabs has been recently completed (Stillman and Reeb, 2001), allowing the application of comparative analytical methods. Latitudinal distribution boundaries of *Petrolisthes* in the Eastern Pacific create four geographic assemblages: North Temperate, Northern Gulf of California, Tropical (Southern Gulf of California to Ecuador), and South Temperate (Fig. 1; Carvacho, 1980). With the exception of one species, *P. armatus*, eastern Pacific species are only found within one geographic assemblage. These four geographic regions comprise three different classes of water temperature. The temperate regions are generally cool (8–18°C), with cooler regions towards the poles (8–11°C). Throughout the tropics, water temperatures are warm (20–30°C) year-round, and in the Northern Gulf of California, water temperatures vary on a seasonal basis (15–30°C). In winter, water temperatures are similar to those in temperate regions, while in summer, water temperatures can exceed those in tropical regions. Thus eastern Pacific porcelain crabs have mean body temperatures in one of three classes: temperate, tropical or seasonally tropical.

In each of the four geographic regions, species are distributed across a vertical gradient in the intertidal and subtidal zones (Romero, 1982; Weber Urbina, 1986; Jensen and Armstrong, 1991; Stillman, 1998).

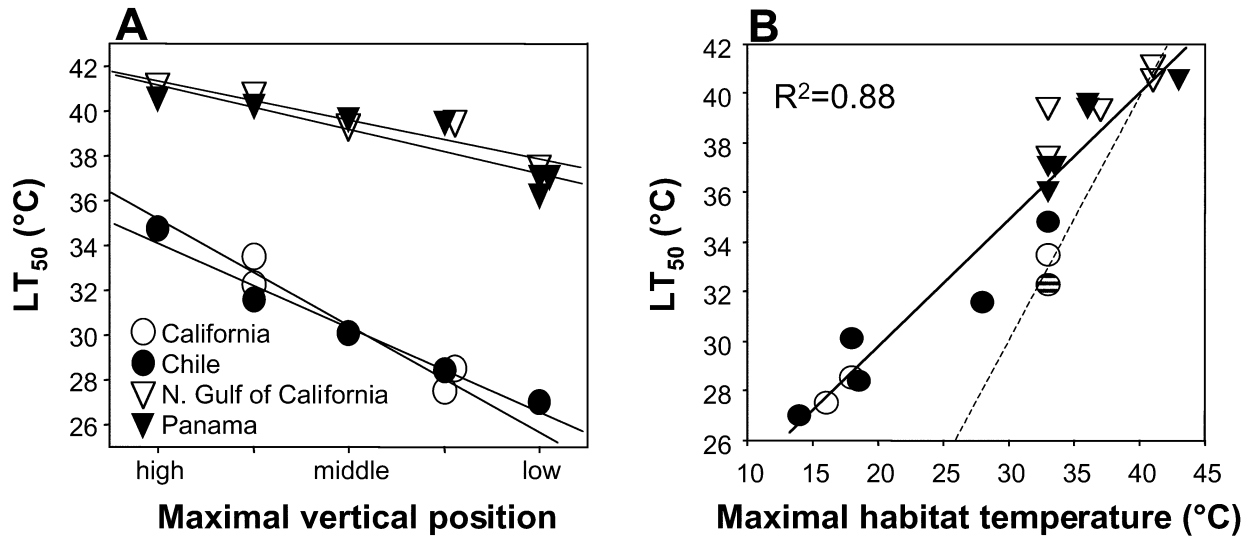


FIG. 2. Upper thermal tolerance limits of porcelain crabs, genus *Petrolisthes*, from throughout the eastern Pacific (Stillman and Somero, 2000). LT_{50} s are the temperature at which 50% mortality occurs during experiments designed to mimic temperature changes in the natural habitat during hot low tide periods (see Stillman and Somero, 1996). A. Thermal tolerance limits plotted as a function of vertical distribution within each of four sites from the four geographic assemblages of *Petrolisthes* in the eastern Pacific. The range of LT_{50} s observed within a site is significantly greater for temperate locations (ANOVA, $P < 0.001$). B. Thermal tolerance limits plotted as a function of maximal microhabitat temperature. The dotted line is where $y = x$. Symbols in B are the same as in A except for one stripe-filled circle to identify this point as *Petrolisthes cinctipes*.

At each site, there are species found strictly in upper-intertidal microhabitats, and species that live in the low-intertidal zone or are strictly subtidal, and therefore never experience emersion during low tide. As a result, individual species of *Petrolisthes* experience a range of microhabitat conditions that are generated by differences in geographic distribution as well as vertical distribution in the intertidal zone. Because small differences in vertical distribution can result in large differences in microhabitat conditions (Doty, 1946; Edney, 1961; Newell, 1979; Stillman and Somero, 1996), patterns of intertidal distribution have the potential to create a much greater range of thermal microhabitat conditions than geographic distribution patterns alone. Annual seawater temperature fluctuations in the eastern Pacific north temperate region, coupled with variation in terrestrial conditions, translate into annual thermal ranges of approximately 8°C–16°C for low intertidal species and approximately 0°C to 32°C for mid- to high-intertidal species (Stillman and Somero, 1996). Species living in the mid- to high-intertidal zone in tropical habitats may encounter body temperatures >40°C during low tides that occur in the hot seasons, but may not be exposed to temperatures below 22°C.

THERMAL TOLERANCE LIMITS OF PORCELAIN CRABS

Comparative analyses

Analyses of upper thermal tolerance limits of *Petrolisthes* from different biogeographic regions and with different intertidal distributions indicate that species have upper thermal tolerance limits that match microhabitat conditions (Jensen and Armstrong, 1991;

Stillman and Somero, 1996, 2000). In 20 species of *Petrolisthes*, maximal thermal tolerance limits, expressed as the temperature at which 50% mortality occurred (LT_{50}) during experiments designed to mimic under-rock temperature changes during extremely hot days, reflected microhabitat conditions in terms of both vertical distribution and maximal microhabitat temperatures (Fig. 2) (Stillman and Somero, 2000). LT_{50} s ranged from approximately 27°C to 35°C for temperate species and from 36°C to 41°C for tropical species (Fig. 2). There was great overlap observed in the LT_{50} s of the two temperate groups as well as for the crabs from Panama and Mexico relative to vertical position (Fig. 2A). A strong positive correlation between LT_{50} s and maximal habitat temperature ($R^2 = 0.88$) was shown across all of these species (Fig. 2B). At a common maximal habitat temperature, 32°C, the LT_{50} s of temperate intertidal species are all lower than the LT_{50} s of tropical subtidal species (Stillman and Somero, 2000). Previous studies of congeneric crabs in rocky intertidal habitats have shown similar patterns (Young, 1980; Burggren and McMahon, 1981; Taylor, 1982), but none of these studies have included as many species as the studies on *Petrolisthes*.

The phenotypic plasticity of upper thermal tolerance limits has also been shown to differ during thermal acclimation to 8°C and 18°C. The LT_{50} s of *Petrolisthes cinctipes*, the upper intertidal species, increased by 1.9°C over that temperature range, while the LT_{50} s of two lower intertidal and subtidal species, *P. erimerus* and *P. manimaculis*, increased by 4°C (Stillman and Somero, 2000). That field acclimatized *P. cinctipes* have LT_{50} s that are approximately equal to maximal

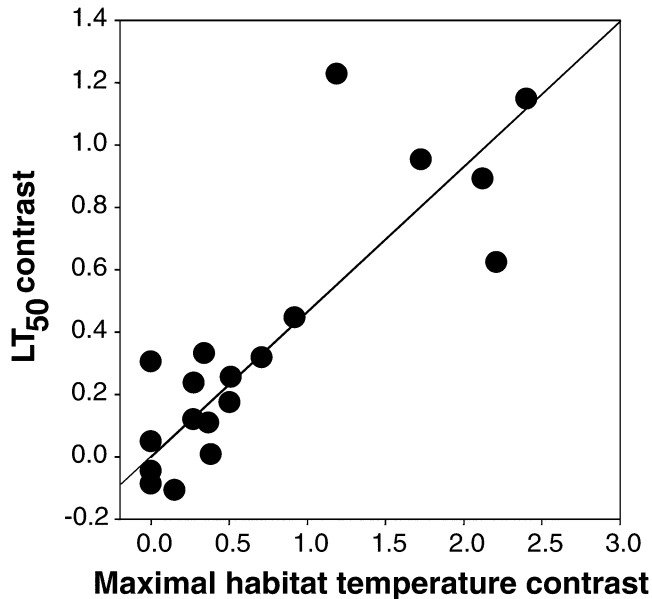


FIG. 3. Phylogenetic independent contrasts analysis of data from Figure 2B using the phylogenetic tree in Figure 1. Regression coefficients are $y = 0.4655x$, $r^2 = 0.72$, $P < 0.05$. From Stillman and Somero (2000).

habitat temperatures (Fig. 2B, hatched circle) and that this species has a limited ability to increase LT_{50} during thermal acclimation suggests that this species is living at the “edge” of its thermal limits. Other upper intertidal species may show the same limited potential for acclimation.

The evolutionary consequences of upper thermal tolerance limits and plasticity of thermal limits are large because only a single exposure to a temperature above the upper thermal tolerance limit before reproduction is required to lower fitness to zero. Thus, there is a great selective advantage for those individuals in a population that have thermal tolerance limits above the maximal habitat temperatures. Evolutionary analyses using phylogenetic independent contrasts suggest that there has been a strong adaptive response of porcelain crabs to evolve thermal tolerance limits that match or exceed maximal habitat temperatures (Fig. 3) (Stillman and Somero, 2000). Because the thermal limits of intertidal species are set so much closer to current maximal habitat temperatures than those of subtidal species (Fig. 2B), we can assume that there are physiological costs associated with maintaining higher thermal tolerance limits and inhabiting the upper intertidal zone. To understand these costs, we must understand the physiological bases that set the thermal limits of an organism.

Physiological mechanisms

The effects of temperature on physiological function can be partitioned into multiple categories. We can consider thermal effects that alter the rates of physiological processes, but do not alter the nature of those processes significantly. We can think of these effects

as altering biological performance, and as ones that occur within the normal temperature range over which an organism lives. Thermal effects that occur within this range could significantly alter species interactions and community structure if those interactions are strong (Sanford, 1999) but do not have fitness consequences. Thermal effects that occur outside of the normal physiological range involve deleterious effects at the cellular level which organisms may not be able to recover from. Frederich and Poertner (2000) have termed these categories of thermal effects as “*optimum*,” for effects that involve only physiological performance, and “*pessimum*,” for effects that are beyond the scope of recovery to normal physiological function. The temperature beyond which physiological recovery is impossible and where tissues switch from aerobic to anaerobic metabolism is the critical temperature (T_c) (Frederich and Poertner, 2000). At both high and low T_c s, then, some or all of the physiological systems involved with oxygen uptake, oxygen delivery, and oxygen utilization must be thermally damaged. Because a functional circulatory system is essential for oxygen uptake and delivery, the thermal sensitivity of cardiac systems have received much attention (Mickel and Childress, 1982; Depledge, 1984a, b; Stillman and Somero, 1996; Brown and Terwilliger, 1999; De Pirro *et al.*, 1999; Styrihave *et al.*, 1999; Frederich *et al.*, 2000a, b; Frederich and Poertner, 2000).

In two sympatric species of *Petrolisthes* living in different vertical zones, the upper and lower thermal limits for heart function were correlated with thermal microhabitat (Stillman and Somero, 1996). In both of these species, the heart beat rate has a similar Q_{10} over a wide range of temperatures, but the thermal limits are different. The heart of *P. cinctipes* (the upper-intertidal species) has an Arrhenius break temperature (ABT) of 31.5°C and the heart of *P. eriomerus* (the low-intertidal and subtidal species) has an ABT of 26.6°C (Stillman and Somero, 1996). Habitat temperatures of *P. cinctipes* can be greater than 30°C, well above the heart ABT of *P. eriomerus* (Stillman and Somero, 1996). Low temperature tolerances of the hearts of these two species are dramatically different. The heart of *P. cinctipes* is not damaged by exposure to 1.5°C, while in comparison, *P. eriomerus* appears dead at 2°C and the heart does not recover after exposure to this temperature (Stillman and Somero, 1996). Recent studies indicate that the hearts of *P. cinctipes* can tolerate temperatures at least as cold as -4.2°C (unpublished observations).

What molecular factors are responsible for setting the differences in heart thermal sensitivity in these two species? Crustacean hearts have a dual myogenic and neurogenic character (Wilkins and McMahon, 1994; Wachter and Wilkens, 1996), thus it is possible that the hearts stop beating because (i) the molecular properties of the heart muscle are damaged, and/or (ii) because the nerves innervating the hearts are damaged. Because membrane order, or fluidity, has been shown

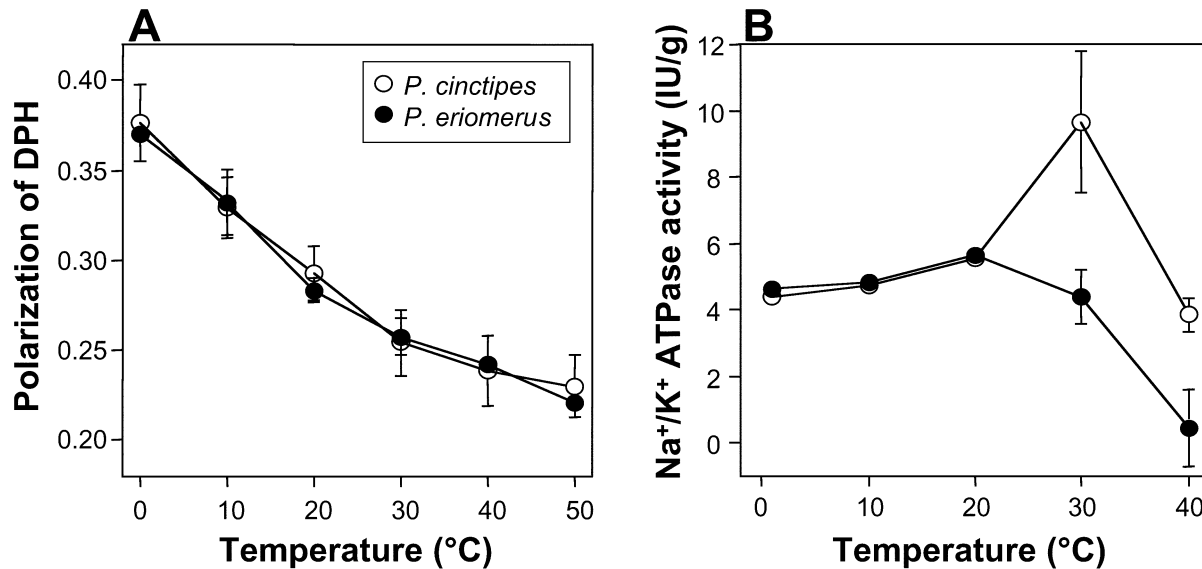


FIG. 4. Thermal sensitivity of molecular properties of *Petrolisthes cinctipes* and *P. eriomerus* hearts. A. Membrane fluidity as a function of temperature. For each sample, hearts were excised from 15–20 specimens, pooled, and homogenized in 50 mM potassium phosphate buffer, pH 6.0 @ 25°C. After a low-speed centrifugation to remove large particles, the homogenate was diluted to an absorbance of 0.150 at 364 nm. Membrane order was determined by fluorescence polarization of diphenylhexatriene following (Williams and Somero, 1996). B. Na⁺/K⁺ATPase activity as a function of temperature. For each sample, hearts were excised from 15–20 specimens, pooled, and enzyme preparation and assays were performed following (Gibbs and Somero, 1989). For both experiments, the entire range of temperatures were tested for each sample, each data point is the mean \pm 1 SEM, and $n = 3$ samples for each species.

to be very temperature sensitive, I examined the physical properties of bulk membranes and a membrane-bound protein (Na⁺/K⁺ATPase) in *Petrolisthes cinctipes* and *P. eriomerus* heart muscle. Because the function of the Na⁺/K⁺ATPase is essential for establishment of the membrane potential needed to generate action potentials, failure of this enzyme renders the heart unable to beat. In specimens acclimated to identical conditions, the temperature effects on bulk membrane properties were identical (Fig. 4A). However, there was some difference in the temperature sensitivity of the ATPase, where at 30°C, the enzyme from *P. cinctipes* functioned at a rate that was much higher than that of *P. eriomerus* (Fig. 4B). From these data, it appears that interspecific differences exist within the protein and/or are localized to lipids that are vicinal to the protein. The differences observed at 30°C are significant because at this temperature the heart beat of *P. eriomerus* fails, although *P. cinctipes* hearts appear undamaged (Stillman and Somero, 1996).

Interspecific differences in nerve thermal sensitivity have recently been shown in four species of *Petrolisthes* from temperate intertidal, temperate subtidal, and tropical intertidal habitats (Knape, 1999 [in Hochachka and Somero, 2002]). At a common temperature, 30°C, the loss of spontaneous activity was quickest in the temperate subtidal species and slowest in the tropical intertidal species, a trend that matches the thermal microhabitat characteristics of these species. Thus, the physiological factors responsible for setting T_c in porcelain crabs include at least both the circulatory and the nervous system.

Ecological consequences

The ecological consequences of upper thermal tolerance limits and plasticity of thermal limits of *Petrolisthes*, especially intertidal species, would be apparent if changes in relative abundance occur. In a survey of intertidal fauna at Hopkins Marine Station, in Monterey California, in which the same transects were sampled from 1931–1933 (Hewatt, 1937) and 1993–1994 (Barry *et al.*, 1995), a decline in abundance of *P. cinctipes* (from 3.2 individuals per m² to 0 per m²) was observed (Sagarin *et al.*, 1999). Records of water temperature at Hopkins Marine Station indicate that the average summer maximum sea surface temperature was 2.2°C higher in the 1993–1994 period than in 1931–1933 (Barry *et al.*, 1995). It is unclear if the differences in water temperature between these periods are directly responsible for the observed decline in abundance of *P. cinctipes*. However, as this species currently experiences maximal habitat temperatures that are near to its thermal tolerance plasticity limits (Stillman and Somero, 2000), slight increases in microhabitat temperature could result in mortality. Mass mortality in nature has been shown for intertidal mussels (Tsuchiya, 1983), but not documented in under-rock fauna. However, the selective importance of those rare days when microhabitat temperatures exceed thermal tolerance limits must still be great.

Understanding the thermal limits of organisms, and the plasticity of those limits, enables us to make some inferences about what will happen to the distribution and abundance of organisms during global climate

change. However, it would be naïve to think that thermal limits are the only important factor. Organisms live within ecological communities and the strength of interaction among groups of organisms can be great. Small increases in temperature that occur well below the lethal limits and that affect the performance of a predator can have large changes in community dynamics (e.g., Sanford, 1999). If different members (both species and age classes) of a community acclimatize to different degrees during global warming, the dynamics of ecosystems could change, and this could have a larger impact on species distribution and abundance than one would expect by examination of the thermal limits of individual species.

In summary, porcelain crabs have proven to be an excellent study system for examination of physiological adaptation to temperature. The groundwork has been set for future studies that investigate further the extent to which thermal tolerance limits contribute to distribution patterns, how thermal limits change with life history, what factors set thermal limits, and what factors contribute to phenotypic plasticity of thermal limits. Because of the diversity of species and microhabitats, porcelain crabs may be one of the best study systems for understanding the causes and consequences of the breadth and plasticity of thermal limits in intertidal organisms.

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