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journal homepage: [www.elsevier.com/locate/jembe](http://www.elsevier.com/locate/jembe)The influence of intertidal location and temperature on the metabolic cost of emersion in *Pisaster ochraceus*Elizabeth K. Fly<sup>a,b,\*</sup>, Cristián J. Monaco<sup>b</sup>, Sylvain Pincebourde<sup>b,c</sup>, Alexa Tullis<sup>a</sup><sup>a</sup> Department of Biology, University of Puget Sound, Tacoma, WA 98416, United States<sup>b</sup> Department of Biological Sciences, University of South Carolina, Columbia, SC 29208, United States<sup>c</sup> Institut de Recherche sur la Biologie de l'Insecte, IRBI CNRS UMR 7261, Université François Rabelais, Faculté des Sciences et Techniques, 37200 Tours, France

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## ABSTRACT

Vertical zonation within the intertidal results from an interaction between the physical environment and an organism's physiological limits. Bioenergetic costs of emersion are likely to vary based on an organism's vertical location in the intertidal. The present study quantified the metabolic costs of microhabitat choice in the important intertidal predator *Pisaster ochraceus*. Rates of oxygen consumption ( $VO_2$ ) were measured at a range of ecologically relevant temperatures in both water and air. In both media, rates increased with increasing temperature but, at any given temperature, aerial  $VO_2$  was approximately 50% that of aquatic  $VO_2$ . These rates, along with biomimetic body temperature data from two field sites in Bodega Bay, California, were used to estimate the metabolism of sea stars at different vertical locations over a 10-day period in the summers of 2006, 2007, and 2010. Results suggest that vertical location would have a much smaller effect on sea star  $VO_2$  than would inter-annual temperature differences. The influence of higher body temperatures experienced by sea stars at low tide in the mid-high intertidal, as compared to the low intertidal, was almost negligible because aerial  $VO_2$  was lower than aquatic  $VO_2$ . By contrast, the higher average water temperature experienced by sea stars in 2006 yielded a 50% higher metabolic cost relative to sea stars in 2007 and 2010. These results suggest that energetic demands of intertidal organisms can vary markedly according to global environmental fluctuations such as El Niño and Pacific Decadal Oscillations.

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## 1. Introduction

The intertidal habitat is physiologically challenging because of the dramatic temporal and spatial variations in temperature. The extent to which an organism is subjected to large temperature changes depends largely on its vertical location in the intertidal. At high tide organisms experience a relatively stable thermal environment because of the high thermal inertia of the large body of seawater (Helmuth, 1998); by contrast, the low tide thermal environment shows comparatively large fluctuations (Broitman et al., 2009; Burnaford, 2004; Helmuth and Hofmann, 2001; Pincebourde et al., 2008; Stillman and Somero, 1996; Szathmary et al., 2009). Fluctuating air temperatures, along with wind and solar radiation, during a summertime low tide can affect the heat flux within an organism, causing body temperature to change by 4–5 °C within a few hours (Helmuth, 1998; Szathmary et al., 2009). In addition to temporal fluctuations, temperatures experienced by intertidal organisms can vary dramatically over short distances according to tidal height and local topography (Burnaford, 2004; Denny

et al., 2011; Harley, 2008; Helmuth and Hofmann, 2001; Schneider and Helmuth, 2007; Szathmary et al., 2009). In some cases, these microhabitat temperature differences can be nearly as extreme as seasonal temperature fluctuations (Burnaford, 2004).

These temporal and spatial variations in temperature during aerial exposure can have dramatic ecological consequences. The most obvious is the vertical zonation within the intertidal that results from the interaction between the physical environment experienced by an organism and its physiological limits (Connell, 1972; Garza and Robles, 2010; Lewis, 1964; Somero, 2002). It is not surprising, therefore, that a considerable amount of effort has gone into determining how temperature influences the physiology of intertidal animals. One of the most direct and pervasive effects of temperature on any ectotherm's physiology is its influence on metabolic rate. In general, a 10 °C increase in body temperature will result in a two- to three-fold increase in metabolic rate until a critical temperature, above which metabolic rate will begin to decrease because of the negative effects of high temperature on physiological processes (Pörtner, 2002). In addition to metabolic rate, temperature has also been demonstrated to affect the growth rate (Sanford, 2002a), activity level (Dahlhoff et al., 2001; Stillman and Somero, 1996), and conversion efficiency (Sanford, 2002a) of intertidal animals. Finally, elaboration of a heat-shock response, an energetically costly process, has been shown to minimize thermally induced

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cellular damages in numerous intertidal species (Parsell and Lindquist, 1993; Tomanek, 2010). Collectively, these temperature-related effects suggest that intertidal organisms incur energetic costs during periods of emersion in which they experience thermal stress.

Accurate estimates of the energetic costs associated with emersion are important for predicting how environmental factors such as temperature contribute to shaping species distributions and intertidal community structures. To this end, the present study examined the effect of physiologically relevant thermal conditions on the metabolic rate of the sea star *Pisaster ochraceus* (Brandt, 1835), an animal which plays a critical role in the community dynamics of rocky intertidal zones on the Pacific coast of North America. In wave-exposed areas *P. ochraceus* is a keystone species that opens space and increases diversity by consuming competitively dominant mussels (Menge et al., 1994; Paine, 1966). Although the sea star does not play a keystone role in wave-protected areas, it is still an important predator of invertebrates (Mauzey, 1966; Mauzey et al., 1968; Menge et al., 1994).

Several studies suggest that the effect of temperature on *P. ochraceus* physiology is complex. Small decreases in water temperatures have been shown to depress the feeding rates of sea stars (Sanford, 2002a, 2002b). In spite of the lower feeding rate, however, these animals still gained biomass, due presumably to a cold-induced decrease in metabolic costs (Sanford, 2002a). Studies examining the effects of aerial exposure on *P. ochraceus* physiology revealed that acute exposure to high temperatures positively influenced feeding rates, while longer term exposure to the same temperatures negatively influenced both feeding and growth rates (Pincebourde et al., 2008). Thus, the temporal patterns of variation of aquatic and aerial body temperatures interactively modulated the feeding response of *P. ochraceus* (Pincebourde et al., 2012). Prolonged exposure to high aerial temperatures also caused *P. ochraceus* to increase the water content of its coelomic fluid (Pincebourde et al., 2009). The fact that this adjustment reduced the rate at which body temperature increased during subsequent low tides (Pincebourde et al., 2009) suggests that prolonged exposure to high aerial body temperatures is potentially costly, and is actively resisted by the animal through this fluid adjustment. In addition, results from a field study showed that sea stars transferred from mid intertidal locations into the high intertidal exhibited reduced feeding, weight loss, and substantial mortality compared to non-transplanted individuals (Petes et al., 2008), all of which suggest some degree of physiological stress. The studies mentioned above provide indirect evidence that high body temperature at low tide can be metabolically costly for *P. ochraceus*, but the metabolic cost of emersion has not been measured under field conditions. This absence of direct measurement impedes quantitative assessment of bioenergetic costs.

As an important step for determining the costs associated with periodic emersion, and to build on the studies mentioned above, the present study measured the oxygen consumption of *P. ochraceus* in both air and water under ecologically relevant thermal conditions. This study focused on standard post-absorptive oxygen consumption to estimate minimal energy requirements of this animal at a given temperature. In this way, the cost of emersion was measured only as it relates to how temperature influences metabolic rate. Insight into this component is a necessary step in understanding the total bioenergetic costs of emersion. Measurements of oxygen consumption were paired with field observations of sea star location and body temperature at low tide to better understand the effects of vertical position and temperature on *P. ochraceus* energetics.

## 2. Methods

### 2.1. Field surveys

Fieldwork was conducted at two different sites within the Bodega Marine Reserve, California (38° 19' N, 123° 4' W), between the low and mid-high intertidal zones (roughly 0–1.9 m above mean lower

low water [MLLW]). In 2006 and 2007, fieldwork took place on the rocky wave-protected shore of Horseshoe Cove while in 2010, it took place on the wave-exposed rocky shore ~400 m north of Horseshoe Cove. Both of these areas have complex topography providing heat-exposed (e.g. exposed to solar radiation on open, flat surfaces) as well as heat-protected (e.g. protected from solar radiation within crevices, tidepools or under algae) microhabitats. Tidepools in this study were considered heat-protected because the majority were located in the low intertidal out of direct sunlight and cooled by wave-splash at both sites (Pincebourde, personal observation). Exposure to solar radiation is a key component in determining an organism's heat exposure, and this categorization is consistent with that used in many previous studies (e.g. Burnaford, 2004; Harper and Williams, 2001; Helmuth, 1998; Pincebourde et al., 2008; Seabra et al., 2011; Williams and Morrill, 1995).

#### 2.1.1. Population surveys

In 2007, 10 population surveys of *P. ochraceus* were conducted in the wave-protected study area between 5/13 and 7/4 (Table 1). The vertical height of each sea star within the intertidal was measured using a Topcon rotating laser-level. Three intertidal zones were defined relative to the position of the mussel bed within the study area: low (<0.6 m), mid (0.6–1.1 m), and mid-high (>1.1 m above MLLW). The microhabitat of each individual was categorized as either heat-exposed or heat-protected. In 2010, four population surveys of *P. ochraceus* were conducted in the wave-exposed site between 5/19 and 6/26 (Table 1). Methods were similar to those in 2007, but the body mass of each individual was also recorded and grouped into one of three size classes: small (<300 g), medium (300–500 g) and large (>500 g). Intertidal zones at this site were low (<0.85 m), mid (0.85–1.5 m), and mid-high (>1.5 m above MLLW). These ranges differed slightly from those used in the wave-protected site (see above) because the mussel bed was generally located higher on the shore (Monaco, personal observation).

#### 2.1.2. *P. ochraceus* temperature biomimetics

In order to estimate the body temperatures *P. ochraceus* were likely to experience over several tidal cycles, biomimetic models that mimicked the thermal properties of a medium-sized (300–500 g) sea star (see Pincebourde et al., 2008 and Szathmary et al., 2009 for detailed descriptions) recorded temperature every 10 min. These biomimetics were placed on flat, heat-exposed surfaces within each intertidal zone to determine the most extreme temperatures sea stars were likely to experience.

In 2006 and 2007, biomimetics were placed at the wave-protected site: three within the low intertidal zone, two within the mid intertidal, and two within the mid-high intertidal (Table 1). Temperatures were recorded from 7/24/06 to 8/21/06 and from 6/6/07 to 7/16/07. In 2010, biomimetics were placed in the low, mid, and mid-high intertidal at the wave-exposed site (Table 1). Due to inherent difficulties in working in wave-exposed areas, complete and overlapping temperature data from only one biomimetic each in the low intertidal and the mid-high intertidal were recovered. These data spanned from 5/13 to 5/24. While the

**Table 1**

Year, site, seasonal period, and type of data collected at the two sites in the Bodega Marine Reserve, California.

Year	Site type	Dates	Survey	Data
2006	Wave-protected	7/24–8/21	Temperature	Biomimetic
2007	Wave-protected	5/13–7/4	Population	Intertidal height Microhabitat
2010	Wave-exposed	6/6–7/16	Temperature	Biomimetic
		5/19–6/26	Population	Intertidal height Microhabitat Body size
		5/13–5/24	Temperature	Biomimetic

number of biomimetics was low, this study focused on the extreme habitats in which these sea stars are found, rather than on the entire range of body temperatures experienced by the population.

Data collected by the Bodega Ocean Observing Node (BOON, <http://bml.ucdavis.edu/boon/index.html>), provided by the University of California, Davis, Bodega Marine Laboratory were used to examine interannual variability in summer water temperatures. These data included average daily shoreline water temperatures between 6/1 and 8/31 for 2006, 2007, and 2010.

## 2.2. Metabolic measurements

*P. ochraceus* individuals used to determine rates of oxygen consumption ( $\text{VO}_2$ ) were collected from a rocky shore on Orcas Island, Washington (48° 37' 33.2" N, 122° 52' 38.0" W). Water temperatures in the San Juan Islands averaged between 10 and 12 °C during the collection period (June 2004 and 2005; SST from meteorological observations at NOAA tide station 9449880 were obtained from <http://tidesandcurrents.noaa.gov>). While this location is farther north than where the field surveys were conducted (see Section 2.1.), biomimetic results from previous studies suggest that northern *P. ochraceus* populations experience very similar water, air, and body temperatures to those recorded in the present study (see Section 3.1.2., Pincebourde et al., 2008; Broitman et al., 2009, and Szathmary et al., 2009). In addition, since *P. ochraceus* larvae can live in the water column for as long as 228 days (Strathmann, 1987), populations occurring throughout the entire distributional range have been shown to be genetically homogeneous (Harley et al., 2006). Indeed, Harley et al. (2006) suggest that local adaptation is unlikely, although acclimation to a specific region is still a possibility.

### 2.2.1. Aquatic oxygen consumption

*P. ochraceus* individuals used to determine rates of aquatic  $\text{VO}_2$  were collected in early June 2004. Animals were maintained at Friday Harbor Laboratories (FHL) in flow-through seawater tanks at ambient temperatures (~12–14 °C) and were fed purple varnish clams (*Nuttallia obscurata*) every few days. Sea stars were fasted for at least 48 h prior to oxygen consumption measurements, and were weighed prior to each measurement.

Aquatic  $\text{VO}_2$  of sea stars (mean  $\pm$  SEM = 403  $\pm$  23.9 g wet weight,  $n = 27$ ) was measured at 10, 15, and 20 °C with closed system respirometry (Ulbricht and Pritchard, 1972). To start each measurement, an individual was placed in a 10-L plastic chamber filled with 1- $\mu\text{m}$  bag-filtered seawater at ambient temperature (12–14 °C). Water temperature was adjusted to the desired experimental temperature at a rate of ~1 °C every 10 min. During this time, the chamber was left open and the water aerated to maintain normoxia. Upon reaching the appropriate temperature, the chamber was sealed and an oxygen electrode (Orion Model 1230; Orion Research Inc., Beverly, Maine) that had been calibrated with its calibration sleeve according to manufacturer specifications was inserted. A stir-bar located beneath a perforated platform at the bottom of the chamber circulated water during a trial. After allowing the system to adjust for 20 min, dissolved oxygen concentration was recorded every 5 min for 70 min or until the oxygen content within the closed chamber reached 80% of normoxic values, whichever occurred first. This time period ranged from 20 to 70 min depending on the individual and experimental temperature. The decline in oxygen content with time was linear over the duration of the trials, and the slope of these lines was used to calculate sea star  $\text{VO}_2$  (see Section 2.3.). Control trials ( $n = 7$  per temperature), that were identical to experimental trials but lacked an animal, were performed and these values were used to correct for any background oxygen consumption. Individual sea stars were tested at all three temperatures, one temperature per day over three consecutive days. The order of temperature treatments was randomly determined for each individual.

### 2.2.2. Aerial oxygen consumption

Aerial  $\text{VO}_2$  was measured in 2005 on another set of *P. ochraceus* individuals collected from the same site as those collected in 2004. Aerial oxygen consumption values collected during a pilot study in 2004 were not significantly different from those measured in 2005 at 10, 15, and 20 °C (ANOVA; 10 °C:  $F_{1,25} = 3.56$ ,  $p = 0.071$ ; 15 °C:  $F_{1,25} = 0.79$ ,  $p = 0.38$ ; 20 °C:  $F_{1,25} = 2.26$ ,  $p = 0.15$ ,  $n = 5$  individuals at each temperature). Thus, any interannual variability in rates of oxygen consumption between 2004 and 2005 should not impact the comparisons made in the present study.

After being maintained for a short time at FHL, animals were transported to the University of Puget Sound in Tacoma, Washington, where they were kept in a re-circulating seawater holding aquarium maintained at approximately 15 °C. Animals were given at least 24 h but not more than five days in the holding aquarium before measuring aerial  $\text{VO}_2$ . Sea stars were not fed while at the University of Puget Sound, and were weighed to the nearest 0.01 g prior to experiments.

Aerial  $\text{VO}_2$  of sea stars (mean  $\pm$  SEM = 387  $\pm$  19.5 g wet weight,  $n = 22$ ) was measured at 10, 15, 20, and 25 °C with flow-through respirometry (Huang and Newell, 2002; Marsden and Weatherhead, 1998). Individual animals were placed into 4.5-L airtight containers that were connected with Tygon tubing to one channel of a dual-channel oxygen analyzer (model S-3A/11; AEI Technologies, Pittsburgh, PA). Air was pulled through the chambers at 57 mL  $\text{min}^{-1}$  with a flow controller (model R-2, AEI Technologies, Pittsburgh, PA). A parallel path lacking an animal chamber led into a second channel of the oxygen analyzer and served as a reference. Before entering the oxygen analyzer, air from both paths (experimental and reference) passed through filters containing Drierite (Acros Organics, Morris Plains, New Jersey) and soda lime (Fisher Chemicals, Fair Lawn, New Jersey) to remove water vapor and carbon dioxide, respectively. The system was calibrated with ambient air prior to data collection, and data were collected at 2 Hz with a PowerLab 2e data acquisition system (ADInstruments, Colorado Springs, Colorado).

Groups of three to four individual animals, each animal in its own airtight container, were tested at two temperatures each day (individuals in different groups did not respond differently to temperature [RM ANOVA; between subjects, group,  $F_{6,15} = 1.364$ ,  $p = 0.291$ ; within subjects, temperature-group,  $F_{18,45} = 1.162$ ,  $p = 0.331$ ]; therefore, data collected on different days were combined). Because the technique of flow-through respirometry continually renews the oxygen within an experimental chamber, aerial trials were run for 5–6 h, which is typically the aerial exposure time for *P. ochraceus* during low tide (Pincebourde et al., 2008). During this time, temperature was controlled by immersing the chambers in a water bath, and the rate of change between any two experimental temperatures was ~1 °C every 10 min. Control trials run at a single temperature demonstrated that sea star  $\text{VO}_2$  was not affected by the length of time they were maintained in experimental chambers (RM ANOVA, effect of time,  $F_{1,9} = 0.506$ ,  $p = 0.50$ ; time-temperature interaction,  $F_{2,9} = 0.051$ ,  $p = 0.951$ ). Although the order of exposure to 10, 15, and 20 °C was random, sea stars were never subjected to 25 °C as the first temperature because preliminary work suggested that this temperature caused the most physiological stress (sea stars were limp and unresponsive after testing at this temperature and many had extruded their stomachs). Steady-state oxygen consumption at a given temperature was determined from the final 5–15 min of a trial when the oxygen content of the air exiting a chamber remained stable (see Section 2.3.). All animals used in the study were tested at all four temperatures.

## 2.3. Data analysis

Mass-specific aquatic  $\text{VO}_2$ , in units of  $\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , was calculated with the following equation:

$$\text{VO}_2 = (\Delta[\text{O}_2] \times V) / (t \times m) \quad (1)$$

where  $\Delta[\text{O}_2]$  is the change in dissolved oxygen,  $V$  is the volume of the chamber,  $t$  is time, and  $m$  is body mass.

Mass-specific aerial  $\text{VO}_2$ , in units of  $\mu\text{mol O}_2 \text{g}^{-1} \text{h}^{-1}$ , corrected to standard temperature and pressure in dry air (STPD), was calculated using the following equation:

$$\text{VO}_2 = (V_E \times \Delta F_{\text{O}_2}) / ((1 - F_{\text{I}_{\text{O}_2}}) \times m) \quad (2)$$

where  $V_E$  is the flow rate of air exiting the respirometer,  $\Delta F_{\text{O}_2}$  is the difference in oxygen content of air entering and exiting the respirometer,  $F_{\text{I}_{\text{O}_2}}$  is the oxygen content of the air entering the respirometer and  $m$  is body mass (Withers, 1977).

For both aquatic and aerial oxygen consumption, temperature sensitivity was determined by calculating temperature coefficients ( $Q_{10}$ ) from the following equation:

$$Q_{10} = (R_2/R_1)(10/(T_2 - T_1)) \quad (3)$$

where  $R_1$  and  $R_2$  are the  $\text{VO}_2$  measured at temperatures  $T_1$  and  $T_2$ , respectively.

Analyses of covariance (ANCOVA) were performed on the aerial and aquatic  $\text{VO}_2$  data sets to determine if temperature or body mass had a significant effect on sea star  $\text{VO}_2$  (SPSS version 17.0). For both aerial and aquatic analyses, temperature was the fixed-factor and body mass (wet weight) was the covariate. Post-hoc analyses using the Sidak test examined the pair-wise comparisons of temperature's effect on  $\text{VO}_2$ .

To examine body size effects on  $\text{VO}_2$  and sea star energetics, both the aquatic and aerial  $\text{VO}_2$  data were split based on the same size classifications used in the population surveys: small (<300 g), medium (300–500 g) and large (>500 g) and average  $\text{VO}_2$  was determined for each temperature for each size class (Table 2). Sample sizes in the small and large size classes for these average  $\text{VO}_2$  values were small (small:  $n=3$  in water,  $n=4$  in air; large:  $n=4$  in water,  $n=3$  in air); however, they were used only to examine any patterns related to body mass in a descriptive manner.

#### 2.4. Calculations of energetic implications

To gain insight into whether or not location at low tide has potential energetic ramifications, oxygen consumption for hypothetical sea stars within different intertidal zones was estimated over a 10-day period in each of the study years: 2006, 2007, and 2010. The time periods examined were: 8/9/06–8/18/06, 6/7/07–6/16/07, and 5/15/10–5/24/10. This analysis was restricted to the low-intertidal and mid-high intertidal zones because these were representative of the vertical distribution range of the sea stars. Using data from the biomimetics, estimations included (a) how long a sea star in each zone would be submerged or emersed, and (b) the time each would spend at, or near, each of the experimental temperatures in both water (10, 15, and 20 °C) and air (10, 15, 20, and 25 °C). Because the biomimetic temperature data were continuous, individual readings were rounded to the closest experimental

temperature such that a reading within  $\pm 2.5$  °C of a given experimental temperature was considered to be that temperature (e.g., a biomimetic temperature of 12.2 °C was rounded down to 10 °C, while a biomimetic temperature of 12.7 °C, was rounded up to 15 °C).

To estimate sea star  $\text{VO}_2$  over each 10-day period, the time a sea star was submerged or emersed at each temperature was multiplied by the average aquatic or aerial  $\text{VO}_2$  at that temperature. These values were multiplied by a wet weight to give the total volume of  $\text{O}_2$  consumed for that amount of time at each temperature/medium condition. Adding these values for a given individual yielded the total volume of oxygen consumed during the 10-day period. Because body size influenced  $\text{VO}_2$  (see Sections 3.2.1. and 3.2.2.), oxygen consumption was estimated for three different sized sea stars: small (250 g), medium (400 g), and large (550 g). The  $\text{VO}_2$  values used in each of these calculations corresponded to the size class used (see end of Section 2.3.).

To estimate whether differences in oxygen consumption could have energetic ramifications, the total volume of  $\text{O}_2$  consumed was converted to joules using  $0.457 \text{ kJ mmol O}_2^{-1}$  (Hill et al., 2008), assuming that the animals were metabolizing a combination of proteins, fats, and carbohydrates (Okumus and Stirling, 1998). The energetic yield of a regularly eaten prey item, blue mussel (*Mytilus* spp.), was estimated from the literature (Okumus and Stirling, 1998), and the amount of mussel tissue necessary to replenish the energy the sea stars used over a 10-day period in the different intertidal zones was calculated.

### 3. Results

#### 3.1. Field surveys

##### 3.1.1. Population surveys

The average daily number of sea stars counted in surveys was  $49.5 \pm 9.3$  in 2007 and  $278.3 \pm 17.6$  in 2010. This difference in numbers is due to a generally higher density of animals at the wave-exposed site (Pincebourde, personal observation). In both years, very few sea stars were found in the mid-high intertidal zone. At the wave-protected site in 2007, only  $5.2 \pm 5.1\%$  of sea stars were found in the mid-high intertidal, as opposed to  $42.9 \pm 14.7\%$  in the mid intertidal and  $52.9 \pm 14.9\%$  in the low intertidal (all values = mean  $\pm$  SD). When categorized by microhabitat type, significantly more individuals were located in heat-protected habitats than heat-exposed habitats at all tidal heights (Pearson Chi-Square test:  $\chi^2 = 57.5$ ,  $p < 0.001$ ; Fig. 1A). In the low intertidal, there were more than 14-times as many sea stars in heat-protected areas than in heat-exposed habitats (Fig. 1A). In the mid intertidal, there were twice as many sea stars in heat-protected areas. Of the small number of individuals found in the mid-high intertidal, approximately equal percentages were found in heat-protected and heat-exposed areas (Fig. 1A).

At the wave-exposed site in 2010, most sea stars,  $64.6 \pm 22.2\%$ , were found in the mid intertidal, while  $29.0 \pm 20.8\%$  were in the low intertidal and only  $6.4 \pm 1.6\%$  were in the mid-high intertidal (all values = mean  $\pm$  SD). Significantly more sea stars were in heat-protected areas than heat-exposed areas (Pearson Chi-Square test:  $\chi^2 = 35.8$ ,  $p < 0.001$ ; Fig. 1B). As with the 2007 data, nearly 14-times as many sea stars were in heat-

**Table 2**

Average aquatic and aerial oxygen consumption rates ( $\mu\text{mol O}_2 \text{g}^{-1} \text{h}^{-1}$ ,  $\pm$  SE) for *P. ochraceus* of different sizes at different temperatures.

	Temperature (°C)	Average oxygen consumption ( $\mu\text{mol O}_2 \text{g}^{-1} \text{h}^{-1}$ )			
		All sizes	Small (<300 g)	Medium (300–500 g)	Large (>500 g)
Aquatic	10	$0.362 \pm 0.048$	$0.456 \pm 0.067$	$0.390 \pm 0.060$	$0.154 \pm 0.013$
	15	$0.604 \pm 0.032$	$0.672 \pm 0.101$	$0.607 \pm 0.040$	$0.541 \pm 0.031$
	20	$0.791 \pm 0.057$	$0.887 \pm 0.140$	$0.818 \pm 0.069$	$0.583 \pm 0.107$
Aerial	10	$0.203 \pm 0.015$	$0.214 \pm 0.042$	$0.211 \pm 0.017$	$0.149 \pm 0.044$
	15	$0.349 \pm 0.026$	$0.449 \pm 0.096$	$0.342 \pm 0.024$	$0.254 \pm 0.047$
	20	$0.535 \pm 0.020$	$0.617 \pm 0.034$	$0.543 \pm 0.018$	$0.384 \pm 0.020$
	25	$0.627 \pm 0.025$	$0.769 \pm 0.086$	$0.611 \pm 0.017$	$0.513 \pm 0.055$

Sample sizes: Aquatic: all sizes,  $n=27$ ; small,  $n=3$ ; medium,  $n=20$ ; large,  $n=4$ . Aerial: all sizes,  $n=22$ ; small,  $n=4$ ; medium,  $n=15$ ; large,  $n=3$ .

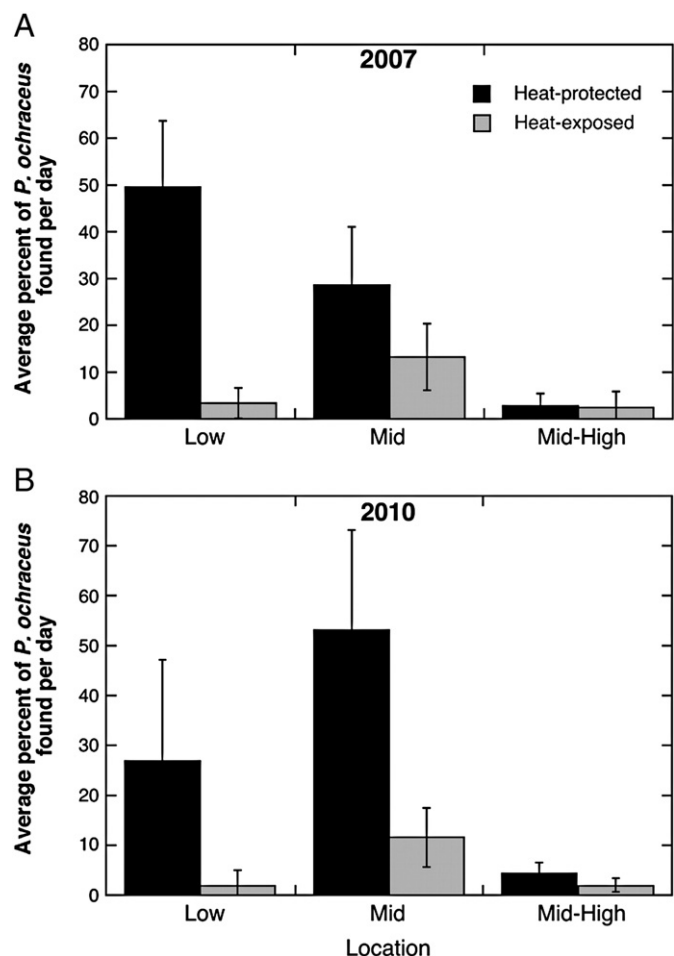


Fig. 1. Average percent of heat-exposed or heat-protected *P. ochraceus* found within the designated intertidal heights during the low tides surveyed. A) 2007, wave-protected site (n = 10 tides; B) 2010, wave-exposed site (n = 4 tides). Individuals categorized as heat-protected (black bars) were located in shaded crevices or other areas out of direct sunlight. Individuals categorized as heat-exposed (gray bars) were located fully exposed to the sun and elements. Values are mean  $\pm$  SD.

protected areas in the low intertidal as compared to heat-exposed areas (Fig. 1B). Over four times as many sea stars were located in heat-protected areas in the mid-intertidal, while twice as many individuals were heat-protected in the mid-high intertidal (Fig. 1B). When data from tidepools were removed, the average percent of *P. ochraceus* found in protected habitats within the low intertidal decreased, although there were still nearly three times more sea stars in protected habitats relative to exposed habitats (data not shown). This observation reveals the presence of many more tidepools in the low intertidal, supporting the categorization of tidepools as heat-protected microhabitats.

Surveys conducted during four spring tides in 2010 showed that microhabitat use also differed with body size. For example, significantly more large sea stars (>500 g) occupied lower intertidal heights than did the smaller sea stars (Pearson Chi-Square test:  $\chi^2 = 103.3$ ,  $p < 0.001$ ; Fig. 2A). Of those individuals in the low intertidal zone,  $54.8 \pm 11.2\%$  were in the large size class, while only  $16.4 \pm 8.9\%$  were in the small size class. In the mid-high intertidal, an average of  $26.4 \pm 31.0\%$  of sea stars were large,  $33.0 \pm 6.9\%$  were medium-sized, and  $40.6 \pm 34.5\%$  were small. The total number of sea stars located in heat-exposed habitats did not differ by body size, but many more large sea stars were found in tidepools than small or medium-sized individuals (Pearson Chi-Square test:  $\chi^2 = 185.8$ ,  $p < 0.001$ ; Fig. 2B). Conversely, fewer large sea stars were found in crevices compared to the smaller animals (Fig. 2B).

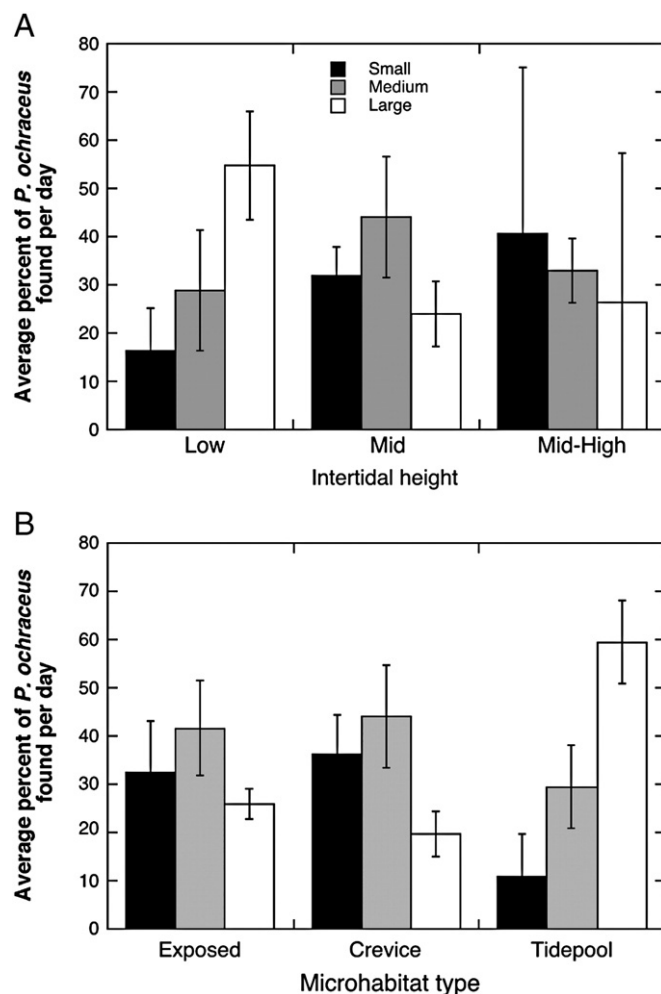
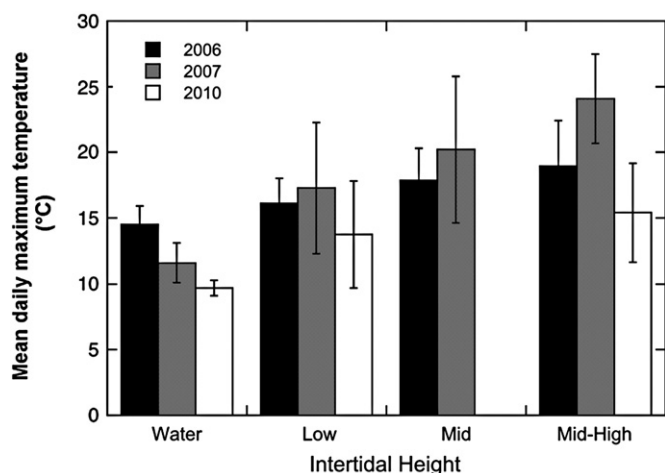


Fig. 2. Average percent of different sized *P. ochraceus* found during four spring-tide surveys in 2010, (A) within the designated intertidal heights, and (B) within different microhabitat types. Size classes were categorized as follows: small (<300 g, black bars), medium (300–500 g, gray bars), and large (>500 g, white bars). Values are mean  $\pm$  SD.

### 3.1.2. Biomimetic temperatures and emersion times

Water temperatures measured by immersed biomimetics differed among the three years examined (Fig. 3). At the wave-protected site in Horseshoe Cove, average daily water temperature was  $14.5 \pm 1.4$  °C between 7/24/06 and 8/21/06. By contrast, water temperature in 2007 averaged only  $11.6 \pm 1.5$  °C from 6/6/07 and 7/16/07. In 2010, average water temperature on the exposed coast was  $9.7 \pm 0.6$  °C between 5/13/10 and 5/24/10. Data collected by the Bodega Ocean Observing Node indicates that the higher water temperatures recorded in 2006 were part of a general trend in this area, and not solely the result of collecting the data later in the summer (BOON, <http://bml.ucdavis.edu/boon/index.html>).

In general, emersion time of the biomimetics increased with increasing height in the intertidal. Between 7/24/06 and 8/21/06, the biomimetics in the low intertidal were exposed an average of  $1.5 \pm 1.4$  h each day, those in the mid intertidal were exposed  $4.9 \pm 2.3$  h, while biomimetics in the mid-high intertidal were exposed for  $9.1 \pm 0.8$  h (mean  $\pm$  SD, n = 29 days for each zone). Emersion times in 2007 also increased with tidal height:  $2.1 \pm 1.7$  h in the low intertidal,  $5.0 \pm 1.5$  h in the mid intertidal, and  $9.0 \pm 2.4$  h in the mid-high intertidal (mean  $\pm$  SD, n = 28 days for low and mid-high, n = 14 days for mid). On the exposed coast, emersion times followed the same pattern with tidal height, although the time spent emersed at a given height tended to be less; between 5/13/10 and 5/24/10, the low intertidal biomimetic was exposed an average of 1.1



**Fig. 3.** Average daily maximum temperature recorded by *P. ochraceus* biomimetics in the water and in the low, mid, and mid-high intertidal zones at the wave-protected site (2006 [black bars] and 2007 [gray bars]), and at the wave-exposed site (2010 [white bars]). Values are mean  $\pm$  SD.

$\pm 2.0$  h, while the mid-high intertidal biomimetic was exposed  $5.9 \pm 1.8$  h (mean  $\pm$  SD,  $n = 12$  days for each zone).

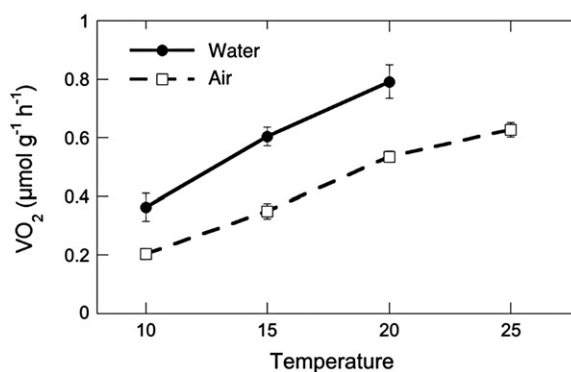
As well as being emersed for shorter periods, biomimetics in the low intertidal recorded lower maximum temperatures than those in the mid or mid-high intertidal for all years investigated (Fig. 3). In 2006, mean daily maximum aerial body temperature ranged from  $16.7 \pm 1.8$  °C in the low intertidal to  $19.0 \pm 3.5$  °C in the mid-high intertidal (mean  $\pm$  SD,  $n = 29$  days for each zone; ANOVA with intertidal height as factor:  $F_{1,86} = 8.29$ ,  $p = 0.001$ ). In 2007, temperatures were higher, ranging from  $19.1 \pm 4.9$  °C in the low intertidal to  $24.1 \pm 3.4$  °C in the mid-high intertidal (mean  $\pm$  SD,  $n = 28$  days for each zone; ANOVA with intertidal height as factor:  $F_{1,71} = 17.53$ ,  $p < 0.0001$ ). The wave-exposed site investigated in 2010 showed cooler temperatures with non-significant differences but similar patterns:  $13.8 \pm 4.1$  °C in the low intertidal to  $15.4 \pm 3.7$  °C in the mid-high intertidal (mean  $\pm$  SD,  $n = 12$  days for each zone; ANOVA with intertidal height as factor:  $F_{1,15} = 0.565$ ,  $p = 0.465$ ). Overall, maximum aerial body temperature measured by biomimetics was obtained at the mid-high intertidal height: 27 °C in 2006 and 35 °C in 2007 at the wave-protected site, but only 22.3 °C at the wave-exposed site in 2010.

### 3.2. Metabolic measurements

#### 3.2.1. Aquatic oxygen consumption

There was no significant interaction between temperature and body mass on aquatic  $VO_2$  (ANCOVA, temperature  $\cdot$  mass,  $F_{2,81} = 2.10$ ,  $p = 0.13$ ), thus the effects of temperature and body mass were examined separately. Temperature had a significant effect on sea star aquatic  $VO_2$  (ANCOVA,  $F_{2,80} = 24.20$ ,  $p < 0.0001$ ; Fig. 4). Over the entire range of temperatures tested, aquatic  $VO_2$  more than doubled between 10 and 20 °C (Table 2, "All sizes"), and post-hoc analysis showed that sea star  $VO_2$  at each temperature was significantly different from one another (Sidak test,  $p < 0.001$  for each comparison). The  $Q_{10}$  value for aquatic oxygen consumption was 2.18 from 10 to 20 °C.

Mass-specific aquatic  $VO_2$  decreased with increasing sea star body mass (ANCOVA,  $F_{1,80} = 12.10$ ,  $p = 0.001$ ), though the exact nature of the relationship between body mass and  $VO_2$  differed among the three experimental temperatures (Appendix A). To refine the estimates of sea star aquatic  $VO_2$  for energetic calculations (Section 3.3), the aquatic  $VO_2$  data were separated into three groups based on the size classifications used in the field data: small (300 g), medium (300–500 g) and large (> 500 g). Averaging the values for each size class clearly shows that  $VO_2$  per gram decreased with increasing body size at each temperature tested (Table 2).



**Fig. 4.** Oxygen consumption rates ( $\mu\text{mol O}_2 \text{g}^{-1} \text{h}^{-1}$ ) of *P. ochraceus* in water (solid line) and air (dashed line). Points represent means  $\pm$  SE (water:  $n = 27$  individuals tested at all three temperatures; air:  $n = 22$  individuals tested at all four temperatures).

#### 3.2.2. Aerial oxygen consumption

As with aquatic  $VO_2$ , there was no significant interaction between temperature and body mass for the aerial data (ANCOVA, temperature  $\cdot$  mass,  $F_{3,87} = 2.29$ ,  $p = 0.084$ ), and temperature had a significant effect on sea star aerial  $VO_2$  (ANCOVA,  $F_{3,87} = 111.39$ ,  $p < 0.0001$ ; Fig. 4). Over the entire range of temperatures examined, average  $VO_2$  of *P. ochraceus* in air increased over three times between 10 and 25 °C (Table 2). Post hoc analysis showed that  $VO_2$  at all temperatures were significantly different from one another (Sidak test,  $p < 0.001$  for each comparison). The  $Q_{10}$  values for aerial  $VO_2$  were 2.63 from 10 to 20 °C, and 2.12 over the entire range tested (10–25 °C).

Mass-specific rates of aerial  $VO_2$  also decreased significantly with body mass (ANCOVA,  $F_{1,87} = 42.96$ ,  $p < 0.0001$ ). Although the strength of the relationship varied among the different experimental temperatures (Appendix A), when averaged by size class, there is a clear trend of decreasing mass-specific  $VO_2$  with increasing body size at all temperatures tested (Table 2).

#### 3.3. *P. ochraceus* energetics

Combining field biomimetic measurements of body temperatures and emersion times with laboratory measurements of  $VO_2$  enabled predictions of the energy expenditure of hypothetical sea stars over a typical 10-day period during the summer. Based on these calculations, a medium-sized sea star (400 g) would have consumed 45–50% more oxygen in 2006 than in 2007 and 2010 (Fig. 5, Table 3). Calculations also suggest that this difference is size-dependent, such that larger individuals would consume approximately 120–210% more oxygen in 2006 than they would have in 2007 and 2010, while small individuals would have consumed approximately 30–40% more oxygen in 2006 than in 2007 and 2010 (Fig. 5, Table 3). In all cases, the increased oxygen consumption estimated for 2006 was primarily caused by a higher average water temperature ( $\sim 15$  °C in 2006 versus 10 °C in 2007 and 2010; Table 3). Comparing the predicted oxygen consumption values for 2010 with those for 2006 and 2007 suggests that there is no systematic difference in the oxygen consumption of sea stars located in a wave-protected site (2006 and 2007) versus a wave-exposed site (2010; Fig. 5, Table 3).

This analysis also suggests that vertical location in the intertidal has a much smaller effect on sea star oxygen consumption than do interannual temperature differences (Fig. 5). For example, oxygen consumption generally differed by only  $\sim 5\%$  for sea stars located in the low versus the mid-high intertidal, the one clear exception being a 26% difference for large sea stars in 2007. Finally, there was no obvious pattern as to whether a sea star's oxygen consumption would be higher in the low or the mid-high intertidal zone (Fig. 5).

The potential energetic implications of differences in oxygen consumption were determined by converting the volumes of oxygen

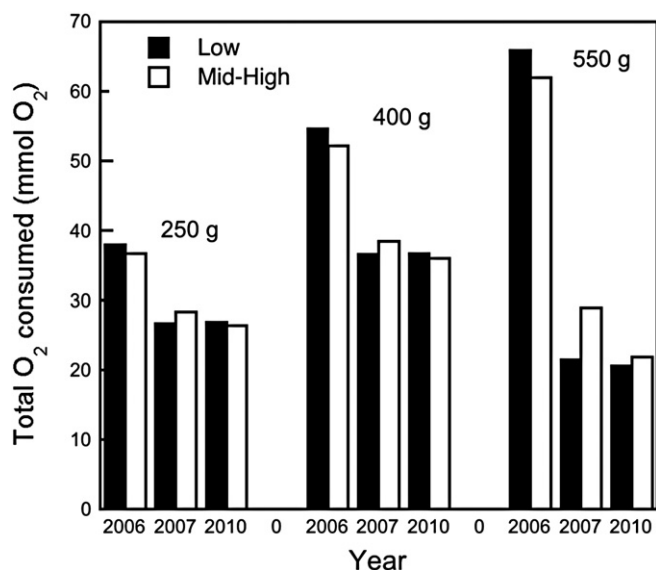


Fig. 5. Total oxygen consumption (mmol O<sub>2</sub>) estimated for different sized sea stars located in the low (black bars) and mid-high (white bars) intertidal over 10 days during the summers of 2006, 2007, and 2010.

consumed into kilojoules of energy (Table 4). This conversion shows that sea stars used between 9.4 and 30.1 kJ over 10 days (Table 4). Interestingly, both the lowest and highest values estimated were for large sea stars in the low intertidal; the lowest was during 2010 while the highest was during 2006 (Table 4). This range of energy expenditure would require between 2 and 6.5 g mussel tissue. Calculations also suggest that large sea stars could have lower energy requirements than most small and all medium-sized sea stars over the 10 days examined in 2007 and 2010 (Fig. 5, Table 4).

#### 4. Discussion

##### 4.1. Oxygen consumption of *P. ochraceus*

Aquatic VO<sub>2</sub> and associated Q<sub>10</sub> values for *P. ochraceus* (Fig. 4, Table 2) are similar to values for aquatic respiration reported for other sea stars tested within a similar temperature range (Cole and Burggren, 1981; McElroy et al., 2012; Murphy and Jones, 1987; Webster, 1975). Comparison of aerial respiration data is more limited given the scarcity of previous research. One notable exception is a study on *Asterina gibbosa*, a subtidal species found off the West coast of Great Britain (Murphy and Jones, 1987). Aerial VO<sub>2</sub> values for *A. gibbosa* were roughly four times higher than those for *P. ochraceus*, a difference that could be largely due to *A. gibbosa* being over 100-times smaller by weight than *P. ochraceus*. The Q<sub>10</sub> for aerial VO<sub>2</sub> was very similar between the two species: 1.90 for a 30 g *A. gibbosa* from 15 to 25 °C (Murphy and Jones, 1987), versus 1.80 for an average 400 g *P. ochraceus* across the same temperature range.

The metabolic response of intertidal animals to aerial exposure is variable, with some species exhibiting an increase in VO<sub>2</sub> relative to aquatic values while others show a decrease. *P. ochraceus* falls within the latter group, with aerial VO<sub>2</sub> being about 50% of that in water (Fig. 4, Table 2). A similar ratio was found for two intertidal snails (McMahon and Russell-Hunter, 1977). Although most intertidal organisms exhibit a lower VO<sub>2</sub> in air than in water, a few species show higher VO<sub>2</sub> in air (e.g., *Pollicipes polymerus*, Petersen et al., 1974). Interestingly, *A. gibbosa*, the only other asteroid species for which these data are available, increased its VO<sub>2</sub> in response to aerial exposure (Murphy and Jones, 1987). The difference between *P. ochraceus* and *A. gibbosa* could be due to differences in body size, typical habitat, and phylogeny, among other more subtle factors. The hypothesis that body size may influence the metabolic response to aerial exposure has precedence in a study demonstrating that metabolism of porcelain crabs responds somewhat differently to air exposure depending on body mass (Stillman and Somero, 1996).

The mechanism by which the VO<sub>2</sub> of *P. ochraceus* decreases in air relative to water is unknown. Studies on other asteroid species demonstrated that gas exchange in seawater occurs over both the aboral and oral surface through papulae and tube feet, respectively (Cole and Burggren, 1981). Observations indicated that the podia of *A. gibbosa* retract in air while the papulae become limp and rest on the aboral surface (Murphy and Jones, 1987), presumably rendering them less efficient at gas exchange by decreasing surface area and increasing diffusion distance. If such a change also occurs in *P. ochraceus*, it could provide a mechanism to explain the reduced VO<sub>2</sub> in air. Lower VO<sub>2</sub> in air relative to water could also indicate increased reliance on anaerobic energy sources, a phenomenon observed in some intertidal bivalves and barnacles (Newell, 1973; Shick et al., 1988). There is evidence that anaerobic pathways may contribute to overall metabolism in echinoderms under all environmental conditions (Greenwood, 1980; Miller and Mann, 1973; Shick, 1983), but this rate appears to be unaffected by aerial exposure (Stickle, 1988). Therefore, a shift to more anaerobic sources by *P. ochraceus* during aerial exposure is unlikely.

##### 4.2. Cost of emersion

###### 4.2.1. Effects of intertidal location

Estimates of sea star VO<sub>2</sub> during the summers of 2006, 2007, and 2010 revealed only modest energetic differences between low and mid-high intertidal locations (Fig. 5, Tables 3 and 4). These small differences are due to two interconnected reasons: (1) the sea stars in both zones spend substantially more time each day submerged than emersed, and (2) their aquatic VO<sub>2</sub> is nearly twice their aerial VO<sub>2</sub> at any given temperature (Table 2). Thus, the oxygen consumed in water would dominate that consumed in air, minimizing the energetic differences between sea stars located in the low and mid-high intertidal. This result seems counter-intuitive, since the mid-high zone is generally regarded as a much harsher location for sea stars than the low zone. Indeed, very few sea stars were located high in the intertidal zone at low tide (Fig. 1). Garza and Robles (2010) found

Table 3  
Estimates of the oxygen consumed (mmol) by hypothetical sea stars in different intertidal zones over 10 days during the summers of 2006, 2007, and 2010.

Year	Intertidal zone	Small (<300 g)			Medium (300–500 g)			Large (> 500 g)		
		O <sub>2</sub> consumed in water	O <sub>2</sub> consumed in air	Total O <sub>2</sub> consumed	O <sub>2</sub> consumed in water	O <sub>2</sub> consumed in air	Total O <sub>2</sub> consumed	O <sub>2</sub> consumed in water	O <sub>2</sub> consumed in air	Total O <sub>2</sub> consumed
2006	Low	35.7	2.3	38.0	51.5	3.1	54.6	62.8	3.1	65.9
	Mid-high	29.9	6.8	36.7	43.2	9.0	52.2	53	9.0	62.0
2007	Low	24.2	2.4	26.7	33.2	3.4	36.6	18.1	3.4	21.5
	Mid-high	16.3	12.1	28.4	22.3	16.3	38.5	22.3	16.7	29.0
2010	Low	25.8	1.0	26.9	35.3	1.4	36.7	19.1	1.4	20.6
	Mid-high	22.6	3.8	26.4	30.9	5.1	36.0	16.8	5.1	21.9

**Table 4**  
Estimates of energy requirements (kJ) of hypothetical sea stars in different intertidal zones over 10 days during the summers of 2006, 2007, and 2010.

Year	Intertidal zone	Small (<300 g)		Medium (300–500 g)		Large (>500 g)	
		Energy requirements (kJ)	Mussel tissue (g)	Energy requirements (kJ)	Mussel tissue (g)	Energy requirements (kJ)	Mussel tissue (g)
2006	Low	17.4	3.74	24.9	5.37	30.1	6.48
	Mid-high	16.8	3.61	23.8	5.13	28.3	6.10
2007	Low	12.2	2.63	16.7	3.60	9.8	2.11
	Mid-high	13.0	2.79	17.6	3.79	13.3	2.87
2010	Low	12.3	2.64	16.8	3.61	9.4	2.02
	Mid-high	12.1	2.60	16.4	3.54	10.0	2.15

that *P. ochraceus* actively avoided being emersed high in the intertidal by moving with the tides. The results of the current analysis suggest that the direct cost of emersion alone cannot explain the vertical distribution of sea stars at low tide (see below).

Comparing results of the analysis for 2007 and 2010, two years with similar water temperatures, also suggests that the direct energetic costs seen in wave-protected and wave-exposed sites can be very similar. However, subtle differences do seem to exist. For example, predictions show that while sea stars within the low-intertidal zone at both sites are predicted to use about the same amount of energy over the 10-day periods in 2007 and 2010, those in the mid-high zone would have greater energy requirements in the wave-protected site than in the wave-exposed site. This difference is due to greater aerial temperatures at the wave-protected site relative to the wave-exposed site. Indeed wave splash induced lower aerial body temperatures for any intertidal height compared to wave-protected sites (Fitzhenry et al., 2004). Moreover, predictions show that this effect appears to increase with increasing body mass (Table 4).

#### 4.2.2. Effects of temperature

While these calculations predict very modest differences in direct energetic costs to sea stars at different intertidal heights, they showed much larger differences between the years examined. All sizes of hypothetical sea stars consumed much more oxygen in 2006 than in 2007 (at the same site) or 2010 (at the wave-exposed site; Fig. 5). At the wave-protected site, aerial temperatures were warmer in 2007 than in 2006, but water temperature averaged 3 °C higher in 2006, causing a large increase in oxygen consumed while submerged (Table 3). Therefore, slight water temperature variations appear to have much larger effects on sea star oxygen consumption than do large differences in aerial body temperature. Nevertheless, Pincebourde et al. (2008) reported that exposure to a single warm low tide event over an eight-day period caused a 60% increase in feeding rate in *P. ochraceus*. The amplitude of this increase is similar to the increase in oxygen consumption between the 15 and 25 °C temperature treatments found in the present study. This result, therefore, corroborates the hypothesis that *P. ochraceus* compensate for the energetic costs associated with an acute exposure to high aerial body temperature by increasing feeding rate (Pincebourde et al., 2008, 2012). Pincebourde et al. (2008) also showed that prolonged increases in aerial body temperature (from 16 °C to 26 °C) have substantial negative effects on feeding rate that cannot be explained by these metabolic rate estimates. This result suggests that energetic costs other than those associated with changes in metabolic rate probably play a large role in determining the energetic and behavioral responses to emersion (Robles et al., 2009). Sanford (1999) found that a 3 °C increase in water temperature caused *P. ochraceus* to consume 29% more mussels at 12 °C than at 9 °C. The current work shows that increasing water temperatures increased oxygen consumption and, therefore, energetic expenditure. To avoid energetic deficits, sea stars likely need to increase their feeding rates to match the higher energetic cost of warmer water temperatures. The calculations presented here suggest that sea stars needed to consume 2–4 g more mussel tissue over 10 days to meet energetic demands in 2006 versus 2007 or 2010

(Table 4). This increase of about 30% for an average-sized sea star is nearly identical to Sanford's (1999) finding. A pertinent next step is to determine whether a 30% increase in feeding rate is enough to alter community structure.

Along the California coast, water temperatures naturally vary with events such as El Niño and the Pacific Decadal Oscillation (PDO). Water temperatures in the summer of 2006 were warmer than in 2007 and, in fact, the summer of 2006 marked an El Niño phase that had passed by the summer of 2007 (Southern Oscillation Index of El Niño phase for 2006 and 2007 was obtained from <http://www.ncdc.noaa.gov/sotc/enso>). Therefore, *P. ochraceus* energetic demands would fluctuate greatly with these natural environmental cycles, which may have implications for rocky intertidal community structure. This fluctuation in *P. ochraceus* energetics with environmental cycles has also been documented by Sanford (2002a,b), as well as by other investigators for other intertidal organisms (e.g. Helmuth, 2002; Urban and Tarazona, 1996; Wethey et al., 2011; Yamane and Gilman, 2009). Indeed, the bioenergetic approach such as developed in this study supports the fact that global environmental fluctuations in aquatic media can be a reasonable proxy to determine the effects of global climate on the metabolism of intertidal organisms, at least for those organisms living in the low intertidal. Measuring the metabolic rate during each lifetime phase of an organism can provide important insights into how environmental fluctuations modulate the bioenergetics of organisms.

Supplementary data related to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2012.04.007>.

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#### References

- Broitman, B.R., Szathmary, P.L., Mislán, K.A.S., Blanchette, C.A., Helmuth, B., 2009. Predator-prey interactions under climate change: the importance of habitat vs body temperature. *Oikos* 118, 219–224.
- Burnaford, J.L., 2004. Habitat modification and refuge from sublethal stress drive a marine plant-herbivore association. *Ecology* 85, 2837–2849.
- Cole, R.N., Burggren, W.W., 1981. The contribution of respiratory papulae and tube feet to oxygen uptake in the sea star *Asterias forbesi* (Desor). *Mar. Biol. Lett.* 2, 279–287.
- Connell, J.H., 1972. Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.* 3, 160–192.



- Dahlhoff, E.P., Buckley, B.A., Menge, B.A., 2001. Physiology of the rocky intertidal predator *Nucella ostrina* along an environmental stress gradient. *Ecology* 82, 2816–2829.
- Denny, M.W., Dowd, W.W., Bilir, L., Mach, K.J., 2011. Spreading the risk: small-scale both temperature variation among intertidal organisms and its implications for species persistence. *J. Exp. Mar. Biol. Ecol.* 400, 175–190.
- Fitzhenry, T., Halpin, P.M., Helmuth, B., 2004. Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. *Mar. Biol.* 145, 339–349.
- Garza, C., Robles, C., 2010. Effects of brackish water incursions and diel phasing of tides on vertical excursions of the keystone predator *Pisaster ochraceus*. *Mar. Biol.* 157, 673–682.
- Greenwood, P.J., 1980. Growth, respiration and tentative energy budgets for two populations of the sea urchin *Parechinus angulosus* (Leske). *Estuar. Coast. Mar. Sci.* 10, 347–367.
- Harley, C.D.G., 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Mar. Ecol. Prog. Ser.* 371, 37–46.
- Harley, C.D.G., Pankey, M.S., Wares, J.P., Grosberg, R.K., Wonham, M.J., 2006. Color polymorphism and genetic structure in the sea star *Pisaster ochraceus*. *Biol. Bull.* 211, 248–262.
- Harper, K.D., Williams, G.A., 2001. Variation in abundance and distribution of the chiton *Acanthopleura japonica* and associated molluscs on a seasonal, tropical, rocky shore. *J. Zool.* 253, 293–300.
- Helmuth, B.S.T., 1998. Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* 68, 51–74.
- Helmuth, B., 2002. How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. *Integr. Comp. Biol.* 42, 837–845.
- Helmuth, B., Hofmann, G.E., 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *Biol. Bull.* 201, 374–384.
- Hill, R.W., Wyse, G.A., Anderson, M., 2008. *Animal Physiology*. Sinauer Associates, Sunderland, MA.
- Huang, S.C., Newell, R.I.E., 2002. Seasonal variations in the rates of aquatic and aerial respiration and ammonium excretion of the ribbed mussel *Geukensia demissa* (Dillwyn). *J. Exp. Mar. Biol. Ecol.* 270, 241–255.
- Lewis, J.R., 1964. *The Ecology of Rocky Shores*. Hodder & Stoughton, London.
- McElroy, D.J., Nguyen, H.D., Byrne, M., 2012. Respiratory response of the intertidal seastar *Parvulastra exigua* to contemporary and near-future pulses of warming and hypercapnia. *J. Exp. Mar. Biol. Ecol.* 416–417, 1–7.
- McMahon, R.F., Russell-Hunter, W.D., 1977. Temperature relations of aerial and aquatic respiration in six littoral snails in relation to their vertical zonation. *Biol. Bull.* 152, 182–198.
- Marsden, I.D., Weatherhead, M.A., 1998. Effects of aerial exposure on oxygen consumption by the New Zealand mussel *Perna canaliculus* (Gmelin, 1971) from an intertidal habitat. *J. Exp. Mar. Biol. Ecol.* 230, 15–29.
- Mauzey, K.P., 1966. Feeding behavior and reproductive cycles in *Pisaster ochraceus*. *Biol. Bull.* 131, 127–144.
- Mauzey, K.P., Birkeland, C., Dayton, P.K., 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound Region. *Ecology* 49, 603–619.
- Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.* 64, 249–286.
- Miller, R.J., Mann, K.H., 1973. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. *Mar. Biol.* 18, 99–114.
- Murphy, C.T., Jones, M.B., 1987. Some factors affecting the respiration of intertidal *Asterina gibbosa* (Echinodermata, Asteroidea). *J. Mar. Biol. Assoc. UK* 67, 717–727.
- Newell, R.C., 1973. Factors affecting the respiration of intertidal invertebrates. *Am. Zool.* 13, 513–528.
- Okumus, I., Stirling, H.P., 1998. Seasonal variations in the meat weight, condition index and biochemical composition of mussels (*Mytilus edulis* L.) in suspended culture in two Scottish sea lochs. *Aquaculture* 159, 249–261.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.* 100, 65–75.
- Parsell, D.A., Lindquist, S., 1993. The function of heat-shock proteins in stress tolerance: degradation and reactivation of damaged proteins. *Annu. Rev. Genet.* 27, 437–496.
- Petersen, J.A., Fyhn, H.J., Johansen, K., 1974. Eco-physiological studies of an intertidal crustacean, *Pollicipes polymerus* (Cirripedia, Lepadomorpha): aquatic and aerial respiration. *J. Exp. Biol.* 61, 309–320.
- Petes, L.E., Mouchka, M.E., Milston-Clements, R.H., Momoda, T.S., Menge, B.A., 2008. Effects of environmental stress on intertidal mussels and their sea star predators. *Oecologia* 156, 671–680.
- Pincebourde, S., Sanford, E., Helmuth, B., 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnol. Oceanogr.* 53, 1562–1573.
- Pincebourde, S., Sanford, E., Helmuth, B., 2009. An intertidal sea star adjusts thermal inertia to avoid extreme body temperatures. *Am. Nat.* 174, 890–897.
- Pincebourde, S., Sanford, E., Casas, J., Helmuth, B., 2012. Temporal coincidence of environmental stress events modulates predation rates. *Ecology Letters*, <http://dx.doi.org/10.1111/j.1461-0248.2012.01785.x>.
- Pörtner, H.O., 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp. Biochem. Physiol. A* 132, 739–761.
- Robles, C.D., Desharnais, R.A., Garza, C., Donahue, M.J., Martinez, C.A., 2009. Complex equilibria in the maintenance of boundaries: experiments with mussel beds. *Ecology* 90, 985–995.
- Sanford, E., 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283, 2095–2097.
- Sanford, E., 2002a. The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. *J. Exp. Mar. Biol. Ecol.* 273, 199–218.
- Sanford, E., 2002b. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. *Integr. Comp. Biol.* 42, 881–891.
- Schneider, K.R., Helmuth, B., 2007. Spatial variability in habitat temperature may drive patterns of selection between an invasive and native mussel species. *Mar. Ecol. Prog. Ser.* 339, 157–167.
- Seabra, R., Wethey, D.S., Santos, A.M., Lima, F.P., 2011. Side matters: microhabitat influence on intertidal heat stress over a large geographical scale. *J. Exp. Mar. Biol. Ecol.* 400, 200–208.
- Shick, J.M., 1983. Respiratory gas exchange in the echinoderms. In: Jangoux, M., Lawrence, J.M. (Eds.), *Echinoderm Studies*, Vol 1. Balkema, Rotterdam, pp. 67–110.
- Shick, J.M., Widdows, J., Gnaiger, E., 1988. Calorimetric studies of behavior, metabolism and energetics of sessile intertidal animals. *Am. Zool.* 26, 161–181.
- Somero, G.N., 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integr. Comp. Biol.* 42, 780–789.
- Stickle, W.B., 1988. Patterns of nitrogen excretion in the phylum Echinodermata. *Comp. Biochem. Physiol.* 91, 317–321.
- Stillman, J.H., Somero, G.N., 1996. Adaptation to temperature stress and aerial exposure in congeneric species of intertidal porcelain crabs (genus *Petrolisthes*): correlation of physiology, biochemistry and morphology with vertical distribution. *J. Exp. Biol.* 199, 1845–1855.
- Strathmann, M.F., 1987. *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast*. University of Washington Press, Seattle.
- Szathmari, P.L., Helmuth, B., Wethey, D.S., 2009. Climate change in the rocky intertidal zone: predicting and measuring the body temperature of a keystone predator. *Mar. Ecol. Prog. Ser.* 374, 43–56.
- Tomaneck, L., 2010. Variation in the heat shock response and its implications for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. *J. Exp. Biol.* 213, 971–979.
- Ulbricht, R.J., Pritchard, A.W., 1972. Effect of temperature on the metabolic rate of sea urchins. *Biol. Bull.* 142, 178–185.
- Urban, H.-J., Tarazona, J., 1996. Effects of El Niño/Southern Oscillation on the population dynamics of a *Gari solida* population (Bivalvia: Psammobiidae) from Bahía Independencia. *Peru Mar. Biol.* 125, 725–734.
- Webster, S.K., 1975. Oxygen consumption in echinoderms from several geographic locations, with particular reference to the echinoidea. *Biol. Bull.* 148, 157–164.
- Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P., Brannock, P.M., 2011. Response of intertidal populations to climate: effects of extreme events versus long term change. *J. Exp. Mar. Biol. Ecol.* 400, 132–144.
- Williams, G.A., Morrill, D., 1995. Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*.
- Withers, P.C., 1977. Measurement of  $VO_2$ ,  $VCO_2$ , and evaporative water loss with a flow-through mask. *J. Appl. Phys.* 42, 120–123.
- Yamane, L., Gilman, S.E., 2009. Opposite responses by an intertidal predator to increasing aquatic and aerial temperatures. *Mar. Ecol. Prog. Ser.* 393, 27–36.