

Body temperature during low tide alters the feeding performance of a top intertidal predator

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Abstract

Although the direct effects of climate change on species distribution and abundance have become increasingly apparent, considerably less is known about the potential for thermal variations to influence community structure indirectly through altered species interactions. We examined how the low tide body temperature of the rocky intertidal sea star *Pisaster ochraceus* affected the rate at which this keystone species fed on the mussel *Mytilus californianus*. Patterns of intertidal distribution and sea star body temperatures were recorded in the field at Bodega Bay, California, in 2006 and 2007. Under controlled laboratory conditions, we separately examined the roles of short-term (acute) and long-term (chronic) exposures to high aerial body temperatures in driving patterns of feeding and growth. Upper limits to thermal tolerance were also quantified in the laboratory. Integrating field data on the vertical distribution, microhabitat, and body temperature of sea stars indicated that individuals typically experienced relatively high body temperatures over a series of short periods of time (acute exposures of a few days) and that they escaped from situations where they would have experienced such temperatures for longer periods (chronic exposure). Although sea stars never approached their upper thermal limit (35°C), laboratory trials demonstrated that chronic exposure to realistic peak aerial body temperatures ($\geq 23^\circ\text{C}$) negatively affected both feeding and growth rates, whereas acute exposure had positive consequences on feeding rates but no effects on growth. Variations in aerial body temperature, and more specifically the frequency of exposure to high body temperatures, can influence interaction strength in this important predator–prey system.

Habitat temperature, which in turn is translated into organismal body temperature in ectotherms, is one of the most influential abiotic factors driving the distribution and abundance of organisms because it influences virtually all biochemical and physiological rates (Somero 1995; Hochachka and Somero 2002). Thus, the direct effect of

climate variations on species distributions, through effects on organismal body temperature, has received considerable attention. Several studies have shown that shifts in species distributions have occurred in recent decades in association with climate change (Perry et al. 2005; Helmuth et al. 2006a; Parmesan 2006). Forecasting future changes in the distribution and abundance of species requires, however, that we fully understand the underlying mechanisms responsible for these range shifts. In particular, climate change is likely to have both direct effects on the physiological performance and survival of organisms, as well as indirect effects mediated through species interactions (e.g., competition, facilitation, and predation) (Southward 1958; Davis et al. 1998; Sanford 2002a). Understanding the nature of these indirect effects may be especially critical in top-down regulated ecosystems because the dynamics of these systems often depend strongly upon one or a few predators (Power et al. 1996) and because species at higher trophic levels may be differentially sensitive to climate change (Voigt et al. 2003).

Our mechanistic understanding of the ecological effects of environmental fluctuations, as mediated through altered species interactions, can be improved by examining the effects of climatic variations on the physiology and behavior of keystone species (Bengtsson 1998; Sanford 1999). Keystone species are important drivers of commu-

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nity structure and diversity and appear to be particularly common in aquatic systems (Paine 1966; Power et al. 1996). Any effect on the physiological ecology of a keystone species may have repercussions on the whole community (Sanford 1999), although the amplitude of the effects depends on both environmental conditions and the relative strength of biotic relationships (Menge and Sutherland 1987; Menge et al. 1994, 2004).

The rocky intertidal zone has long served as a model ecosystem for examining the ecological effects of thermal stress over a wide range of scales (Helmuth et al. 2006a). However, it is also among the most thermally complex environments on Earth. The body temperature of intertidal species during low tide is driven by multiple climatic parameters and is strongly affected by an organism's morphology and behavior. Moreover, the timing of aerial exposure is exceedingly complex given geographic variability in the timing of low tide (Helmuth et al. 2006b). As a result, only a few studies have examined the indirect effects of aerial body temperature on species interactions in the intertidal zone (Williams 1994; Sanford 1999; Dahlhoff et al. 2001).

In this study, we explicitly examined the effects of fluctuating aerial body temperatures on the feeding rate of a keystone predator, the sea star *Pisaster ochraceus* feeding on the mussel *Mytilus californianus* in the rocky intertidal zone, a marine ecosystem thought to be especially susceptible to climate change (Helmuth et al. 2006a). Paine's classic experiments showed that *P. ochraceus* maintains high species diversity in low-intertidal habitats by preying on *M. californianus* (Paine 1966, 1974). Following the experimental removal of *P. ochraceus*, this mussel outcompeted all other sessile animals and macroalgae for primary space in the low-intertidal zone. Paine (1966) coined the term "keystone species" to describe a species, like *P. ochraceus*, with disproportionate community effects. His results helped motivate an extensive body of subsequent research that demonstrated the importance of top-down control in structuring a variety of aquatic communities (Power et al. 1996; Menge 2000). Although environmental stress has long been known to modify the strength of top-down forces (Menge and Sutherland 1987), these abiotic effects have been explored at a mechanistic level only recently (Sanford 1999; Dahlhoff et al. 2001; Menge et al. 2002).

Thus, although the ecological effects of *P. ochraceus* are well studied (Paine 1974; Menge et al. 1994; Robles et al. 1995), surprisingly little is known regarding the thermal tolerance of this sea star. *P. ochraceus* forages and feeds when underwater (at high tide), but during low tide, it regularly experiences exposure to aerial conditions (Landenberger 1969). Physiological stress experienced at low tide is assumed to set the upper vertical foraging limit of *P. ochraceus*, and thus to indirectly maintain the lower boundary of the mussel bed distribution (Feder 1956; Paine 1974). Recent works indicate that the predation rate of *P. ochraceus* is highly sensitive to small changes ($\sim 3^\circ\text{C}$) in water temperature (Sanford 1999, 2002b), but it is not clear how variations in aerial conditions during low tide might affect the performance of this sea star (Petes et al.

2008). Thus, we do not fully understand how fluctuations in terrestrial climatic factors (such as air temperature and solar radiation) may indirectly affect the distribution of mussels. Here, we recorded the body temperature patterns of *P. ochraceus* over a year in the field, and we determined thermal tolerance (LT50) to examine whether this species is living near its thermal tolerance limits. Then, under controlled laboratory conditions, we separately examined the roles of short-term (acute) and long-term (chronic) exposures to sublethal aerial body temperatures in potentially driving patterns of feeding and growth in this predator.

Methods

Species, field site, and collection—The ochre sea star *P. ochraceus* is very common along the Pacific coast of North America (Menge et al. 2004). It preys on a broad range of invertebrates, but the California mussel, *M. californianus*, is one of its preferred prey (Feder 1956; Landenberger 1968) and is the primary species through which *P. ochraceus* exerts its community-level effect (Paine 1974). Measurements of body temperature patterns were made on a rocky shore in the Bodega Marine Reserve (California, $38^\circ 19' \text{N}$, $123^\circ 4' \text{W}$). This outer coast site was sheltered from large waves due to its location inside a semiprotected cove (Horseshoe Cove). This site was exposed to solar radiation from sunrise until the end of the afternoon due to local topography. All laboratory experiments were conducted at the Bodega Marine Laboratory, where animals were supplied with seawater continuously flowing through tanks. The sea stars used for feeding experiments were collected at several outer coast sites, all sheltered from large waves and within ~ 15 km of the Bodega Marine Reserve. All individuals collected had a body wet weight between 100 g and 250 g (mean \pm SD = 204.1 ± 45.5 g, $n = 326$), which corresponds to the most common wet mass range in populations of this sea star along the central coast of California (Menge et al. 2004). Distributions of body mass were similar in each feeding experiment. Mussels (*M. californianus*) were collected at a single site inside the Bodega Marine Reserve, and all had a shell length of 4–6 cm (mean \pm SD = 5.04 ± 0.51 cm, $n = 2,213$).

Field temperature measurements and intertidal distribution—A biomimetic data logger mimicking the thermal properties of *P. ochraceus* and developed by Lauren Szathmary (University of South Carolina, Columbia) was used to obtain continuous records of sea star body temperature in the field. Briefly, the biomimetic data logger consists of a solid disc made of foam (Aquazone single-cell foam, Reilly Foam) with a height of 3.7 cm and a diameter of 8.5 cm. A temperature data logger (i-Button, Dallas Semiconductor) was inserted into the disc and recorded temperature to the nearest 0.5°C every 10 min. The biomimetic data logger was fixed on the rock using epoxy putty (Z-spar splash zone compound A-788, Kop-Coat).

Six biomimetic data loggers were deployed at different intertidal elevations from July to August 2006, and then from March to July 2007. The position of the loggers

spanned the wider vertical range of *P. ochraceus* distribution (see Results). Intertidal elevations were recorded using surveyor's equipment (laser level). Data loggers were attached to relatively flat rocky surfaces (inclination angle between 0° and 14°), with two loggers in the upper midintertidal zone (103.5 cm and 124.8 cm above mean lower low water [MLLW] in 2006; 133.8 cm and 138.9 cm above MLLW in 2007), two in the lower midintertidal zone (88.5 cm and 94.8 cm above MLLW in 2006; 85.2 cm and 86.1 cm above MLLW in 2007), and two in the low-intertidal area (36.3 cm and 43.2 cm above MLLW in 2006; 35.7 cm and 35.1 cm above MLLW in 2007). Three loggers were also deployed in crevices in the lower midintertidal zone during summer 2006.

Although the biomimetic data logger was found in previous trials to estimate the *P. ochraceus* body temperature with an average absolute error of $\sim 1^\circ\text{C}$ (Lauren Szathmary pers. comm.), its accuracy was verified at our study site by comparing its records and body temperatures measured in live sea stars located near data loggers, within a radius of about 1 m, during four nonconsecutive days (dates: 27 July in 2006; 18 and 21 June and 4 July in 2007). Body temperatures were recorded using a digital thermometer and thermocouple (type T, Omega Engineering) during the last hour of the emersion period ($n = 46$ sea stars).

The intertidal distribution of *P. ochraceus* was surveyed monthly in early spring 2007 and in June to August of both 2006 and 2007, i.e., for 9 d total. Intertidal elevation of all individuals present in the study site at low tide was recorded using surveyor's equipment (laser level). The microhabitat of each individual was also noted as "open area" (i.e., sea star was found on a relatively flat surface that could potentially receive solar radiations) or "nonexposed area" (i.e., sea star was under algae, in a crevice, or on a north-facing vertical surface). Upper and lower edges of mussel bed were also measured every 50 cm along a 25-m horizontal transect crossing the entire study site in April 2007.

Feeding experiments: the setup—A set of 12 identical tanks (volume 75 liters) was used for all feeding experiments during summer 2007 (Fig. 1). Each tank was supplied continuously with flow-through seawater at a rate of 6 L min^{-1} . A tidal cycle was simulated by alternating periods with tanks full vs. nearly empty of water. A stand pipe (height 30 cm) was used to set the high tide and then removed manually to drain the tank at low tide. The low tide was set 50 min later on each subsequent day to mimic the natural tidal rhythm. Duration of aerial exposure during low tide was set to 6 h, which corresponds to a realistic value for low-intertidal to midintertidal organisms. Sea stars were placed on an inclined ramp (inclination 30°) in each tank (Fig. 1). The tanks were also slightly inclined to facilitate draining at low tide. Flow of incoming seawater was kept constant throughout the experiments so that water flowed across the bottom of the tank even during low tide periods. This system allowed animals to be out of water during the low tide while relative humidity inside the tanks was maintained high and roughly constant throughout the low tide duration. A 150-W heat-wave lamp (ceramic heat

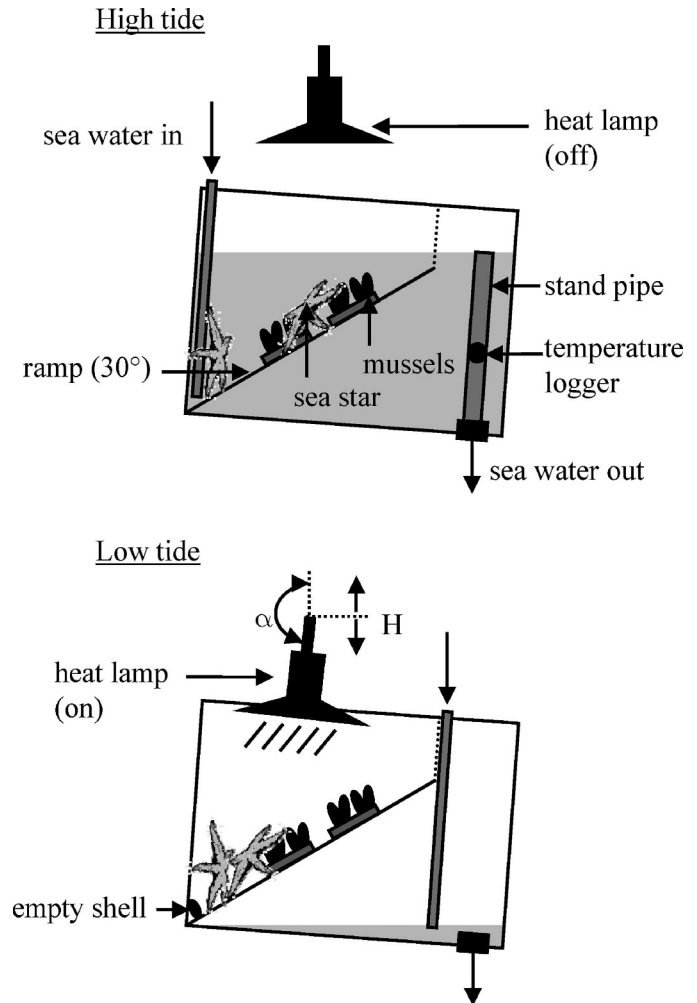


Fig. 1. Experimental design of aquaria involving control of aerial body temperatures in intertidal sea star *P. ochraceus*. A stand pipe was used to fill tank at high tide, and it was removed to drain tank at low tide. Both height (H) and inclination from vertical (α) of heat lamp were modified daily according to position of sea stars within tanks and recorded body temperatures.

emitter, Rolf C. Hagen) was mounted above each tank. Polystyrene plates insulated adjacent tanks from one another. Aerial body temperature of sea stars (i.e., during the low tide) was controlled by adjusting both the distance and the view angle between sea stars and heat lamps (Fig. 1). *P. ochraceus* body temperatures were checked every 15 min with an infrared imaging camera (ThermaCAM 695, FLIR Systems). Body temperature of each individual was calculated as the mean of five measurements taken on the body center (i.e., excluding the arms). An i-button was fixed along the stand pipe to measure water temperature every 10 min during high tides.

In all experiments, each of the 12 tanks contained four sea stars. A new set of animals was used for each experiment (chronic and acute exposure experiments) to prevent any side effect caused by thermal history. To place all animals in a similar physiological condition, sea stars were acclimated in the tanks for 8 d prior to the start of each experiment. During this period, sea stars were held

without any food and at a body temperature between 13°C and 15°C during daily low tides. *M. californianus* were added to the tanks on the first day of each experiment and were provided ad libitum throughout the trial. Groups of 12 mussels were placed in Petri dishes (diameter 10 cm) about 1 week before each experiment to allow them to reattach their byssal threads to each other and to the Petri dish as well (Sanford 2002b). Four Petri dishes were fixed on the inclined ramp in a similar position for each tank. Because the use of heat lamps altered the temperature of mussels as well, we verified that thermal history of mussels did not affect sea star feeding rates (see Web Appendix 1: www.aslo.org/lo/toc/vol_53/issue_4/1562a1.pdf). No effect of mussel body temperature on *P. ochraceus* feeding rate was detected (analysis of variance [ANOVA], mussel temperature treatment as main factor: $F_{3,8} = 0.22$; $p = 0.88$).

All sea stars were weighed both at the start of the acclimation period and at the end of every trial to estimate growth rate. Wet mass was measured immediately at the end of a high tide (i.e., after 18 h of submersion). Sea stars were individually identified by taking digital pictures of their dorsal surface. The geometry of the madreporite and surrounding tubercles was used as an individual signature. Throughout all experiments, care was taken to not disturb sea stars as handling can negatively alter feeding.

Feeding experiments: effect of chronic thermal exposure—Four body temperature treatments were applied daily during periods of aerial exposure, for 16 consecutive days in summer 2006 ($n = 3$ replicate tanks per treatment). In the four treatments, the aerial body temperatures (mean \pm SD over the 16 d) were $16.7 \pm 1.5^\circ\text{C}$ (control), $19.6 \pm 0.6^\circ\text{C}$, $23.3 \pm 0.8^\circ\text{C}$, and $26.1 \pm 0.8^\circ\text{C}$. Heat lamps were switched on after 1 h of aerial exposure, and body temperature was increased slowly to treatment level over the next 2 h. Sea stars were held at the experimental temperature for the last 3 h of aerial exposure. All empty mussel shells were collected and replaced by fresh mussels on day 8 and day 16. After day 16, sea stars were left fully submerged for an additional 8 d (corresponding to a neap tide period in the field when sea stars are seldom emersed). Empty shells were collected again at the end of day 24. Mean (\pm SD) seawater temperature (averaged over the 24 d) was $15.2 \pm 1.2^\circ\text{C}$.

Feeding experiments: effect of acute thermal exposure—This experiment tested the effects of varying the frequency of exposure to warm aerial conditions. Four temperature treatments were applied ($n = 3$ replicate tanks per treatment) during an experimental period of 8 d in summer 2006. In the first treatment (control), sea stars were maintained at a body temperature of $16.2 \pm 1.1^\circ\text{C}$ during the daily low tides. In a second treatment (called “1 d”), body temperatures were also $16.1 \pm 0.9^\circ\text{C}$ except for day 3 when body temperatures were increased to $26.6 \pm 1.2^\circ\text{C}$ using the same method described above. In another treatment (called “2 consecutive days”), body temperatures were increased to $26.1 \pm 1.4^\circ\text{C}$ on both days 3 and 4. In the last treatment (called “2 distant days”), body temperatures

were increased to $26.3 \pm 0.9^\circ\text{C}$ during days 3 and 6. All sea stars were observed feeding in all tanks during the first 2 d, before any temperature treatment was applied. Empty shells were collected and replaced by fresh mussels at the end of the second day to verify that feeding rates were similar in all tanks (Kruskal–Wallis test: $p = 0.98$). All empty shells were collected at the end of the experiment. Mean (\pm SD) water temperature over the experimental period was $14.6 \pm 0.6^\circ\text{C}$.

Estimating feeding and growth rates—The feeding rate of *P. ochraceus* was measured by recording the total amount of mussel tissue consumed during a treatment period in each tank. An allometric relationship was found from a set of 60 mussels (shell length range 4–6 cm) between mussel size [length (mm) \times width (mm)] and wet mass (including the shell) of mussels (linear regression model: $y = 0.01x - 4.18$; $R^2 = 0.91$; $F_{1,58} = 585.06$; $p < 0.001$). Empty shells were dried using absorptive paper, weighed, and their dimensions were measured using calipers, immediately after collection. The amount of wet tissue consumed in a single mussel (A , in g) was computed from

$$A = [0.01(L \times w) - 4.18] - E \quad (1)$$

where L is the shell length (mm), w is the shell width (mm), and E is the weight of the empty shell (g). A per capita feeding rate was computed by dividing the total amount of mussel tissue consumed in a tank by the number of sea stars (Sanford 2002b). In this study, we were interested in quantifying the average performance of sea stars rather than determining interindividual variation in behavioral responses, because *P. ochraceus* exerts its community-level effects through the performance of the whole population.

Growth rate was estimated as the change in wet body mass between the start and the end of a temperature treatment. Obviously, it was not possible to measure dry body mass nondestructively before a feeding trial. However, estimating growth rate from a change in wet body mass assumes that body water content remains unchanged through time regardless of the temperature treatment. This assumption could be violated, for example, if sea star body water content during high tide varied as a response to thermal and/or desiccation stress experienced during previous low tides. We tested this possibility in a separate trial by measuring wet body mass, daily, right before low tide, for 9 d. Sea stars were held in tanks without food, and three aerial body temperature treatments were applied (16°C , 23°C , and 26°C ; $n = 9$ sea stars for each) from day 1 to day 6 during daily low tides following the same method described above. All sea stars were held at a body temperature of 16°C during low tides from day 7 to day 9 to test whether wet body mass varied with previous temperature exposure. A fourth treatment (control) consisted of five sea stars left underwater continuously, to test whether any variation in wet mass was due to repetitive aerial exposures. Sea stars were dissected immediately after the last wet body mass record (i.e., at the very end of last simulated high tide), drained of fluid, and left drying on paper towels for 1 h. Body mass was then measured again

to estimate the amount of water in the coelomic cavities. Dry body mass was subsequently measured by holding sea stars in an oven at 75°C for 48 h. Body masses were checked frequently during the last 24 h to ensure that they remained stable, indicating that the sea stars had reached a final dry mass.

Aerial lethal temperature—The aerial lethal temperature threshold of *P. ochraceus* was estimated as the temperature at which 50% of individuals die of heat death (LT50). It was measured in a 75-liter tank. A flat, elevated platform was installed inside the tank allowing seawater to run continuously while sea stars were not in contact with water. This method was used to keep the relative humidity constant and high. Two heat lamps (150 W) were positioned above the tank, and the height of the lamps relative to the sea stars was adjusted to vary body temperatures during aerial exposure. The size of the tank permitted us to test the tolerance of seven individuals at the same time. Sea stars were placed in a flat position and were not overlapping with each other. Body temperature differed between the seven animals due to their positions relative to the lamps, and body temperatures were difficult to predict from the height of the heat lamps. Therefore, 10 groups of seven sea stars each were tested using different heat lamp heights. This method ensured against having an unbalanced sampling in the different temperature ranges with a 2°C increment from 26°C to 42°C. Each group was exposed to aerial conditions for 6 h. Body temperatures were gradually increased for 3 h until they reached the experimental temperature that was then maintained for 3 h. Body temperatures were checked every 15 min throughout the treatment using the infrared camera. Body temperature was measured as the mean of five measurements made on the body. Survival was first assessed for all individuals immediately after the treatment by placing the animal on its dorsal surface and looking for movement of the tube feet, a response seen in live sea stars. The tank was then filled with seawater. Sea stars were left submerged for a 24-h recovery period and then the survival test was repeated. A sea star was considered alive only when movement of the tube feet was observed after 24 h (all individuals alive after 24 h were still alive after 3 weeks spent submerged in a holding tank).

Statistical analysis—The biomimetic data logger was tested for its accuracy by performing Pearson correlations between actual body temperature and temperature measured by the data loggers. The mean root mean square of error (RMSE) relative to the 1:1 relationship was computed to quantify the data logger's accuracy. Any variation in field elevation patterns of sea stars was verified through an ANOVA with month as the main factor and distribution of individual elevations as the dependent variable. A Bonferroni post hoc test was used subsequently for multiple comparisons. Survival data established by the aerial lethal temperature experiment were treated as binary data (0, when individuals died, and 1, when they survived). Binary data were plotted against body temperature, allowing us to fit the logistic dose response model using

TableCurve 2D (SYSTAT Software). The transition center of the model corresponds to the LT50.

The effect of aerial temperature treatment on cumulative wet mass change was assessed by performing a multivariate analysis of variance (MANOVA) with a repeated measures analysis to consider the effect of time. Main factors were therefore thermal treatment and time (9 consecutive days). The dependent variable was daily cumulative wet mass change. Post hoc tests, however, cannot be done in a MANOVA preventing any detailed analysis of the daily patterns. Therefore, an ANOVA with a Tukey post hoc test for multiple comparisons was subsequently performed independently for each day (main factor was thermal treatment) to test whether wet body mass change in temperature treatments differed from that in the control.

The effects of aerial body temperature on feeding rates were assessed through ANOVA with the Tukey post hoc test for multiple comparisons (the main factor was temperature treatment and the dependent variable was feeding rate in a tank). Additionally, the general trends in the chronic exposure scenario were assessed using linear regressions. A *t*-test was used to compare the slope of the regression lines for the three different periods of 8 d of chronic thermal events (i.e., days 1–8, 9–16, 17–24) (Zar 1998). Gains or losses of wet body mass were tested for their significance (i.e., difference from zero) performing a one-sample *t*-test that was set to compare a given sample to a mean of zero (i.e., no gain or loss of mass) with a 95% confidence interval. The effect of aerial temperature treatment on growth rate was assessed by performing a nested ANOVA to analyze individual growth rates by considering the variability in both tank replicates and temperature treatments. Tank effect was therefore nested within each temperature treatment effect (i.e., 12 sea stars distributed among three tanks for each temperature treatment) according to the method described in Gotelli and Ellison (2004). A Tukey post hoc test was subsequently used for multiple comparisons.

A probability threshold of 0.05 was used for all statistical tests, and analyses were performed using SYSTAT software version 10.2 (Systat Software).

Results

Field patterns—The biomimetic data logger accurately estimated body temperatures of nearby sea stars in the actual body temperature range 10.2–27.1°C (Pearson correlation: $p < 0.001$, RMSE = 0.70°C) (Fig. 2). Daily maximal body temperatures during low tide, as assessed using biomimetic data loggers, were highly variable temporally as well as spatially (Fig. 3A). Aerial body temperature generally increased with intertidal elevation. During aerial exposure, the mean maximal body temperature in the upper midintertidal zone was up to 17°C above that recorded in the low-intertidal zone. Body temperature also differed greatly from air temperature: daily maximal body temperature was on average 3.5°C and 8.3°C above ambient, with peak body temperatures up to 14.3°C and 16.6°C warmer than ambient, in the low intertidal and the upper midintertidal, respectively. From May to early July

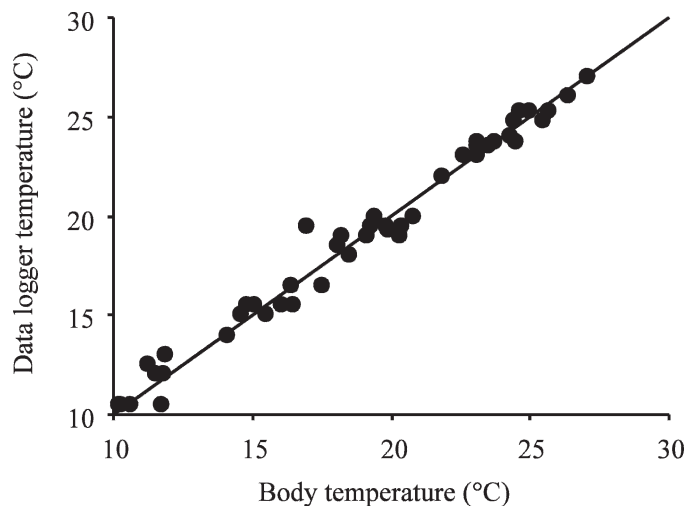


Fig. 2. Accuracy of biomimetic data logger. Temperature recorded by biomimetic data loggers are plotted against actual body temperature of sea stars located in field near loggers. Line indicates the 1:1 relationship.

2007, daily maximal body temperatures were frequently above 23°C, the threshold at which effects of chronic exposure are significant (*see below*). Temperatures above 23°C occurred more frequently in the upper and lower midintertidal zones than in the low intertidal. By contrast, during summer 2006, daily maximal body temperatures were above 23°C only in the upper midintertidal. The three temperature loggers deployed in cracks in the lower midintertidal during summer 2006 recorded body temperatures that were always lower than those recorded in open areas in the lower midintertidal but also always higher than those in the low intertidal (data not shown).

Intertidal elevation patterns of sea stars indicated that *P. ochraceus* tended to remain higher on the shore at low tide during summer months than during spring (Fig. 3B). Also, more individuals were found in open areas than in nonexposed areas during summer months, whereas individuals were observed mostly in nonexposed areas during the spring. In fact, the number of individuals found in open areas during low tide increased linearly from April to August (linear regression model: $y = 0.46x - 40.53$; $R^2 = 0.67$; $F_{1,7} = 14.12$; $p = 0.007$). No relationship was found between intertidal elevation and the microhabitat of individuals (Pearson correlation: $p > 0.05$, for all comparisons), indicating that habitat choice at low tide was independent of vertical height in the intertidal.

Upper lethal temperature—The effect of aerial body temperature on survival was described well by the logistic dose response model (Fig. 4). The model indicated that the transition occurred at the body temperature 35.3°C, suggesting that the LT50 was about 35°C. Only two individuals survived at a mean body temperature slightly above 35°C, whereas no sea star mortality occurred at body temperatures below 35°C (Fig. 4).

Wet and dry body mass—Overall, wet body mass varied through time and with temperature treatment (Fig. 5). A

more detailed analysis (ANOVA ran for each day: $F_{3,28} > 3.89$; $p < 0.02$ for all) indicated that the cumulative changes of wet mass in the 16°C and 23°C aerial body temperature treatments were similar to that in the control ($p > 0.05$ for all daily comparisons). The cumulative change of wet mass in the 26°C treatment, however, was similar to that in the control only during the first 2 d and the last day of the experiment ($p > 0.05$ for all), and it was higher otherwise ($p < 0.001$ for all). These results indicated that sea stars increased water uptake at high tide following exposure to warm aerial conditions during low tides and that body mass subsequently decreased back to its initial level about 3 d after the end of the exposure period. The mean maximal water uptake, obtained after 5 d of exposure, was about 15 g (Fig. 5).

When pooling all treatments (i.e., $n = 32$), dry body mass could be predicted from wet body mass measured on the last day of the experiment, i.e., day 9 (linear regression model: $[\text{dry mass}] = 0.23 [\text{wet mass}] + 9.96$; $R^2 = 0.93$; $p < 0.0001$). On average, the dry-to-wet ratio was 0.40 ± 0.02 .

Effect of chronic thermal exposure—Increasing aerial body temperatures of sea stars led to a substantial decrease in their feeding rate during the first 8-d period of the experiment (Fig. 6A). Relative to the control (16°C), reduced feeding was apparent starting at ~23°C (Tukey: $p < 0.05$ solely at 23°C and 26°C). The per capita feeding rate was about 30% lower at a mean aerial body temperature of ~26°C than at ~16°C. A similar relationship held for the following 8-d period. The per capita feeding rate was decreased by about 44% at ~26°C compared with ~16°C (Fig. 6B). The slope of the two regression lines did not differ between the first period (days 1–8) and the second period (days 9–16) ($p > 0.05$). The feeding rate was quite similar in all tanks during the third 8-d period when all sea stars were kept continuously submerged (Fig. 6C). Overall, the per capita feeding rate in the control was slightly lower in the second period than in the first one and was much more reduced in the third period (Fig. 6), presumably due to satiation on the ad libitum diet of mussels. The mean gain of wet body mass was significant (i.e., different from 0) in all body temperature treatments ($p < 0.05$) except the 26°C treatment ($p = 0.235$). Overall, the mean gain of wet mass decreased as body temperature increased (Fig. 7).

Effect of acute thermal exposure—Acute exposure to high temperature affected the per capita feeding rate of *P. ochraceus* (Fig. 8). The mean per capita feeding rate was higher in the 1-d treatment than in the control by about 60%. It was also significantly increased in the 2-consecutive-days treatment. The feeding rate in the 2-distant-days treatment did not differ from any other treatment. The gain of wet body mass was significant only in the 1-d treatment. Overall, however, temperature treatment had no detectable effects on growth rate (Fig. 8).

Discussion

Our results reveal that aerial body temperatures experienced by *P. ochraceus* have profound effects on predation

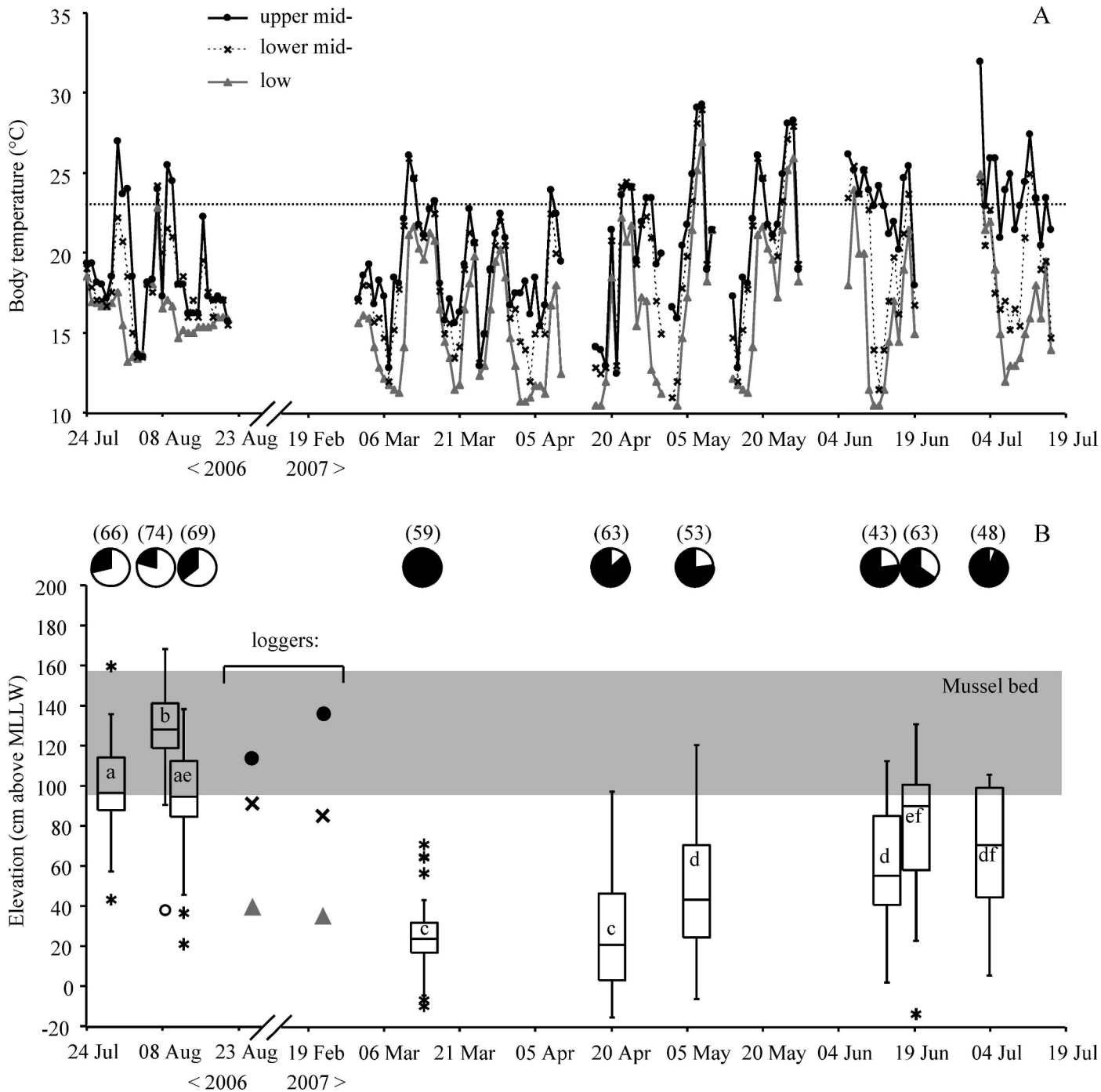


Fig. 3. (A) Daily mean body temperatures, as recorded by biomimetic data loggers in low, lower midintertidal, and upper midintertidal during summer 2006 and spring and summer 2007. SD eliminated for clarity. Horizontal dashed line shows temperature threshold (23°C) at which thermal stress effects can be detected (see Results). (B) Monthly intertidal elevation patterns of *P. ochraceus* populations (box plot charts). In each box plot, center horizontal line marks median of sample. Length of each box indicates range within which central 50% of the values fall, with box edges at first and third quartiles. Whiskers: range of values that fall within inner fences. Asterisks: values within inner and outer fences. Empty circles: far outside values. Statistically different distributions indicated by different letters within each box plot (ANOVA: $F_{8,529} = 104.67$, $p < 0.0001$, Tukey test for multiple comparisons). Gray zone indicates mean elevation of mussel bed in the area. Mean elevation of biomimetic data loggers for both 2006 and 2007 also shown. Pie charts at top show proportion (%) of *P. ochraceus* population located in open areas (white) vs. nonexposed microhabitats (black) (see Methods for additional details). Pie charts and box plots correspond to each other. Numbers of individuals sampled during quantification of sea star elevation and microhabitat are in brackets.

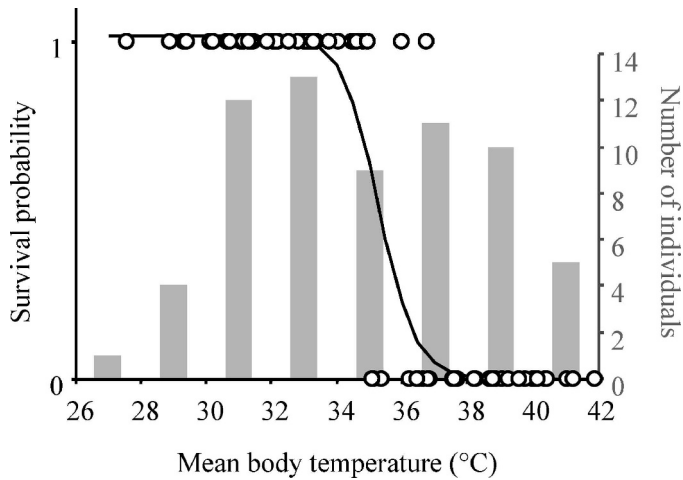


Fig. 4. Lethal temperature threshold of *P. ochraceus*. Survival likelihood (1 means individuals survived, 0 means they died) is shown as function of aerial body temperature. Logistic dose response model adequately fits dataset ($R^2 = 0.84$, $F_{2,67} = 172.5$, $p < 0.001$). Sampling distribution (gray bars = number of individuals sampled per 2°C temperature range) indicates that about as many individuals were sampled within a 6°C range below and above lethal threshold.

by this sea star, a keystone species in rocky intertidal communities. Although tolerance level to environmental stress has long been assumed to limit the upper vertical foraging range of this predator (and hence the lower vertical boundary of mussel beds), surprisingly little attention has been paid to testing the influence of aerial exposure on *P. ochraceus*. The likelihood of reaching a high body temperature during a low tide increased with the vertical position of sea stars, a phenomenon that has been reported in other intertidal organisms (Denny et al. 2006). Overall, biomimetic data loggers indicated that the period from March through early July was relatively warmer than during late July and August for sea stars in the area of Bodega Bay, California. This observation can be explained by the tidal cycle. Relative to other locations along the Pacific North American coast, Bodega Bay is a cool site, and the cumulative hours of midday exposure to aerial conditions is low during summer (Helmuth et al. 2002, 2006b). For example, sea stars were exposed to aerial conditions only early in the morning and in the evening in August, while low tides occurred more frequently around midday in May–June when the amount of solar radiation reaches maximal level (Helmuth et al. 2006b). These relatively hotter conditions during spring relative to summer may thus explain the lower foraging location of sea stars observed in spring at this site.

Although the biomimetic loggers are quite accurate in estimating *potential* sea star body temperature, the estimate corresponds to *actual* body temperature only if sea stars are located in the same microhabitat and at the same elevation as the loggers. For example, no sea stars were recorded at the same elevation as the loggers in the upper midintertidal during spring 2007, and all individuals were in microhabitats shielded from solar radiations in March 2007 (Fig. 3B). Integrating data on sea star tidal elevation,

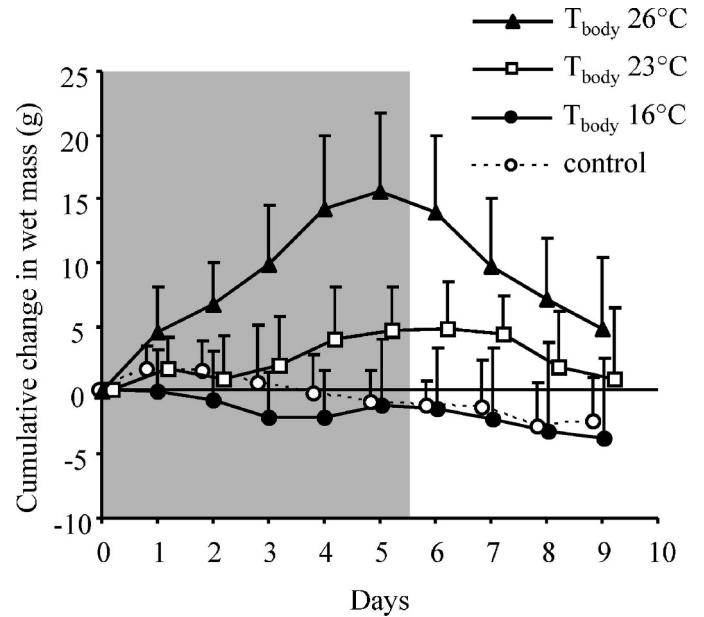


Fig. 5. Cumulative change in wet body mass (mean \pm SD) when sea stars experienced body temperatures of 16°C, 23°C, and 26°C at low tide (MANOVA among temperature treatments, $F_{3,28} = 17.82$, $p < 0.001$; repeated measure analysis, time \times temperature treatment, $F_{24,224} = 4.5$, $p < 0.001$). Sea stars in control were held underwater all the time. Period highlighted in gray indicates days when temperature treatments were actually applied during low tide. All sea stars were at body temperature of 16°C during last three low tides (days 7, 8, and 9).

microhabitat, and body temperature indicates a seasonal variation in the aerial body temperature patterns actually experienced by sea stars (Fig. 3). In early spring (March and April), a major portion of the population was in crevices or beneath algae during low tide, and their body temperature in these microhabitats was similar to that recorded in open areas in the low intertidal. In late spring and early summer (May to early July), individuals were mostly in the low intertidal and lower midintertidal, and a small portion of the population was in open areas where they experienced body temperatures above 23°C during several series of no more than 3 or 4 consecutive days. Sea stars avoided the upper midintertidal where body temperatures above 23°C would have been experienced for 8 consecutive days in June and 14 d in early July. In late summer (late July and August), sea stars mainly experienced aerial body temperature as recorded in the upper midintertidal, where they reached body temperatures above 23°C for no more than two series of 3 consecutive days.

Sea stars in the field frequently experienced body temperatures above 23°C for short periods of time (3–4 d), and the laboratory trials indicate that these conditions positively affect sea star performance in opposition to chronic exposure to such temperatures. The negative effects of chronic exposure were detected at body temperatures above 23°C, suggesting that 23°C is the threshold inducing thermal stress. This result is consistent with a field study in Oregon that did not find any effect of aerial body temperature on predation rate in low-intertidal habitats

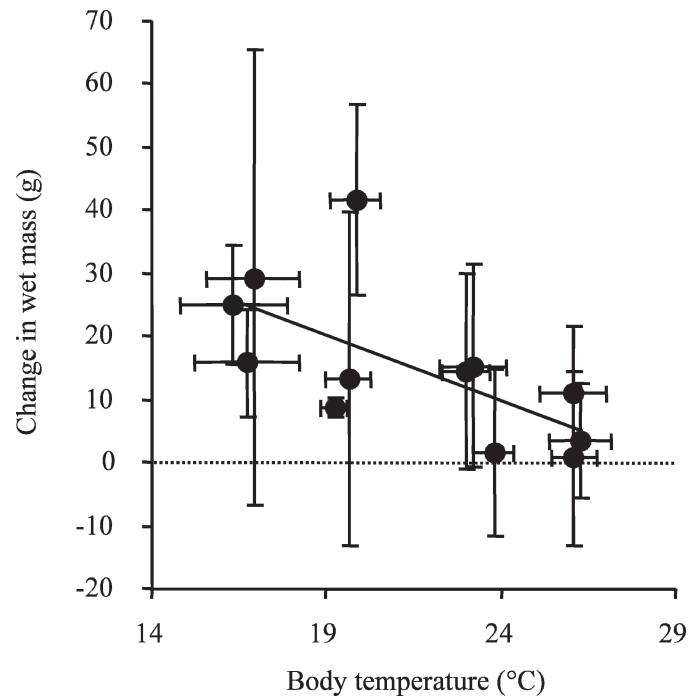
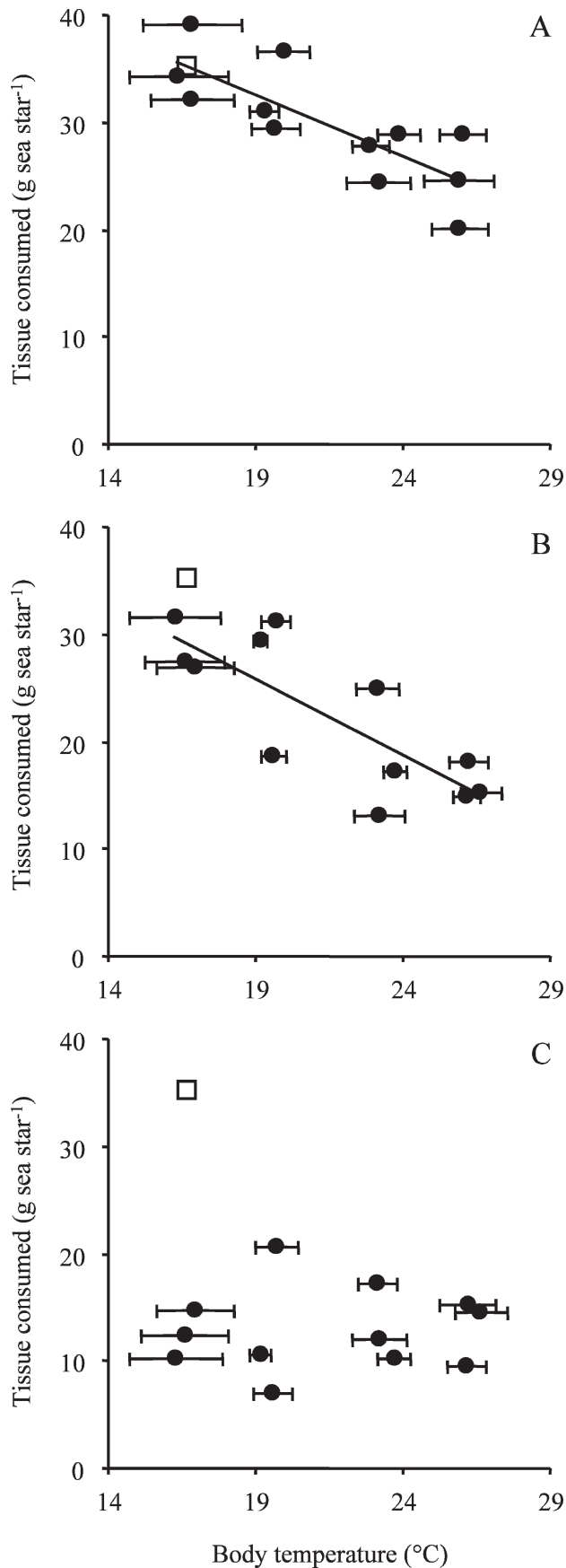


Fig. 7. Mean change in *P. ochraceus* wet body mass as function of aerial body temperature during chronic exposure treatment (linear regression model, $y = -2.03 x + 58.59$; $R^2 = 0.41$; $p = 0.025$). Dots represent means for each tank. SD given for both mean body temperatures and mean change of wet mass. Nested ANOVA indicated that mean gain of wet mass decreased as body temperature increased (among treatments, $F_{3,8} = 4.60$, $p = 0.038$) and that there was no significant replicate (tank) effect (among replicates, $F_{3,36} = 0.17$, $p = 0.99$).

where body temperatures seldom reached 23°C (Sanford 2002a). In contrast to the negative effects of chronic thermal stress, short-term exposure to warm aerial conditions had a positive effect on sea star feeding performance. Surprisingly, a 1-d exposure to warm body temperatures induced a substantial increase in the feeding rate of *P. ochraceus* (Fig. 8). This suggests that *P. ochraceus*'s initial

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Fig. 6. Effect of chronic thermal stress on *P. ochraceus* feeding rate. Total amount of mussel tissue consumed per sea star is shown as function of their body temperature averaged over a given period: (A) days 1 to 8 (ANOVA, $F_{3,8} = 5.45$, $p = 0.025$; linear regression model, $y = -1.16 x + 54.51$; $R^2 = 0.64$; $p = 0.002$); (B) days 9 to 16 (ANOVA, $F_{3,8} = 4.83$, $p = 0.033$; $y = -1.41 x + 52.67$; $R^2 = 0.64$; $p = 0.002$); (C) days 17 to 24 (ANOVA, $F_{3,8} = 0.02$, $p = 0.99$), when sea stars were kept underwater permanently. In final case (C), feeding rate is shown as a function of mean body temperature experienced over entire previous treatment period (i.e., previous 16 d). Each dot represents per capita feeding rate estimated in a single tank (therefore no SD along y-axis is available). White squares indicate mean per capita feeding rate in treatment 16°C of first period (days 1 to 8) and can be used as a reference point for comparisons among periods. SD given for body temperatures (horizontal bars).

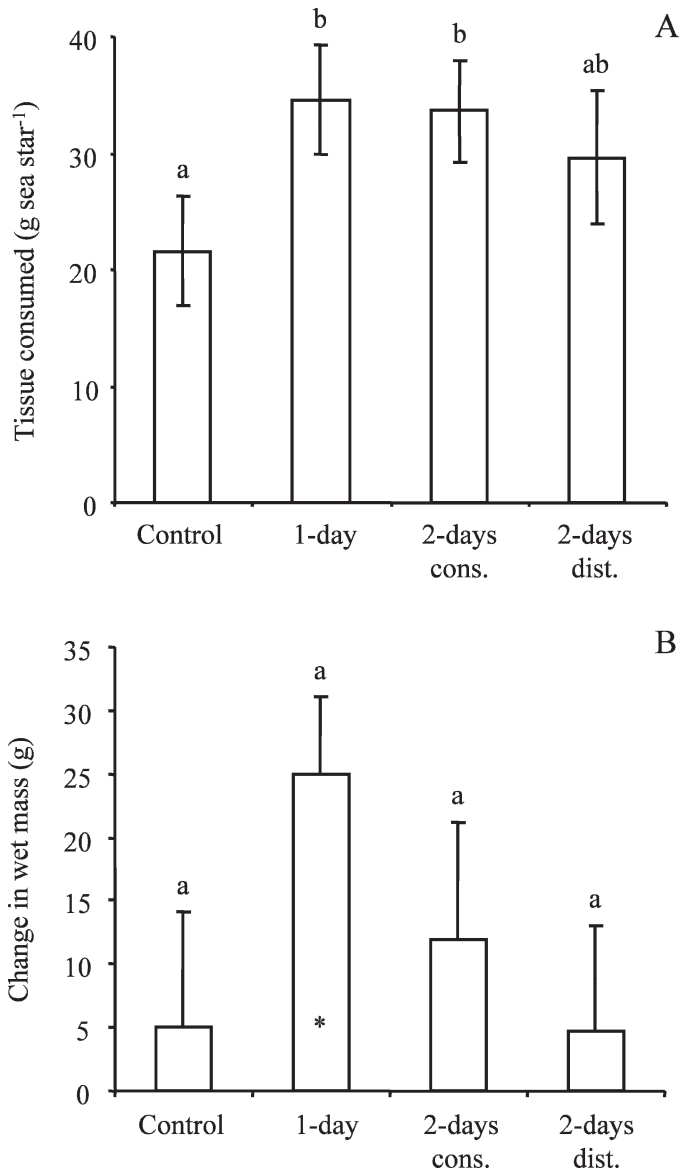


Fig. 8. Effect of acute thermal exposure on (A) the total amount of mussel tissue consumed (mean \pm SD) over the whole experimental period (ANOVA, $F_{3,8} = 4.42$, $p = 0.041$), and (B) growth rate (mean \pm SD) (Nested ANOVA among treatments, $F_{3,8} = 2.34$, $p = 0.15$; among replicates, $F_{3,36} = 0.04$, $p = 0.99$), in control, 1 d of exposure to warm aerial body temperature, 2 consecutive days, and 2 distant days with thermal exposure. Shared letters above bars indicate groups whose means do not differ (Tukey, $p > 0.05$). Asterisk at bottom of a bar indicates when change of wet mass differs significantly from zero (t -test, $p < 0.05$).

response to potentially stressful conditions may be to increase feeding rates perhaps to compensate for energetic costs of elevated metabolic rate over a short temporal window. A similar response to acute exposure to warm water temperature has been noted in oysters (Beiras et al. 1995) and in a stream fish (Quigley and Hinch 2006).

Physiological stress usually refers to a reduction in performance or fitness of an organism (Menge and

Sutherland 1987). Here we show that exposure to potentially stressful conditions can lead to increased feeding under certain circumstances depending on the frequency of thermal events. It is unclear, however, whether this increase in consumption has a positive effect on growth or merely compensates for the energetic costs of a response to sublethal stress. The effect on growth tended to be positive (Fig. 8B), although it is possible that this positive trend could have resulted from aerial conditions inducing an increase in body water content. The acute experiment was conducted for 8 d, and such a temporal window was probably too brief to detect any significant change in the dry body mass of sea stars.

Chronic exposure to high aerial body temperature tends to negatively alter the growth rate of sea stars. Growth rate was estimated from wet body mass measurements. Such an estimate is accurate only if variation in body mass is due to a gain or loss of dry mass, and not of body water content, which is especially critical in the case of marine organisms. In fact, our results show that body water content varied with aerial body temperature (Fig. 5). Wet body mass at the end of high tide increased by about 15 g on average (representing about 7.5% of initial body mass) when sea stars experienced body temperature of $\sim 26^{\circ}\text{C}$ during the previous low tide. Sea stars, including *P. ochraceus*, can regulate the volume of internal fluid through the madreporite, the external opening to the water vascular system (Ferguson 1992). It is possible that sea stars associate exposure to high body temperatures with desiccation stress and respond by increasing their body water content, but this remains to be investigated further. These data suggest, however, that we overestimated growth rate by about 15 g in the warmest treatment during the chronic exposure experiment. Therefore, the negative effect of chronic exposure to high body temperatures on growth rate is probably even greater than what we report (Fig. 7).

P. ochraceus forages while submerged at high tide (Feder 1956) and is forced to remain immobile once emerged at low tide. Our results clearly reveal a delayed effect of aerial body temperature experienced during low tide on the feeding rate of sea stars when they are resubmerged again at high tide. This effect may continue beyond a single tide series, since sea stars in the 23°C treatment continued to show reduced feeding rates during the third period of the chronic exposure experiment (i.e., when underwater all the time) while they were clearly not satiated, since they fed much less than individuals in the 16°C treatment (Fig. 6C). Abiotic factors like aerial exposure duration and water temperature experienced by intertidal organisms are known to affect physiological processes including feeding rate (Sanford 1999, 2002b), growth rate (Bishop and Peterson 2006), and reproduction (Petes et al. 2007). Aerial body temperature, however, has been traditionally considered for its direct effect on survival and intertidal zonation, and most studies put a greater emphasis on the morphological, behavioral, physiological, and biochemical adaptations that allow organisms to increase their thermal tolerance and to live higher on the shore near this threshold (Stillman and Somero 1996; Somero 2002; Williams et al. 2005). Our

results indicate that aerial conditions can also affect species interaction strength, e.g., by altering feeding rates. By doing so, aerial body temperature may alter community structure not only through acute mortality events but also by driving the predation rate of a keystone species. This is consistent with results reported by Dahlhoff et al. (2001), suggesting that aerial physiological stress modifies activity of another intertidal predator, a carnivorous snail. The physiological mechanisms underlying our results are not known, although exposure to air during low tide often incurs physiological costs in intertidal organisms (Newell 1973; Somero 2002). It is unlikely that thermal conditions altered the ability of sea stars to forage (i.e., underwater movement) because they were in relatively small tanks and as such they were always very close to prey. It has been suggested recently that this predator responds behaviorally to thermal stress, but not physiologically (i.e., no differential production of heat shock proteins with increasing vertical height on the shore; Petes et al. 2008), making it quite sensitive to prolonged exposures if it does not thermoregulate by moving to more favorable locations.

The upper vertical distribution limit of many intertidal species has been traditionally thought to be set by abiotic conditions (e.g., temperature) that become intolerable for a given organism at a given vertical height in the intertidal zone (Connell 1972; Stillman 2002; Davenport and Davenport 2005). This is especially true in the case of sessile and sedentary organisms for which the occurrence of mortality events during extreme thermal periods sets the upper vertical limit of intertidal distributions (Wolcott 1973; Chan et al. 2006). Thermal stress is also thought to determine the vertical range of mobile species such as *P. ochraceus* (Paine 1966, 1974; Robles et al. 1995). Our results suggest, however, that the upper foraging limit of *P. ochraceus* may not be set directly by intolerable levels of environmental conditions, at least at Bodega Bay, since body temperatures never approached the lethal threshold. Rather, *P. ochraceus* was often located in zones where it experienced relatively elevated body temperatures (about 27°C) for short periods of time (1–3 d), and it did not remain in locations where it would likely have suffered from chronic exposure to warm body temperatures (e.g., in the upper midintertidal during spring months). The upper vertical limit of mobile predators may therefore reflect that tidal height that minimizes chronic exposure to sublethal stress (with negative effects on growth), in favor of a tidal height that combines easy access to prey (middle of the mussel bed, see Fig. 3B) with a tolerable exposure to acute thermal events. Consequently, predation pressure might be high at the lower mussel edge during spring, since sea stars were located right below the mussel bed, whereas predation pressure could extend higher into the mussel bed during summer in the Bodega Bay region (see Fig. 3). This broadening of perspective to include behavioral choices that may maximize fitness (rather than those that simply avoid lethal conditions) has important consequences for predicting the indirect effects of climate variations on prey distribution through the effects on their mobile consumers.

References

- BEIRAS, R., A. PÉREZ CAMACHO, AND M. ALBENTOSA. 1995. Short-term and long-term alterations in the energy budget of young oyster *Ostrea edulis* L. in response to temperature change. *J. Exp. Mar. Biol. Ecol.* **186**: 221–236.
- BENGTSSON, J. 1998. Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *App. Soil Ecol.* **10**: 191–199.
- BISHOP, M. J., AND C. H. PETERSON. 2006. Direct effects of physical stress can be counteracted by indirect benefits: Oyster growth on a tidal elevation gradient. *Oecologia* **147**: 426–433.
- CHAN, B. K. K., D. MORRITT, M. DE PIRRO, K. M. Y. LEUNG, AND G. A. WILLIAMS. 2006. Summer mortality: Effects on the distribution and abundance of the acorn barnacle *Tetraclita japonica* on tropical shores. *Mar. Ecol. Prog. Ser.* **328**: 195–204.
- CONNELL, J. H. 1972. Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.* **3**: 169–192.
- DAHLHOFF, E. P., L. A. BUCKLEY, AND B. A. MENGE. 2001. Physiology of the rocky intertidal predator *Nucella ostrina* along an environmental stress gradient. *Ecology* **82**: 2816–2829.
- DAVENPORT, J., AND J. L. DAVENPORT. 2005. Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. *Mar. Ecol. Prog. Ser.* **292**: 41–50.
- DAVIS, A. J., J. H. LAWTON, B. SHORROCKS, AND L. S. JENKINSON. 1998. Individualistic responses invalidate simple physiological models of community dynamics under global environmental change. *J. Anim. Ecol.* **67**: 600–612.
- DENNY, M., L. P. MILLER, AND C. D. G. HARLEY. 2006. Thermal stress on intertidal limpets: Long-term hindcasts and lethal limits. *J. Exp. Biol.* **209**: 2420–2431.
- FEDER, H. M. 1956. Natural history studies on the starfish *Pisaster ochraceus* (Brandt, 1835) in the Monterey Bay area. Ph.D. thesis. Stanford Univ.
- FERGUSON, J. C. 1992. The function of the madreporite in body fluid volume maintenance by an intertidal starfish, *Pisaster ochraceus*. *Biol. Bull.* **183**: 482–489.
- GOTELLI, N. J., AND A. M. ELLISON. 2004. A primer of ecological statistics. Sinauer Associates.
- HELMUTH, B., C. D. G. HARLEY, P. HALPIN, M. O'DONNELL, G. E. HOFMANN, AND C. BLANCHETTE. 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* **298**: 1015–1017.
- , N. MIESZKOWSKA, P. MOORE, AND S. J. HAWKINS. 2006a. Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 373–404.
- , AND OTHERS. 2006b. Mosaic patterns of thermal stress in the rocky intertidal zone: Implications for climate change. *Ecol. Monogr.* **76**: 461–479.
- HOCHACHKA, P. W., AND G. N. SOMERO. 2002. Biochemical adaptation: Mechanism and process in physiological evolution. Oxford Univ. Press.
- LANDENBERGER, D. E. 1968. Studies on selective feeding in the Pacific starfish *Pisaster* in Southern California. *Ecology* **49**: 1062–1075.
- . 1969. Effects of exposure to air on Pacific starfish and its relationship to distribution. *Physiol. Zool.* **42**: 220–230.
- MENGE, B. A. 2000. Top-down and bottom-up regulation of marine rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* **250**: 257–289.

- , E. L. BERLOW, C. BLANCHETTE, S. A. NAVARRETE, AND S. B. YAMADA. 1994. The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.* **64**: 249–286.
- , A. M. OLSON, AND E. DAHLHOFF. 2002. Environmental stress, bottom-up effects, and community dynamics: Integrating molecular-physiological with ecological approaches. *Integr. Comp. Biol.* **42**: 892–908.
- , AND J. P. SUTHERLAND. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* **130**: 730–757.
- , AND OTHERS. 2004. Species interaction strength: Testing model predictions along an upwelling gradient. *Ecol. Monogr.* **74**: 663–684.
- NEWELL, R. C. 1973. Factors affecting the respiration of intertidal invertebrates. *Am. Zool.* **13**: 513–528.
- PAINE, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* **100**: 65–75.
- . 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* **15**: 93–120.
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669.
- PETES, L. E., B. MENGE, AND G. D. MURPHY. 2007. Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. *J. Exp. Mar. Biol. Ecol.* **351**: 83–91.
- , M. E. MOUCHKA, R. H. MILSTON-CLEMENTS, T. S. MOMODA, AND B. A. MENGE. 2008. Effects of environmental stress on intertidal mussels and their sea star predators. *Oecologia* **156**: 671–680.
- PERRY, A. L., P. J. LOW, J. R. ELLIS, AND J. D. REYNOLDS. 2005. Climate change and distribution shifts in marine fishes. *Science* **308**: 1912–1915.
- POWER, M. E., AND OTHERS. 1996. Challenges in the quest for keystones. *Bioscience* **46**: 609–620.
- QUIGLEY, J. T., AND S. G. HINCH. 2006. Effects of rapid experimental temperature increases on acute physiological stress and behaviour of stream dwelling juvenile chinook salmon. *J. Therm. Biol.* **31**: 429–441.
- ROBLES, C., R. SHERWOOD-STEPHENS, AND M. ALVARADO. 1995. Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* **76**: 565–579.
- SANFORD, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* **283**: 2095–2097.
- . 2002a. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. *Integr. Comp. Biol.* **42**: 881–891.
- . 2002b. 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.
- SOMERO, G. N. 1995. Proteins and temperature. *Annu. Rev. Physiol.* **57**: 43–68.
- . 2002. Thermal physiology and vertical zonation of intertidal animals: Optima, limits, and costs of living. *Integr. Comp. Biol.* **42**: 780–789.
- SOUTHWARD, A. J. 1958. Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. *J. Mar. Biol. Assoc. UK* **37**: 49–66.
- STILLMAN, J. H. 2002. Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, genus *Petrolisthes*. *Integr. Comp. Biol.* **42**: 790–796.
- , AND G. N. SOMERO. 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.
- VOIGT, W., AND OTHERS. 2003. Trophic levels are differentially sensitive to climate. *Ecology* **84**: 2444–2453.
- WILLIAMS, G. A. 1994. The relationship between shade and molluscan grazing in structuring communities on a moderately-exposed tropical rocky shore. *J. Exp. Mar. Biol. Ecol.* **178**: 79–95.
- , M. DE PIRRO, K. M. Y. LEUNG, AND D. MORRITT. 2005. Physiological responses to heat stress on a tropical shore: The benefits of mushrooming behaviour in the limpet *Cellana grata*. *Mar. Ecol. Prog. Ser.* **292**: 213–224.
- WOLCOTT, T. G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): A critical look at “limiting factors”. *Biol. Bull.* **145**: 389–422.
- ZAR, J. H. 1998. *Biostatistical analysis*, 4th ed. Prentice-Hall.

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