



Shore-level size gradients and thermal refuge use in the predatory sea star *Pisaster ochraceus*: the role of environmental stressors

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ABSTRACT: The body size of a mobile intertidal invertebrate can determine its access to different microhabitats, and thus alter its exposure to environmental stressors. We surveyed a rocky intertidal keystone predator, the sea star *Pisaster ochraceus*, and characterized size-dependent distribution, defined by individuals' shore level and refuge use. At 2 field sites (in California and Oregon, USA) we examined temporal and geographical variability in habitat selection. We evaluated the hypothesis that environmental drivers measured on-site and body temperatures measured using biomimetic sensors (i.e. 'robo-sea stars'), explained the observed distribution patterns, including shore-level size gradients, with larger animals lower on the shore. We tested the effect of size on animals' thermo- and desiccation-tolerance. Using robo-sea star data, thermal performance curves and critical temperatures of different size classes, we investigated potential physiological and survival consequences of microhabitat use (shaded vs. sun-exposed). *Pisaster* is mostly found in thermal refugia during low tide even when the risk of thermal stress in sun-exposed areas is low, suggesting a risk-avoidance strategy. In sheltered microhabitats, *Pisaster* exhibited shore-level size gradients; in sun-exposed microhabitats, this pattern disappeared. The proportion of individuals found in shaded microhabitats increased with air temperature, solar radiation, and body temperature. Size-dependent sensitivity to stressful temperatures and wind speed did not explain the observed distribution patterns, suggesting that in the field, size constraints prevent larger animals from occupying refuges that small individuals can use. Our data reveal that, despite generally mild conditions, *Pisaster* risk-avoidance strategy buffers against rare but potentially highly stressful events.

KEY WORDS: Ecology · Physiology · Rocky intertidal · Environmental stress · Climate change · Temperature · Desiccation · Solar radiation · Body size · Behavior

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INTRODUCTION

A variety of mobile intertidal species exhibit shore-level gradients in body size. Several hypotheses have been put forward to explain these patterns, each of which yield different predictions of whether smaller individuals should be more common higher on the shore, or lower on the shore. Vermeij (1972) found

that smaller individuals of shelled gastropod species common to the low intertidal zone were typically found only at higher shore elevations, presumably because predation and competition pressures on those vulnerable individuals decrease at those heights (see also Paine 1969). Bertness (1977) provided evidence that energy maximization played a role for the predatory snails *Nucella* spp. that chose

shore heights based on their preference for consuming specific prey sizes. In contrast, shore-level size gradients in some grazing gastropods appear to be related to environmental stress gradients. Frank (1965) argued that differential sensitivity to temperature and desiccation between size classes leads to larger limpets *Lottia digitalis* occurring higher on the shore. In contrast, studying the topshell snail *Oxytele variegata*, McQuaid (1982) noted that higher desiccation experienced by smaller individuals due to their increased surface area to volume ratio prevents these individuals from occupying higher shore levels, as larger ones do. Raffaelli & Hughes (1978) showed that the availability and size of refuges can drive size gradients across the intertidal zone in *Littorina* spp. snails.

Here, we examined microhabitat use by a keystone predator, the rocky intertidal sea star *Pisaster ochraceus* (Brandt, 1835) (hereafter, *Pisaster*) in order to distinguish among alternative mechanisms responsible for shore-level size gradients. Because of its role as a keystone predator, *Pisaster* has been the subject of extensive ecological and physiological research (e.g. Paine 1966, 1974, Robles et al. 1995, Sanford 1999). *Pisaster* inhabits wave-exposed rocky shores on the Pacific coast of North America, where cyclic tides, recurrent upwelling, and topographic complexity set the scene for an extremely heterogeneous thermal environment (Helmuth & Hofmann 2001, Broitman et al. 2009, Jackson 2010).

The impact of *Pisaster* on populations of its main prey, the mussel *Mytilus californianus*, is indirectly mediated by body temperatures experienced during periods of low and high tide (Sanford 1999, Pincebourde et al. 2008). *Pisaster* forages during submersion at high tide, and then either retreats to a shelter prior to emersion at low tide or else remains in place, continuing to ingest its prey (Robles et al. 1995). As a result, depending on where a sea star finds itself when the tide recedes, it can either be exposed to potentially stressful thermal and desiccation stresses, or protected in crevices, tide pools, or under algae (Burnaford & Vasquez 2008, Fly et al. 2012). Being exposed to waves while foraging at high tide may also imply having to cope with the impact of wave-generated forces (Denny et al. 1985). Previous studies have observed shore-level size gradients in *Pisaster*, with larger individuals found lower on the shore (Feder 1956, Fly et al. 2012). Unlike other smaller species, however, the size range of *Pisaster* (~0.1 to 20 cm arm length) is quite large and in some cases similar to that of the physical habitat. Thus, a microhabitat that may serve as an effective refuge for

a small animal may be inaccessible to a larger individual (Raffaelli & Hughes 1978, Gedan et al. 2011). Additionally, these highly mobile animals can travel several meters per day during high tide (Robles et al. 1995), and individuals can thus be found at different elevations (from shallow subtidal to mid-high intertidal; Pincebourde et al. 2008, Garza & Robles 2010), implying exposure to different degrees of physical stress (Marshall et al. 2013).

Here, we approached the issue through both field- and laboratory-based observations. First, using data from repeated field surveys (2010–2012) conducted at 2 sites 770 km apart, we characterized *Pisaster* refuge use and shore level to assess how consistent patterns were through space and time. Second, we tested whether the variability in these patterns could be explained by changes in environmental drivers (air temperature, seawater temperature, solar radiation, wind speed, and wave action) or by their cumulative impacts on body temperature. Third, we conducted laboratory experiments to determine whether differences in thermo- and desiccation-tolerance between size classes can explain the observed pattern. According to the oxygen-limitation hypothesis (Pörtner 2002, 2006), and supporting evidence (Peck et al. 2009, 2013), we hypothesized that smaller individuals can withstand higher temperatures than larger ones because they have a proportionately larger respiratory surface area relative to volume of tissue.

One might also expect that the larger surface area to volume ratio exhibited by small animals would increase water loss during exposure to wind, with a consequent reduction in performance, relative to larger individuals (Stevenson 1985, Allen et al. 2012). However, previous accounts for *Pisaster* (Feder 1956, Landenberger 1969) have suggested that this may not be the case. Feder (1956) found that smaller *Pisaster* are not more vulnerable to losing water through evaporation, nor of showing earlier signs of physical distress (i.e. body wall flattening, failure of tube feet to attach) (Landenberger 1969). To test the hypothesis that size does not have a strong effect on desiccation tolerance, we exposed individuals to a constant wind speed that paralleled average *in situ* measurements made during a representative low-tide period, and measured performance during simulated high tides.

The relevant hypotheses depend on small-scale differences in temperature, but there are almost no records from the exact spots occupied or avoided by *Pisaster* over the course of the tides. We met this need with biomimetic temperature loggers ('robo-sea

stars'). Using these approaches, we aimed to determine the mechanisms driving patterns of distribution in *Pisaster*, and their role in defining zonation patterns. As previously recognized, *Pisaster* upper shore limits at low tide are set by high air temperatures (Robles et al. 1995), a process that is likely mediated by sublethal effects of temperature on physiological performance (Pincebourde et al. 2008, Robles 2013). Because vertical movement may imply increased energy expenditure to cope with physiological thermal stress (either acute or chronic, *sensu* Pincebourde et al. 2008), we expected *Pisaster* to behaviorally compensate for these costs by preferentially seeking protected microhabitats.

MATERIALS AND METHODS

Study sites

We conducted field surveys at 2 study sites: Strawberry Hill (44° 14' 59.4" N, 124° 06' 54.7" W, Oregon, USA), and Bodega Marine Reserve (38° 19' 07.7" N, 123° 04' 27.0" W, California, USA), separated by ~770 km of coastline. We limited our analysis to wave-exposed rocky shores, where this keystone predator plays a more critical ecological role (Paine 1966, 1974, Menge et al. 1994, Power et al. 1996). Both sites had dense mid-intertidal mussel beds and were topographically complex, providing alternative microhabitats for sea stars to occupy, including crevices, tide pools, kelps, and open spaces. At the time of the surveys, wasting disease (Hewson et al. 2014) had not yet affected populations, and abundances at all sites were high.

Intertidal distribution surveys

To describe *Pisaster* microhabitat use (shore level and refuge use) at each study site and survey date, we sampled every individual encountered along 5 belt-transects (2 m wide), placed non-randomly 1 m apart and perpendicular to the coastline. Transects extended from the height of the highest *Pisaster* individual found to the low water level limit set by the spring tide. We conducted all surveys during the time of negative tide heights, as predicted by NOAA (stations 9435380 and 9415020 for Strawberry Hill and Bodega, respectively). For each sea star, we recorded body size and microhabitat use. We determined size from wet weight measurements taken with a portable balance (Ohaus SP202, 200 g)

or a spring scale (Pesola, 1000 g), depending on the animal's size. We characterized the microhabitat by (1) shore level (cm above MLLW), measured using a surveying laser level (Topcon), and (2) refuge use, which was designated as either heat-protected (i.e. crevice, tide pool, under kelp) or sun-exposed (i.e. flat, receiving solar radiation). We used regression analysis to determine shore-level size gradients from the data collected during each survey (see 'Statistical analyses' below).

To evaluate temporal dynamics in sea star distribution patterns, we surveyed Strawberry Hill and Bodega on multiple spring tide periods during the summer of 2012 (Strawberry Hill: 24 May, 22 June, 20 July, and 3 August; Bodega: 22 May, 8 June, 20 June, 19 July, and 1 August). Bodega was additionally surveyed during the summers of 2010 (2, 16, and 28 June) and 2011 (19 May, 4 June, 15 June, 1 July, and 14 July); thus inter-annual comparisons could be performed. To examine spatial variability, we compared data between sites collected in the same year (2012).

Population density and foraging activity

The intertidal distribution surveys were additionally used to quantify population densities at both sites and to describe foraging activity. During 2011 and 2012 at Bodega, and 2012 at Strawberry Hill, we recorded (1) whether sea stars were found consuming mussels (i.e. digesting with stomach everted), and (2) distance to closest mussel bed edge.

Influence of environmental drivers

We examined the effect of changes in relevant environmental variables on the intertidal distribution patterns (shore-level size gradients and refuge use) exhibited by *Pisaster*. We tested the effects of seawater temperature (Sanford 1999), air temperature (Pincebourde et al. 2008), wind speed (Landenberger 1969), wave action (Sanford 2002), and solar radiation (Burnaford & Vasquez 2008), since all have been shown to affect sea star physiology, body temperature, and/or behavior (Szathmary et al. 2009). We used data collected hourly by a weather station (200 m from the survey area) and associated wave height radar and seawater temperature sensors maintained by the Bodega Ocean Observing Node (www.bml.ucdavis.edu/boon/). Because on-site data were not available for Strawberry Hill, we

conducted this analysis only for Bodega. We manipulated the data series as follows. First, we used aerial data corresponding to 1 d prior to each population survey, since aerial conditions would have had their impact during the previous day's aerial exposure (Szathmary et al. 2009). We only used seawater temperature and wave height data recorded during high tide periods (>1 m above MLLW), and only used air temperature, wind speed, and solar radiation data recorded during low tide periods (≤ 1 m above MLLW). For each driver, we determined the daily maxima, which were regressed against our field observations of *Pisaster* distribution.

The analysis addressed 2 main elements of *Pisaster* distribution that could potentially depend on environmental variability. First, we looked for relationships between shore-level size gradients and the 5 environmental drivers; second, we tested whether these drivers explained changes in refuge use.

Size-dependent aerial thermotolerance: laboratory experiment

To evaluate the effect of *Pisaster* body size on its aerial thermotolerance, we conducted experiments to estimate the lethal temperature (LT_{50} , temperature at which 50% of the individuals die) of 2 size classes, small (25–75 g, $N = 34$) and large (250–400 g, $N = 33$). We ran these experiments in July 2011, at the Bodega Marine Laboratory (BML, University of California – Davis).

We collected the *Pisaster* at Bodega, and held them in tanks with running seawater and food (*Mytilus californianus*) provided ad libitum. We withdrew their food supply 24 h before the start of the experiment to standardize physiological condition. Before beginning the experimental treatments, we recorded each individual's wet weight. We placed specimens (up to 2, avoiding contact between them) on gray acrylic platforms positioned 25 cm above the bottom of 75 l tanks. Below the platform, we provided a constant stream of seawater to maintain high levels of ambient humidity. A heat lamp (150 W) was used to adjust animals' temperature during each trial. Using an infrared thermometer (Model OS36, Omega), we measured the surface temperature of each individual's central disc every 15 min. We ran each trial for 6 h. During the first 3 h, we gradually increased body temperature from ambient seawater temperature ($\sim 12^\circ\text{C}$) to the treatment temperatures (24–40°C, in 2°C increments). During the last 3 h, we maintained the treatment

temperature at constant levels. At the end of 6 h, animals were returned to running seawater at 12°C. Survival was assessed after 24 h in running seawater by probing the tube feet and evaluating their response.

Size-dependent desiccation tolerance: laboratory experiment

To evaluate the effect of *Pisaster* body size on its tolerance to desiccation, we quantified the performance of individuals ranging in size (7.1–780.1 g, $N = 26$) after consecutive, 6 h daily exposures to wind of 3.5–4.0 m s⁻¹. We ran these experiments during July 2011 at BML.

We collected and prepared the animals as described for the thermotolerance experiment. We determined each individual's performance on 4 consecutive days: (1) Day 0, 1 d prior to beginning the experiment, which defined a baseline; (2) Day 1, after a first exposure to the wind treatment; (3) Day 2, after a second wind exposure; and (4) Day 3, after a final, third wind exposure. We assessed performance based on righting response time (*RT*; seconds), the length of time required to move to an upright position. We calculated an activity coefficient: $AC = 1000/RT$ (Lawrence & Cowell 1996). The mean *AC* from Days 1, 2, and 3 was subtracted from the Day 0 reference *AC* of each individual, thus obtaining a relative measure of the effect of desiccation. These data were modified by adding a positive offset value in order to have only positive numbers, which were then analyzed in relation to body size.

Robo-sea star temperature records

To assess the temperatures individuals would experience in different microhabitats (potential body temperature), we used biomimetic temperature loggers (iButton DS1922, 0.0625°C resolution) embedded within a solid disc of foam (Aquazone single cell, Reilly Foam) to resemble the thermal properties of an average size *Pisaster*, ~ 200 g (Szathmary et al. 2009). We deployed the sensors (robo-sea stars) at Strawberry Hill and Bodega during the summer of 2012, and continuously recorded (15 min sampling interval) *Pisaster* body temperature in sun-exposed (high, mid-, and low intertidal heights) and heat-protected microhabitats (crevices and tide pools).

Physiological performance and survival consequences of body temperature

We used the robo-sea star temperature data to evaluate the physiological implications, as well as potential mortality effects, of selecting each microhabitat type. Physiological consequences were quantified based on a *Pisaster* thermal performance curve (Monaco et al. 2014), to calculate the temperature dependence of respiration rates (a proxy for physiological performance). Mortality was estimated from cumulative survival curves for each microhabitat type, size class, and site. The cumulative probability of survival was calculated daily using the exponential function, based on estimates from the LT_{50} logistic models.

Statistical analyses

All statistical analyses were conducted using R 3.0.1 (R Core Team 2013). To determine the effect of body size on individuals' intertidal height (i.e. shore-level size gradients) we ran regression analyses using data collected during each survey (e.g. Bertness 1977, Hobday 1995). To test whether microhabitat use would change the nature of these relationships, microhabitat type was included in the models as a categorical variable. Due to lack of normality in the data, we used generalized linear models (GLMs) and generalized linear mixed effects models when appropriate, assuming gamma (modified with 'identity' link function) error distributions, which yielded the lowest dispersion (determined using the 'gamma.dispersion' function from the MASS package in R). Because the sample sizes were unbalanced between surveys, we computed significance of model parameters via likelihood ratio tests (LRTs) using Type II sums of squares. We checked for homogeneity of variances by visual inspections of diagnostic plots of residuals vs. fitted data (R package car; <http://CRAN.R-project.org/package=car>).

To determine whether shore-level size gradients and refuge use patterns varied among survey dates (i.e. temporal variability) at each site and year, we ran ANCOVAs with date as the main factor. We did not combine data from different years because population densities varied annually. To examine whether shore-level size gradients and microhabitat use patterns varied between sites, we ran ANCOVAs with site as the main factor, using data from 2012 because surveys at Strawberry Hill were only conducted that year.

To examine the relationships between shore-level size gradients and daily maxima of the 5 environmental drivers, we ran multiple regression analyses, where the slope of the regression lines between *Pisaster* intertidal height and wet weight (see Table 1) was the response variable (weighted by the inverse of their associated SE), and all 5 drivers were treated as independent variables. We tested whether these drivers explained changes in the proportion of individuals found in sun-exposed microhabitats during low-tide surveys (i.e. refuge use) using multiple logistic regressions, treating exposure (heat-protected/sun-exposed) as response and the 5 environmental drivers as independent variables. Air temperature and solar radiation were collinear (variance inflation factor >10; Quinn & Keough 2002). To avoid collinearity problems, we ran the regressions twice, once including air temperature and excluding solar radiation, and vice versa.

We compared *Pisaster* population density data and distance to mussel beds between sites using Wilcoxon rank-sum tests. To evaluate the effect of site on the proportion of *M. californianus* found in the diet of *Pisaster*, we used GLM with binomial error distributions and computed the significance of model parameters via LRT.

Pisaster thermotolerance survival data for each size class were fitted using logistic regression models estimated by GLMs with binomial error distributions. We determined LT_{50} s from these models, and compared them using a 1-tailed *z*-score test (Quinn & Keough 2002).

The relationship between body size and *Pisaster* relative performance after desiccation (wind) was described by a 2-parameter asymptotic exponential model. The asymptote of the fitted curve was the size at which performance was least affected by desiccation. Individuals performing below 2 SEs of the asymptote were regarded as significantly affected by desiccation.

To compare the temperature time series obtained from the robo-sea stars at different tidal elevations and microhabitat types, we calculated mean absolute errors (MAEs) and ran paired *t*-tests using daily maximum values. For each site, we used the high intertidal sun-exposed robo-sea star (expected to have the highest temperatures) as the reference time series against which all other robo-sea stars were compared. Physiological implications of selecting each microhabitat were quantified using a thermal performance curve for *Pisaster* (Monaco et al. 2014). Using the thermal performance breadth parameter (17.2–23.8°C, i.e. the temperature range where per-

formance is $\geq 69\%$ of maximum; Sharpe & DeMichele 1977), we calculated the percentage of time *Pisaster* would have spent below, above, and within that range at each microhabitat. Potential mortality effects of body temperature were evaluated based on cumulative survival curves for each microhabitat, size class, and site. We calculated survival using the logistic functions modeled from our size-dependent thermotolerance experiments, and the robo-sea stars' temperature records.

RESULTS

Pisaster intertidal distribution

Year-to-year changes in *Pisaster* demographics (density and size-frequency distribution) at Bodega were large (mean density 2011: 0.52 m^{-2} , 2012: 0.01 m^{-2}). Therefore, we grouped the data by year and site, and examined temporal dynamics occurring among survey dates. The relationships between intertidal height, refuge use, and body size in *Pisaster* were highly variable (Table 1 and see Figs. S1 & S2 in the Supplement, available at www.int-res.com/articles/suppl/m539p191_supp.pdf), although some generalizations could be made. We provide specific findings below.

Most individuals were found protected from the sun either in crevices, tide pools, or under algae (Table 1). We found extensive evidence for shore-level size gradients. At Bodega, in 8 of 12 surveys from 2010 to 2012, there was a negative relationship between body size and shore height in heat-protected microhabitats (Table 1). In sun-exposed microhabitats, we found no relationship between body size and shore height in 11 of 12 surveys (Table 1). In the remaining case in sun-exposed microhabitats, there was a positive relationship. At Strawberry Hill, the patterns were less clear. In 2 of 4 cases in heat-protected microhabitats, significant relationships were evident between body size and shore level, but 1 relationship was positive and the other negative. In no case was there a relationship in sun-exposed microhabitats at Strawberry Hill (Table 1).

Table 1. *Pisaster ochraceus* size-dependent distribution. Regression lines were fitted using a generalized linear model (gamma error distribution). NaN indicates that the parameter could not be calculated because no individual was found in that location. Significance of model parameters were computed via likelihood ratio tests (LRTs) using Type II sums of squares. HP: heat-protected, SE: sun-exposed; * $p < 0.05$, ** $p < 0.01$; date: mo/d/yr

Site/ survey date	Micro- habitat	N	% at micro- habitat	Slope mean \pm SE	p
Strawberry Hill, OR					
05/24/2012	HP	49	62.82	-0.147 ± 0.021	0.008**
	SE	29	37.18	0.089 ± 0.059	0.129
06/22/2012	HP	37	71.15	0.091 ± 0.061	0.205
	SE	15	28.85	0.019 ± 0.070	0.789
07/20/2012	HP	49	63.64	0.126 ± 0.052	0.042*
	SE	28	36.36	-0.022 ± 0.044	0.659
08/03/2012	HP	66	92.96	0.027 ± 0.037	0.518
	SE	5	7.04	0.181 ± 0.179	0.246
Bodega Marine Reserve, CA					
06/02/2010	HP	198	71.22	-0.021 ± 0.015	0.156
	SE	80	28.78	-0.003 ± 0.025	0.908
06/16/2010	HP	234	84.78	-0.054 ± 0.012	0.000**
	SE	42	15.22	-0.015 ± 0.023	0.488
06/28/2010	HP	267	88.41	-0.023 ± 0.009	0.010**
	SE	35	11.59	-0.004 ± 0.016	0.791
05/19/2011	HP	107	74.31	-0.058 ± 0.022	0.007**
	SE	37	25.69	0.015 ± 0.039	0.713
06/04/2011	HP	110	77.46	-0.004 ± 0.023	0.871
	SE	32	22.54	0.072 ± 0.024	0.004**
06/15/2011	HP	153	82.26	-0.046 ± 0.015	0.003**
	SE	33	17.74	0.052 ± 0.050	0.314
07/01/2011	HP	160	87.91	-0.062 ± 0.017	0.000**
	SE	22	12.09	-0.046 ± 0.123	0.713
07/14/2011	HP	139	83.23	-0.055 ± 0.017	0.001**
	SE	28	16.77	0.015 ± 0.028	0.595
05/22/2012	HP	37	100.00	-0.027 ± 0.010	0.010*
	SE	0	0	NaN	NaN
06/08/2012	HP	19	100.00	-0.003 ± 0.012	0.804
	SE	0	0	NaN	NaN
06/20/2012	HP	21	84.00	-0.023 ± 0.012	0.034*
	SE	4	16.00	0.040 ± 0.025	0.248
07/19/2012	HP	20	90.91	-0.014 ± 0.013	0.304
	SE	2	9.09	NaN	NaN

Population density and foraging activity

At Strawberry Hill, individual sea stars were found farther from beds of *Mytilus californianus* mussels, their preferred prey, compared to at Bodega (mean \pm SD: $256.7 \pm 207.8 \text{ cm}$ vs. $77.8 \pm 63.3 \text{ cm}$, respectively; Wilcoxon test, $W = 5746.5$, $p < 0.01$). This is possibly a result of the higher population density at Strawberry Hill (mean \pm SD: 3.95 ± 0.86) vs. Bodega (mean \pm SD: 0.31 ± 0.27 ; Wilcoxon test, $W = 0$, $p < 0.05$), and consequently a stronger predation pressure, which would push mussel bed boundaries higher on the shore. At Bodega, where

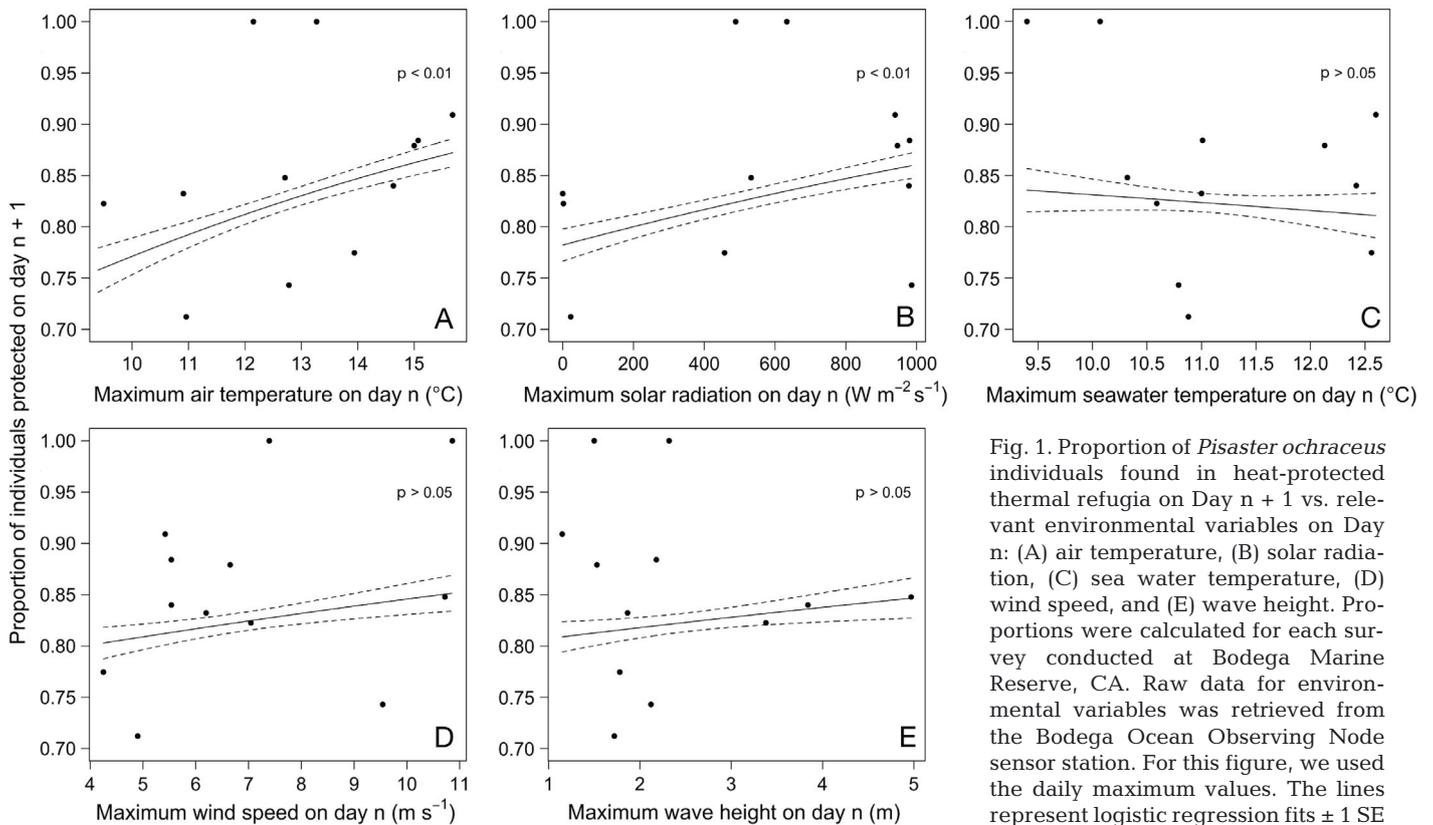


Fig. 1. Proportion of *Pisaster ochraceus* individuals found in heat-protected thermal refugia on Day $n + 1$ vs. relevant environmental variables on Day n : (A) air temperature, (B) solar radiation, (C) sea water temperature, (D) wind speed, and (E) wave height. Proportions were calculated for each survey conducted at Bodega Marine Reserve, CA. Raw data for environmental variables was retrieved from the Bodega Ocean Observing Node sensor station. For this figure, we used the daily maximum values. The lines represent logistic regression fits ± 1 SE

Pisaster were closer to *M. californianus* than at Strawberry Hill, sea stars were found eating proportionally more mussels (mean \pm SD: 0.83 ± 0.29 , 0.31 ± 0.19 , respectively; LRT, $\chi^2 = 58.6$, $df = 1$, $p < 0.01$) than small, less profitable prey (e.g. barnacles). These observations may account for the higher proportion of sun-exposed individuals observed at Strawberry Hill vs. Bodega (see above).

Role of environmental drivers and how they translate to the organism

Contrary to expectations, we observed no relationship between any of the 5 environmental variables (air temperature, solar radiation, seawater temperature, wave height, wind speed) and the shore-level size gradients of *Pisaster* at Bodega. This was true for both heat-protected and sun-exposed individuals (Table S1 in the Supplement). Although the proportion of individuals found in sun-exposed microhabitats was consistently low (Table 1), the proportion of sun-exposed animals was negatively correlated with both air temperature (Fig. 1A; LRT, $\chi^2 = 22.5$, $df = 1$, $p < 0.01$) and solar radiation (Fig. 1B; LRT, $\chi^2 = 12.8$, $df = 1$, $p < 0.01$)

during the day prior to our field population surveys. While the model that included solar radiation as an independent variable did not detect an effect of seawater temperature on *Pisaster* refuge use (Fig. 1C; LRT, $\chi^2 = 1.9$, $df = 1$, $p > 0.05$), the model that considered air temperature revealed a positive influence of seawater temperature (LRT, $\chi^2 = 4.3$, $df = 1$, $p < 0.05$). We detected no relationship between proportion of *Pisaster* in refuge and wave height (Fig. 1E; LRT, $\chi^2 = 0.48$, $df = 1$, $p > 0.05$), or wind speed (Fig. 1D; LRT, $\chi^2 = 0.07$, $df = 1$, $p > 0.05$) recorded during summer months.

Because ectotherm body temperatures are driven by multiple environmental variables (Helmuth 2002, Broitman et al. 2009, Szathmary et al. 2009), we examined the influence of maximum temperatures recorded by robo-sea stars 1 d prior to the surveys. Contrary to expectation, there were no significant relationships between shore-level size gradients and robo-sea star temperatures in low, mid-, and high intertidal heights as measured by the regression slopes in Table 1 (LRT; $p > 0.05$ in all cases). However, there was a positive association between temperatures recorded by robo-sea stars deployed at low (Fig. 2A; LRT, $\chi^2 = 10.2$, $df = 1$, $p < 0.01$) and mid- (Fig. 2B; LRT, $\chi^2 = 17.2$, $df = 1$, $p < 0.01$) intertidal

heights and *Pisaster* refuge use on the next day. There was no association between high intertidal robo-sea star temperature and the proportion of individuals in heat-protected microhabitats (Fig. 2C; LRT, $\chi^2 = 0.2$, $df = 1$, $p = 0.35$). Daily potential body temperature maxima as measured by robo-sea stars were higher than daily air temperature maxima (cf. Figs. 1A & 2; MAE = 3.18°C).

Size-dependent tolerance to thermal and desiccation stress

Contrary to expectation, large *Pisaster* individuals showed a significantly higher median lethal temperature (LT_{50}) than small animals (Fig. 3; mean \pm SE; large = $33.3 \pm 0.9^\circ\text{C}$; small = $31.6 \pm 0.5^\circ\text{C}$; $z = -1.76$; $p = 0.04$).

Consistent with expectation, the effect of wind (and hence desiccation) on the activity coefficient of *Pisaster* depended on individual size (Fig. 4). According to the 2-parameter asymptotic exponential model, all animals smaller than 83.7 g (7 individuals) had significantly reduced performance with respect to the asymptote after exposure to continuous wind during simulated low tide periods. Of 19 individuals larger than 83.7 g treated, only 3 (15.7%) reduced their activity coefficient with respect to the model's asymptote.

Robo-sea star temperature records

Pisaster body temperatures, as determined using robo-sea stars, varied among microhabitats and sites during low tides. We focused on daily temperature maxima due to their importance for individual survival and fitness. At both sites, the high intertidal sun-exposed robo-sea star temperatures were consistently higher than other microhabitats (mean differences; Bodega = 9.05°C ; Strawberry Hill = 2.07°C ; paired t -tests, $p < 0.01$ in all cases) and more variable (mean variance ratios; Bodega = 10.13; Strawberry Hill = 4.58; F -tests, $p < 0.01$ in all cases, except for the low intertidal and tide pool robo-sea stars at Strawberry Hill; Fig. 5). MAE and variance ratios between sun-exposed and heat-protected microhabitats were greater at Bodega than Strawberry Hill (Fig. 5). At Strawberry Hill, the coolest microhabitats were crevices; at Bodega, low intertidal, crevices, and tide pools were coolest (Fig. 5). As a caveat, the relatively high temperatures recorded by low intertidal and tide pool robo-sea stars at Strawberry Hill are likely

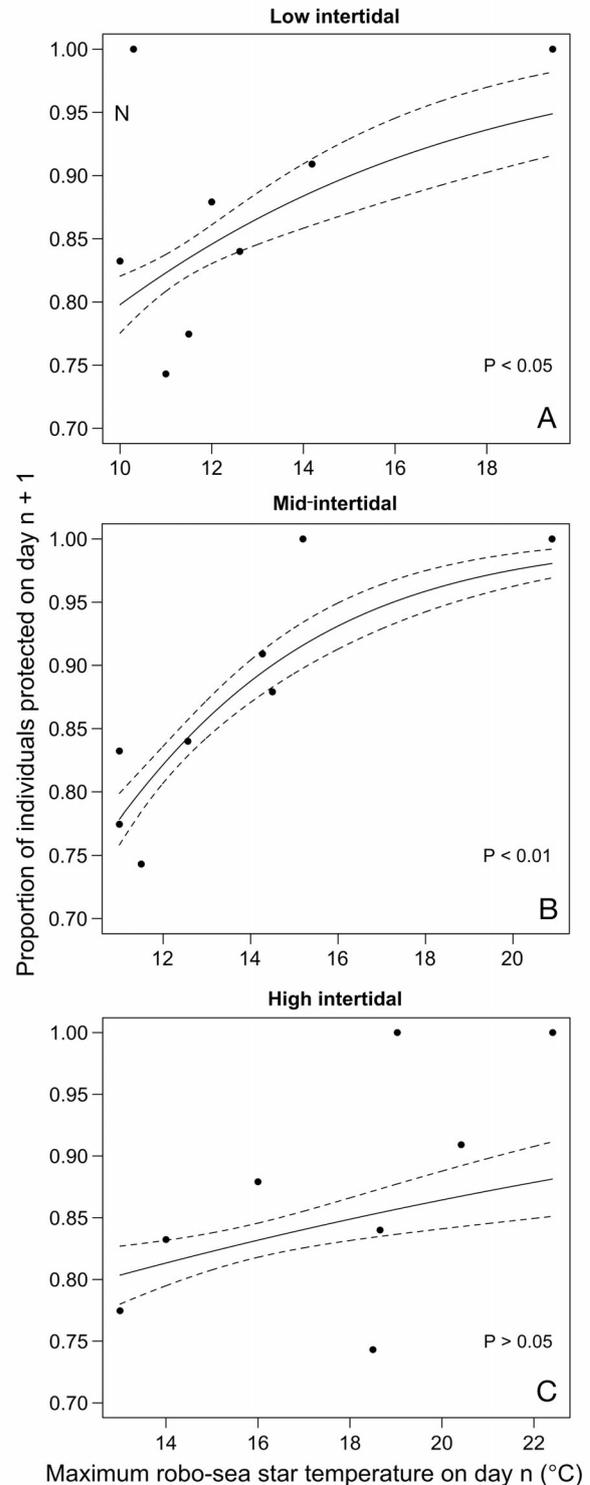


Fig. 2. Proportion of *Pisaster ochraceus* individuals found in heat-protected thermal refugia on Day n + 1 vs. potential maximum body temperatures on Day n experienced at 3 intertidal heights: (A) low, (B) mid, and (C) high (0, 1, and 1.5 m above MLLW, respectively). Data were collected at the Bodega Marine Reserve, CA, in 2011 and 2012. Temperatures were recorded using robo-sea stars. The lines represent logistic regression fits ± 1 SE

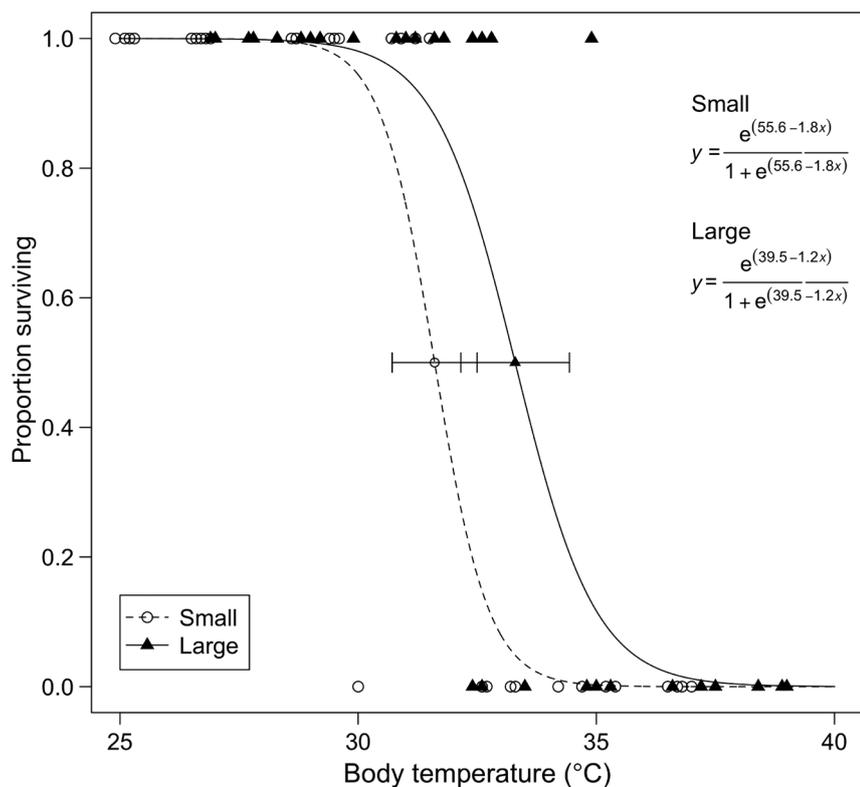


Fig. 3. Proportion of *Pisaster ochraceus* individuals surviving a series of aerial body temperature treatments. Lethal temperatures were experimentally determined for 2 size classes, small (25 to 75 g, N = 34) and large (250–400 g, N = 33), by fitting independent logistic regressions. The body temperatures (\pm SE) at which 50% of individuals die (i.e. LT_{50}) are indicated on each logistic regression line. The logistic model equations for each size class, and their estimated parameter values, are also provided

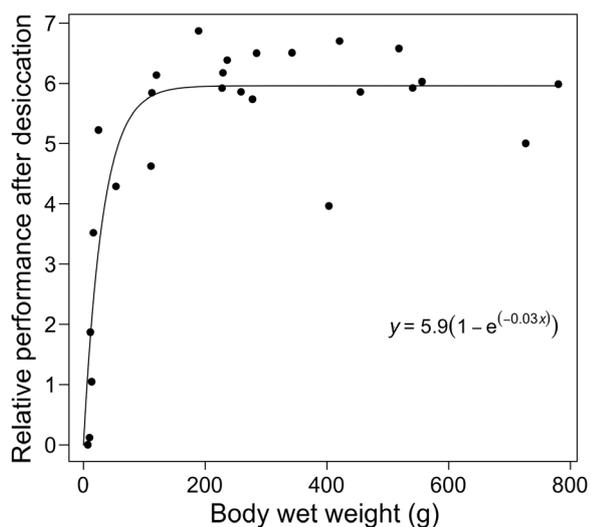


Fig. 4. *Pisaster ochraceus* relative performance after 3 d experiencing simulated 6 h low tide periods with 3–4 $m s^{-1}$ wind speeds, in relation to body size (7.1 to 780.1 g, N = 26). 2-parameter asymptotic exponential model parameters are indicated

explained by their specific location: the former received more solar radiation than the rest, and the latter was in a rather shallow pool which may have heated more than deep ones.

Thermal conditions differed between sites. High intertidal temperatures at Bodega were higher than at Strawberry Hill ($22.5 \pm 4.4^{\circ}C$, vs. $19.9 \pm 3.6^{\circ}C$, mean \pm 1 SD; paired t -test, $t_{47} = -3.44$, $p < 0.01$). In crevices, mean daily maxima were much more similar ($13.4 \pm 1.6^{\circ}C$ at Bodega, $12.8 \pm 1.8^{\circ}C$ at Strawberry Hill; paired t -test, $t_{46} = -2.15$, $p < 0.05$). The variance in daily temperature maxima did not vary with site (F -test, $p > 0.05$ comparing high intertidal and crevice loggers).

Physiological consequences of microhabitat selection

Consistent with our expectation, the percentage of time spent at temperatures above the optimal thermal performance breadth ($>23.8^{\circ}C$) was small, $<5\%$ in every case (Table 2). In mid- and high intertidal microhabitats, *Pisaster* at Bodega experienced slightly more time above this threshold than at Strawberry Hill. However, contrary to expectation, the proportion of time spent within the thermal performance breadth ($17.2\text{--}23.8^{\circ}C$) was also low ($<5\%$) for every microhabitat, except the high intertidal at Strawberry Hill and Bodega, where it reached values of 7.5 and 6.4%, respectively. For all microhabitats at both sites, *Pisaster* spent most of the time ($>90\%$) at body temperatures markedly lower than the optimal thermal performance breadth ($<17.2^{\circ}C$; Table 2, Fig. 5).

Survival probability

The cumulative probability of survival was markedly high at both sites, and for both large and small individuals (Fig. 6). Only the high intertidal zone at Bodega showed potentially risky conditions for large and small *Pisaster*, for which final cumulative survival was 0.87 and 0.59, respectively (Fig. 6B,D).

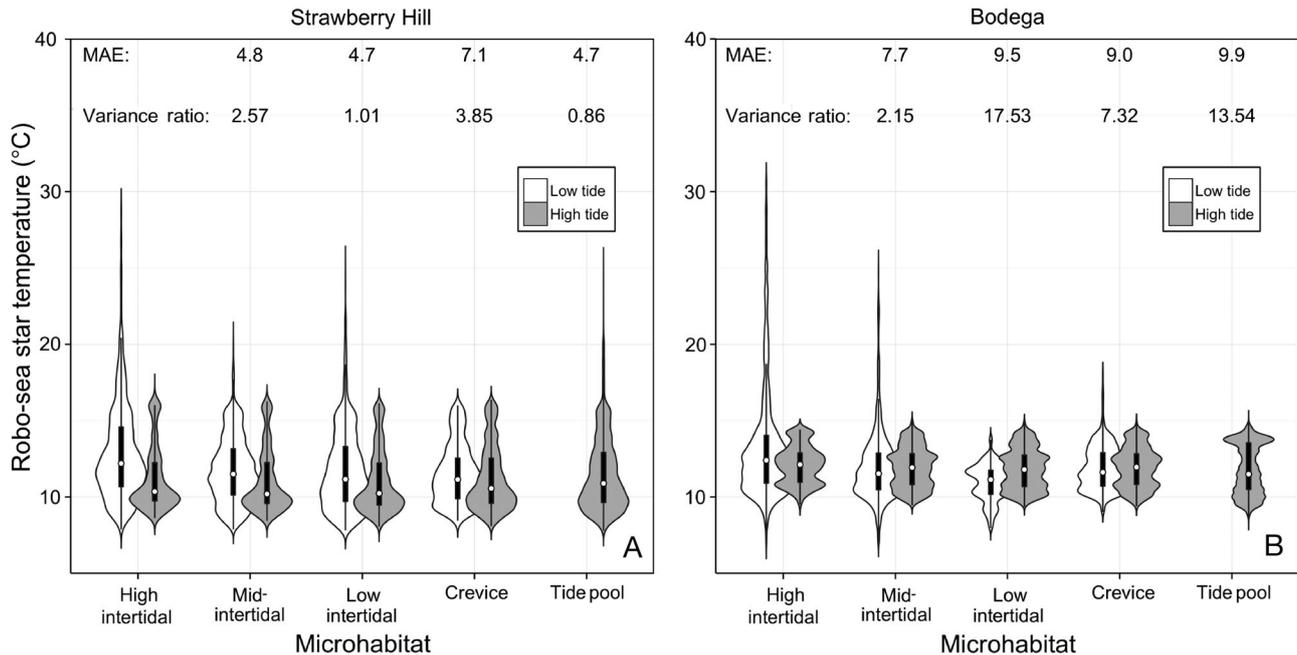


Fig. 5. *Pisaster ochraceus* body temperatures recorded by robo-sea stars (15 min sampling frequency) deployed in 5 different microhabitats at (A) Strawberry Hill, OR, and (B) the Bodega Marine Reserve, CA, between 6 June and 22 August 2012. High, mid-, and low intertidal are sun-exposed, while crevice and tide pool are heat-protected. Data are provided as violin plots with box plots embedded; the line represents the range, the box defines the 25th and 75th% quartile, and the dot represents the median. For each microhabitat, data were split between measurements taken while loggers were exposed to air (white) or submerged under water (gray). Comparisons between daily temperature maxima of each microhabitat and the high intertidal (reference) were made based on mean absolute errors (MAEs), and variance ratios are given. The MAE values were calculated for each microhabitat without discriminating between tide periods

DISCUSSION

This study was designed to test among alternative mechanisms responsible for microhabitat selection and shore-level size gradients. Previous studies have attributed observed patterns to predation risk (Vermeij 1972), preference for prey of a given size based on their energetic profitability (Bertness 1977), differential sensitivity to temperature and desiccation between size classes (Frank 1965), and differences in the risk of desiccation due to the effect of size on surface area to volume ratios (McQuaid 1982). Our results are most consistent with those of Raffaelli & Hughes (1978), who suggested that the availability of refuges can determine shore-level size gradients.

Shore-level size gradients

Consistent with previous work (Feder 1956, Fly et al. 2012), *Pisaster* exhibited shore-level size gradients, with larger individuals found lower on the shore. We found this in 2/3 of surveys of protected animals, but not for animals in sun-exposed microhabitats (Table 1). This pattern varied both temporally and

Table 2. Potential physiological consequences for *Pisaster ochraceus* of occupying different microhabitats. Data represent percentage of time experiencing potential body temperatures (as measured by robo-sea stars) that fall below ($<17.2^{\circ}\text{C}$), within ($17.2\text{--}23.8^{\circ}\text{C}$), and above ($>23.8^{\circ}\text{C}$) *Pisaster* thermal performance breath (69% of maximum performance). Thermal performance breath was determined from a performance curve empirically derived by Monaco et al. (2014)

Site/Microhabitat	% Below	% Within	% Above
Strawberry Hill, OR			
High intertidal	91.33	7.51	1.19
Mid-intertidal	98.88	1.12	0.00
Low intertidal	97.77	2.20	0.03
Crevice	100.00	0.00	0.00
Tide pool	97.76	1.99	0.25
Bodega Marine Reserve, CA			
High intertidal	90.99	6.45	2.56
Mid-intertidal	98.82	1.05	0.13
Low intertidal	99.97	0.03	0.00
Crevice	99.92	0.08	0.00
Tide pool	100.00	0.00	0.00

geographically (Figs. S1 & S2 in the Supplement, Table 1). Given that this species can travel several meters during high tide periods (Robles et al. 1995), it

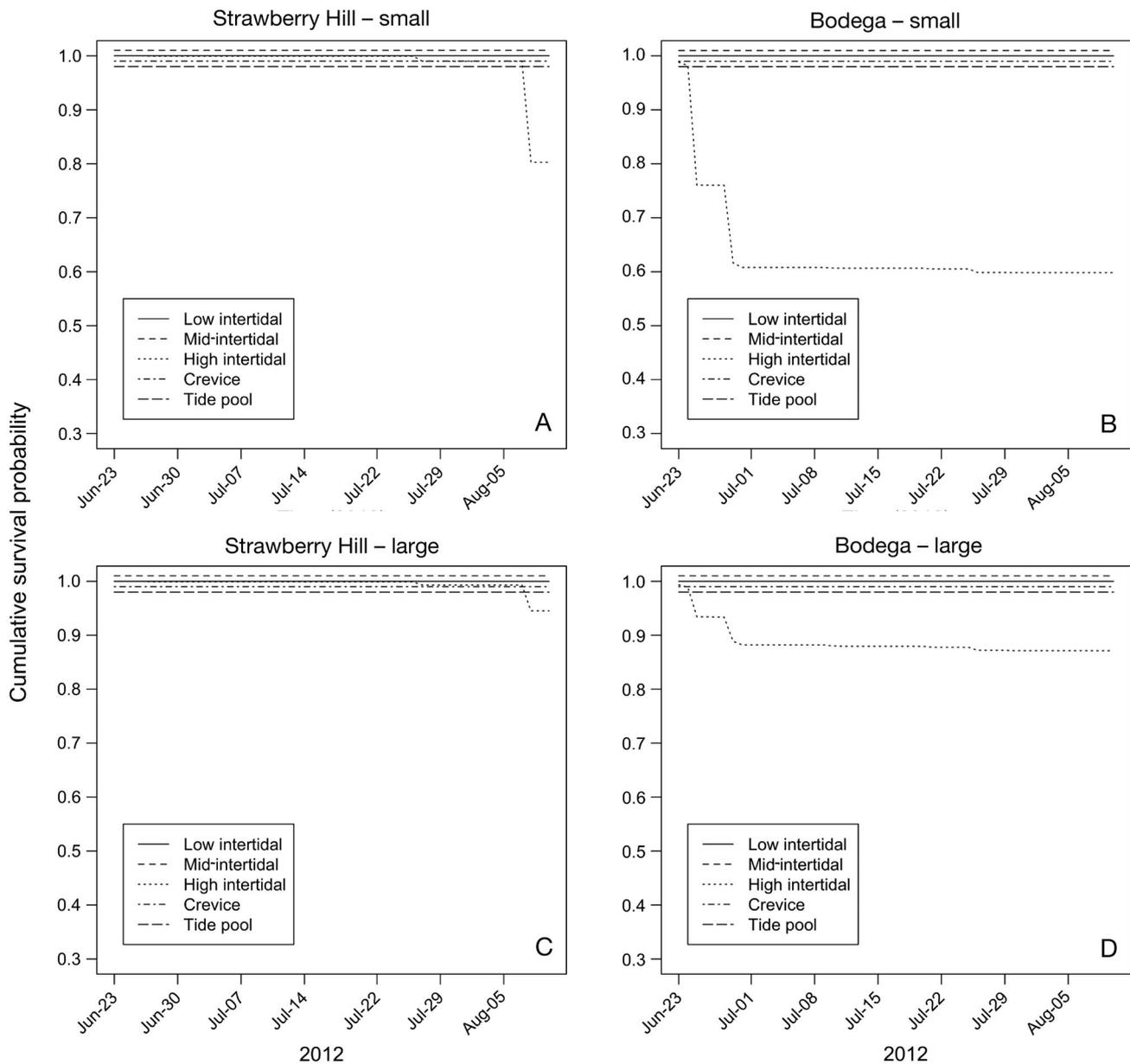


Fig. 6. Cumulative survival curves for hypothetical small (25–75 g) and large (250–500 g) *Pisaster ochraceus* individuals occupying various microhabitats (sun-exposed high, mid-, and low intertidal, and heat-protected in crevices or tide pools) available at the Bodega Marine Reserve, CA, and Strawberry Hill, OR. Survival was calculated based on our empirical estimates of mortality in relation to body temperature (see 'Materials and methods'). We slightly displaced curves that overlapped one another

is not surprising that its distribution patterns changed over time. The bulk of the week-to-week variation (Table 1) was driven by vertical displacements of larger animals (Figs. S1 & S2 in the Supplement). We speculate that 2 main factors determine this phenomenon. First, while submerged during high tide, larger *Pisaster* are more active and travel faster than small individuals (C. Monaco unpubl.). Second, *Pisaster* avoids physical stressors by seeking protection before low tide (Garza & Robles 2010, Robles et al. 1995); however, we suggest that because larger animals can-

not benefit from small crevices, they are often forced to move towards the milder subtidal zone. Therefore, only sheltered animals exhibit shore-level size gradients. Exposed animals are presumably not seeking refuge, and do not exhibit this pattern.

Microhabitat selection

As expected, most *Pisaster* were found in microhabitats protected from the elements (Table 1), which

reinforces the idea that this species avoids physical stressors (Robles et al. 1995, Burnaford & Vasquez 2008, Pincebourde et al. 2008, Garza & Robles 2010, Fly et al. 2012) and possibly predators like gulls (Morris et al. 1980) during low tide. A larger fraction of the *Pisaster* was in sun-exposed microhabitats at Strawberry Hill than Bodega (Table 1). At Strawberry Hill, sea star densities are significantly higher than at Bodega, so predation pressure on *Mytilus californianus* is higher and prey densities are lower. Consequently, *Pisaster* at Strawberry Hill consume fewer *M. californianus*, forage longer, and eat less profitable prey. We suggest that this foraging behavior might explain the longer time spent by Strawberry Hill *Pisaster* in sun-exposed microhabitats during low tides.

Role of microclimate in habitat selection

To estimate the influence of microclimate on habitat selection, we examined the slopes of the regressions between intertidal height and body size (shore-level size gradients), and refuge use (sun-exposed/heat-protected). We found no association between shore-level size gradients and air temperature, solar radiation, seawater temperature, wind speed, or wave height on the previous day (Table S1 in the Supplement). However, the proportion of individuals found in thermal refugia was positively correlated with air temperature and solar radiation on the previous day (Fig. 1).

We also evaluated the effect of body temperatures measured *in situ* using biomimetic loggers (Szathmary et al. 2009). Although body temperature recorded by robo-sea stars were not correlated with shore-level size gradients, they were positively correlated with the fraction of individuals found in heat-protected microhabitats (Fig. 2A,B), consistent with active selection of sheltered microhabitats (Robles et al. 1995, Garza & Robles 2010). Selection of heat-sheltered microclimates may also explain Sanford's (1999) observation that the strength of interaction between *Pisaster* and its prey was not related to air temperature conditions in Oregon.

Body temperatures across microhabitats and potential consequences

To determine physiological consequences of microhabitat selection, we used the body temperature time series from the robo-sea stars, and a ther-

mal performance curve for *Pisaster* (Monaco et al. 2014). *Pisaster* selects cool microhabitats (Table 1) where respiratory performance is low (Table 2) rather than warmer sites where respiratory performance is higher, and where its predation rates on mussels are higher (Sanford 1999). Behavioral selection for temperatures below the performance optimum has been widely documented in ectotherms (e.g. Martin & Huey 2008, Tepler et al. 2011). The concept of 'sub-optimal is optimal' (Martin & Huey 2008) maintains that ectotherms select temperatures lower than those that yield the highest fitness based on (1) the negatively skewed shape of a thermal performance curve, including that of *Pisaster* (Monaco et al. 2014), and (2) the fact that ectotherms are imperfect behavioral thermoregulators. A negatively (left) skewed curve means that, if field body temperatures are close to or at optimal, an increase in body temperature (to the right) generates a greater depression in performance than a decrease in temperature by the same amount. Accordingly, given the high thermal heterogeneity in the rocky intertidal, selecting for cool and thermally homogeneous microhabitats (e.g. crevices) may grant *Pisaster* a higher cumulative fitness than what can be expected from warmer (seemingly more profitable) microhabitats (e.g. sun-exposed high intertidal) through the avoidance of rare but damaging extreme temperatures. Thus, in heat-protected microhabitats (Table 1) where conditions are cooler and homogeneous (Fig. 5), *Pisaster* avoids upper critical temperatures (Martin & Huey 2008).

It has been commonly documented that intertidal organisms live very close to their thermal tolerance limits (Stillman 2002, Wetthey 2002, Jones et al. 2009, Denny et al. 2011; but see Mislán et al. 2014). However, given *Pisaster*'s preference for cool microhabitats (Table 1), cumulative probability of survival with respect to body temperatures was high in all microhabitats (Fig. 6).

Size-dependent tolerance to thermal and desiccation stress

Contrary to expectation (Landenberger 1969, Pörtner 2002, Peck et al. 2009), the upper critical temperature (LT_{50}) (Fig. 5) and resistance to desiccation from wind stress was higher for the large size class of *Pisaster* (Fig. 6). The latter finding matches biophysical predictions based on surface area to volume ratios (McQuaid 1982, Allen et al. 2012). Neither of these results would explain the presence of larger animals

lower on the shore. Although we observed a relationship between body size and intertidal height of *Pisaster*, it was only evident for individuals found in refugia.

Consistent with Vermeij (1972), as a low intertidal organism, *Pisaster* exhibited a negative relationship between body size and shore level; however, negative biotic interactions do not appear to drive the pattern. Bertness' (1977) hypothesis that prey size can drive the predator shore level was not tested here but may be applicable to *Pisaster*, given this predator's preference for consuming particular mussel sizes (Paine 1974, McClintock & Robnett 1986, Gooding & Harley 2015). Despite differential sensitivity to temperature and desiccation between sizes, this relationship was opposite to the distribution patterns observed in the field, not supporting the hypotheses by Frank (1965) and McQuaid (1982). As argued by Raffaelli & Hughes (1978), we suspect that the shore-level size gradient shown by *Pisaster* might be better explained by the availability of proper refugia. Because most individuals are found in protected microhabitats (Table 1), among which potential body temperatures are quite similar (Fig. 5), conditions experienced between size classes are ultimately very similar. Thus, as long as suitable microhabitats are available, the refuge-seeking behavior of *Pisaster* (Robles et al. 1995, Garza & Robles 2010) is not dependent on size.

We have explored the possibility that life-threatening exposure to critical temperatures may drive *Pisaster* intertidal distribution, and suggested a bet-hedging strategy against rare but potentially fatal events. We did not evaluate the subtle effects of temperatures on energy balance components (investment in maintenance, growth, and reproduction), which, as argued by Robles (2013), directly translate to Darwinian fitness in *Pisaster*. Energy maximization may be an important driver of sea stars' behavior and therefore deserves further research.

Although we only worked at 2 coastal locations, we believe that the range of environmental conditions studied is representative of conditions found over much of the geographic range of the species. As documented by investigators on both the US Pacific coast (Helmuth & Hofmann 2001, Helmuth et al. 2006, Denny et al. 2011) and the European coast (Seabra et al. 2015), the difference in thermal conditions between sun-exposed and shaded microhabitats is often greater than the thermal difference between sites separated by as much as 1000 km.

CONCLUSIONS

Our results indicate that shore-level size gradients in the keystone predator *P. ochraceus* result primarily from a preference for cool microhabitats and the low availability of sheltered sites for large individuals at high shore levels. Contrary to expectation, the small difference in LT_{50} between size classes, and the fact that wind stress has a greater effect on small individuals (Fig. 4), suggests that size-dependent sensitivity to high temperature and desiccation does not explain the distribution patterns. Avoidance of lethal temperatures during normal daily low tide exposures appears to be unlikely, since body temperatures were rarely high enough to cause mortality (Fig. 6). However, these results match a growing body of literature that suggests that some animals may sacrifice increased performance in order to ensure a wider safety margin during rare but potentially lethal conditions (e.g. Martin & Huey 2008).

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