Thermal tolerance of the hermit crab *Pagurus samuelis* subjected to shallow burial events

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Abstract.— Sedimentation and increasing temperature caused by human disturbances and global climate change are additive in their effects on coastal areas. To assess their influence on intertidal organisms, we studied the hermit crab, *Pagurus samuelis*, under acute temperature changes and shallow burial conditions. We applied three temperatures (5°C, 20°C, and 30°C) and two burial depths (3 cm and 6 cm) with a control at the surface (0 cm), and monitored survival, shell abandonment, and burial escape. Survival was primarily affected by temperature, with hermit crabs twice as likely to survive at 20°C than at 30°C, and at 5°C than at 30°C. The combined conditions of 30°C and 6 cm were the least favorable for survival. Hermit crabs which abandoned their shells were more likely to survive burial at 20°C and 30°C than those retaining their shells. Fewer hermit crabs abandoned their shells when exposed to 5°C than to 20°C and 30°C. Crabs buried at 6 cm were 85.0% less likely to abandon shells than those buried at 3 cm, and heavier shells were less readily abandoned than lighter shells. Although overall, 35% of hermit crabs escaped burial to the sediment surface, hermit crabs buried in the combined conditions of 30°C and 6 cm were significantly slower to reach the surface. Our results show that the combined stresses of temperature and burial can impact survival of hermit crabs in intertidal zones. While human activities, including dredging, industrial and domestic dumping, and coastal construction, result in relatively immediate increased inputs of sediment in coastal environments, climate change may endanger intertidal organisms, such as *P. samuelis*, living near their thermal tolerance over the long term, with both increasing temperature and sedimentation from more frequent storm events.

■ Introduction

The rocky intertidal zone is a highly variable region exposed to cyclical changes in pH, temperature, salinity, and oxygen. Temperature is a crucial abiotic factor in determining the distribution of organisms in this harsh environment. During low tides, organisms found in the high and mid intertidal zones experience higher temperatures than low intertidal and subtidal organisms (Morris & Taylor, 1983; Dunbar, 2005; Benedetti-Cecchi & Trussell, 2014).

Helmuth and Hofmann (2001) measured temperature changes in a small tide pool (1.5 m × 1 m × 15 cm deep) in Central California from July 1999 to June 2000. The maximum acute temperature they recorded in the tide pool (29.8°C) was twice as high as the maximum seawater temperature (15°C) at high tide. High temperatures in tide pools without algae result in decreased solubility of oxygen in seawater (Martin & Bridges, 1999). This results in the combined threat of low oxygen availability and high water temperatures in tide pools. Howev-

er, in those pools with abundant algae, night time metabolic activity of algae and other organisms, rather than temperature, results in low oxygen conditions (Taylor & Butler, 1973; Truchot & Duhamel-Jouve, 1980; Morris & Taylor, 1983; Hill *et al.*, 1991; Grieshaber *et al.*, 1994; Dunbar, 2001).

Warm-adapted intertidal organisms are already living close to their thermal tolerance limits (Stillman & Somero, 1996; Tomanek & Somero, 1999; Stillman & Somero, 2000; Stillman, 2003), so that further increases in temperature associated with global climate change may be detrimental to them. Somero (2002) reported that elevated levels of thermal stress in high intertidal regions produced metabolically costly heat shock proteins in the black turban snails, *Chlorostoma* (formely *Tegula*) *funebralis*, which were associated with a reduction in growth rates of these snails compared to their mid intertidal and subtidal congeners, *C. brunnea* and *C. montereyi*, respectively. Abele *et al.* (2002) found that heat stress resulted in an increased production of reactive oxygen species (ROS) in the intertidal mud clam, *Mya arenaria*, increasing the risk of cellular damage. Additionally, Stillman and Somero (1996) found that when porcelain crabs of the genus *Petrolisthes* were exposed to temperatures close to their highest habitat temperatures, these crabs succumbed to heart failure. Temperature increases associated with global climate change may thus cause changes in abundance and distribution of intertidal organisms. Barry *et al.* (1995) reported significant changes in the abundance of 32 out of 45 invertebrates surveyed along the central California coast after 60 years, following an increase in temperature of only 0.75°C. Northward range shifts in the distribution of marine organisms, such as the Zebra perch fish, *Hermosilla azurea* (Sturm & Horn, 2001), and the Kellet's whelk, *Kelletia kelletii* (Zacherl *et al.*, 2003), have already been measured in California. Other studies have identified the presence of "hotspots" and

"coldspots" where maximal and minimal daily temperatures are relatively higher and lower, respectively, than expected at their latitudes (Helmuth *et al.*, 2006). Intertidal organisms in these regions are susceptible to temperatures outside their normal physiological range which may result in lethal alterations of biological and physiological processes (Stillman, 2002), since almost all biological structures and processes are affected by temperature (Hochachka & Somero, 2002). However, temperature alone, is not the only factor impacting intertidal organisms.

Tidal movements of sand result in periodic burial of intertidal organisms (Grant, 1983). Other physical disturbances, such as storms, currents, and strong winds further increase the risk of burial in this dynamic environment. The immediate threats of sedimentation from urban development and increasing human population growth, dredging, beach replenishment, land reclamation, and industrial and domestic discharges along shorelines can lead to increased rates of sediment loading into the intertidal region (Airoldi, 2003). For instance, Hewawasam *et al.* (2003) reported that intense rainfall increased terrestrial runoffs and sediment deposition into intertidal zones in Sri Lanka. Heavy sedimentation can prevent trapped animals from escaping. Burial beyond a certain depth can result in compaction (overburden stress), thereby inhibiting any movement or vertical migration of the organism (Nichols *et al.*, 1978). In the long term, because storm intensity is on the rise as a consequence of global climate change (Villarini, 2013), we expect more extensive and rapid sediment depositional events in intertidal regions. Additionally, burial in sediment can also lead to a reduction in availability of oxygen for intertidal organisms triggering them to switch to anaerobic metabolism. Environmental hypoxia has become more extensive due to increasing eutrophication resulting from enhanced nutrient loading (especially nitrates) into coastal waters and marine

systems (Diaz & Rosenberg, 1995; Wu, 2002). Global warming may exacerbate the problem, since an increase in seawater temperature may also decrease oxygen solubility. Sensitivity of intertidal organisms to changes in environmental conditions makes the intertidal zone an important system in which to study potential impacts of climate change.

In this study, we investigated responses of the hermit crab, *Pagurus samuelis*, to the combined stresses of burial and temperature change. *Pagurus samuelis* is the most widespread intertidal hermit crab species in southern California (Morris *et al.*, 1980), may represent a good indicator species, and additionally is an important food source for species at higher trophic levels (Reese, 1969; Bertness, 1981). The range of *P. samuelis* extends from Nootka Sound, British Columbia to northwest Baja California, Mexico (McLaughlin, 1974; Jensen, 2014). Individuals are usually found in the mid to high rocky intertidal where they are important detritivores (Morris *et al.*, 1980; Hazlett, 1981; Laidre & Greggor, 2015) and contributors to energy recycling. The high levels of biological turnover in intertidal zones result in abundant carrion (Laidre & Greggor, 2015) available to scavengers, such as *P. samuelis*, which thrive in these habitats. A distinct feature of hermit crabs is that they occupy empty gastropod shells. *Pagurus samuelis* has a strong preference for *Chlorostoma funebralis* shells whose internal shape is similar to the morphology of the hermit crab (Mesce, 1993). The shells of hermit crabs influence many aspects of their biology, including growth rate, fecundity, and susceptibility to predation (Vance, 1972; Fotheringham, 1976; Bertness, 1981; Caruso & Chemello, 2009). Body size is highly correlated with shell biometrics, so that crabs select shells proportional to their size (de Souza *et al.*, 2015). Larger shells (which are typically heavier and thicker) provide better protection from predators, and are beneficial for higher growth rate and increased fecundity.

However, shells beyond optimal size and weight require more energy to carry and may limit mobility, growth, and reproduction (Hazlett & Baron, 1989; Osorno *et al.*, 1998; Dominciano *et al.*, 2009). Hermit crabs can abandon shells as a behavioral strategy that may prolong their survival when they experience life-threatening stressors, such as entrapment and burial (Shives & Dunbar, 2010; Turra & Gorman, 2014). There is a greater tendency among hermit crabs to abandon shells in low predation environments compared to rocky areas, where predation is high (Gorman *et al.*, 2015). Negative impacts of climate change on this essential scavenger may also result in adverse impacts at other trophic levels in the intertidal environment. To better understand how both long-term climate change and short-term sedimentation events may affect intertidal organisms, we tested combinations of acute temperature change and sedimentation on survival and shell abandonment behavior in the hermit crab, *P. samuelis*. We also investigated factors that impact escape from burial. We expected the mortality rate of hermit crabs subjected to 30°C and buried at 6 cm to be higher than at 20°C and 5°C and in 3 cm depth due to low oxygen levels at 30°C and 6 cm. We also anticipated the highest rate of shell abandonment and escape in hermit crabs subjected to 20°C and buried at 3 cm, because these represent the average temperature normally experienced in the field, and the treatment depth at which there was least potential for overburden stress.

■ Methods

Pre-burial Methods

Prior to the start of the experiment, we analyzed the size of the sediment used in the experiment by dynamic light scattering methods using a laser diffraction particle size analyzer (LS13 320, Beckman Coulter, Brea, CA, USA). Particles were suspended in deionized water at room temperature. We added a few

drops of dilute surfactant and sonicated the sample before analysis. An obscuration level of 10–12% was used. The grain sizes of 10 samples of sand collected from southern California beaches, including one from the hermit crab collection site, were measured. All measurements were obtained in duplicate.

Oxygen monitoring at the three burial depths and three experimental temperatures was also carried out using a static YSI 5739 field probe connected to a TPS-90D oxygen meter (TPS, Brisbane, Australia). The oxygen sensor was calibrated in oxygen-free solution (2% sodium sulphite) followed by air calibration. Salinity values were measured using a WP-84 conductivity-salinity-temperature meter (TPS, Brisbane, Australia).

Collection and care of hermit crabs

Specimens of the hermit crab, *Pagurus samuelis*, were caught by hand at low tide from White Point Beach, Los Angeles County, California (33°42.57N, 118°19.6W) in August 2013 and January 2014. A long acclimation period ensured complete acclimation (Bowler, 1963; Cuculescu *et al.*, 1998) which should lessen seasonal variation in temperature tolerance among individuals. Immediately after being transported to the laboratory, hermit crabs were transferred to aquaria containing natural seawater. Hermit crabs were acclimated to ambient temperature in the laboratory (19 ± 2°C) for a minimum of 14 days before testing. Water was changed every week. Sea water salinity was maintained at 34.2 ± 1.2 ppK throughout the experiment. Crabs were fed a diet of defrosted krill *ad libitum*, with feeding stopped two days prior to the start of each treatment. Hermit crabs were not sexed in the following investigations since other studies found no effect of sex on behavioral responses in hermit crabs (Briffa *et al.*, 2008; Gorman *et al.*, 2015).

Experimental procedure

Experiments were conducted in a 62 L water

bath. Initial burial of hermit crabs was performed at room temperature before the crabs were exposed to the temperature of the water bath. The burial medium took on average 15 min, 20 min, and 50 min to reach the incubated conditions of 20°C, 30°C, and 5°C, respectively. We considered these acclimatory treatments. Nine trials were performed using a total of 135 hermit crabs (including 45 control animals) in acclimatory treatments. A second set of experiments was run where hermit crabs were acutely exposed to the experimental temperature. Acute exposure trials were repeated 9 times (n = 135, including 45 control animals). Fifteen 10 cm-graduated plastic containers (8 diameter) were filled with sand to a depth of 8 cm and placed randomly in the water bath (Fig. 1) thermostatted to one of three temperatures (5°C, 20°C, or 30°C) for 1–1.5 hrs. Temperature of the water bath was controlled by a refrigerated recirculating chiller/heater (Polyscience 5205, Niles, IL, USA). Hermit crabs were selected at random, dried of excess water, and weighed. One container at a time was removed from the water bath and the sediment dug down 3 cm or 6 cm from the surface (Fig. 2). A single hermit crab was placed upside down (with shell aperture up) in the sediment and buried with a mixture of sand and water up
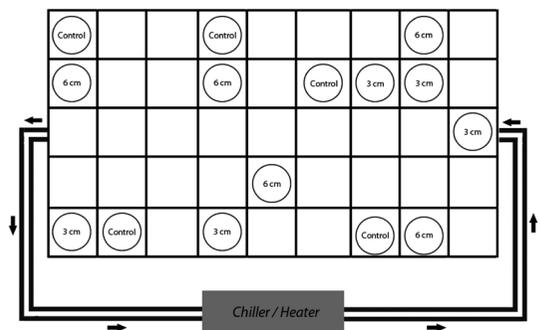

Fig. 1. Experimental layout of sand-filled plastic containers in the water bath. Control hermit crabs (at the surface) and crabs buried at 3 cm and 6 cm were placed randomly in the water bath. A chiller/heater kept water temperature constant at 5°C, 20°C or 30°C.
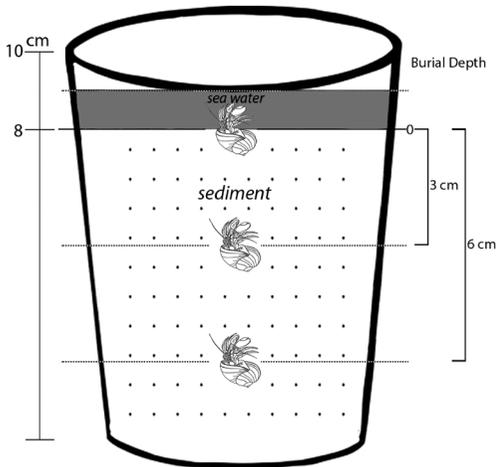
Fig. 2. Experimental setup showing hermit crabs (*Pagurus samuelis*) buried with their aperture up at two burial depths (3 and 6 cm) and the control (at the surface). A slurry mixture of sand and natural seawater was used to bury the hermit crabs. One hermit crab was buried per container.

to the 8 cm mark, corresponding to 0 cm depth (Fig. 2). The plastic container was placed back in the water bath and the buried hermit crab was monitored for 6 hours, corresponding to the approximate time period of a tidal cycle. A total of fifteen crabs was used per trial, 5 crabs at each burial depth and 5 control animals which were placed with their shell apertures on the sediment surface at the 8 cm mark (at 0 cm depth) and were not buried. Sea water (32.8 ± 0.4 ppK salinity) was maintained at 1 cm above the sediment. Water temperatures at each depth were recorded every minute using iBut-ton thermochron data loggers (Dallas semicon-ductor, Dallas, TX, USA) accurate to $\pm 0.5°C$. Six data loggers were used per trial, two data loggers at each burial depth. The distribution of data loggers for each trial was set at random. Shell abandonment and time to escape burial were monitored every 30 seconds over 6 hours with the use of a Logitech webcam Quickcam[®] S5500 and Booru webcam 2.0 software. The number of hermit crabs alive following 6 hours of burial was also noted at the end of the ex-periment. We pooled acclimatory and acute ex-

periments and performed a total of eighteen burial trials (n = 270).

After burial treatments, the shell of each her-mit crab was gently cracked open using a bench vise. The wet mass of each crab and sep-arate shell fragments were measured using a digital balance (Mettler Toledo, PG603-S Delta Range, Columbus, OH, USA). Hermit crabs were occupying almost exclusively *C. funebra-lis* shells (268 out of 270), which is known to be the preferred shell of *P. samuelis* (Abrams, 1987; Mesce, 1993; Hahn, 1998; Absher *et al.*, 2001). Shells were in good condition, with few shells bearing extensive physical abrasions or epiphytes. The shell lengths of 60 hermit crabs (which abandoned their shells) were measured along the shell base-apex axis to the nearest 0.05 mm using Vernier calipers. Shell width and crab mass were also measured in a sample of 50 hermit crabs (inhabiting *C. funebralis*) subsequently collected at White Point Beach. This was done to investigate if there was a re-lationship between the size of shell and size of crab.

Statistical Analysis

We carried out simple linear regressions to find relationships between shell length and shell mass (n = 60) and between shell width and crab mass (n = 50). Analysis of residuals confirmed that assumptions of normality, lin-earity, and homogeneity of variance were met. Crabs tested in acclimatory and acute condi-tions were pooled, since the responses of her-mit crabs to acclimatory and acute exposures were not significantly different following chi-square and t-test analyses (survival $\chi^2_{(1)} = 0.124$, p = 0.724; shell abandonment $\chi^2_{(1)} = 0.217$, p = 0.642; escape behavior $\chi^2_{(1)} = 0.611$, p = 0.435; time to escape $t_{(61)} = 0.284$, p = 0.777). There-fore, we decided not to perform an experimen-tal conditions-stratified analysis. We performed Chi-square analyses at each treatment tempera-ture to test if hermit crabs were less likely to survive in the experimental group than the con-

trol group. We then used log-binomial regression analyses to predict the survival of hermit crabs under different conditions of temperature, depth, and shell mass. We were unable to perform multivariate analyses due to sample size limitations in some categories, and instead ran bivariate log-binomial regression analyses. Because the assumption of linearity for shell mass was violated, we arbitrarily classified this continuous variable into 3 categories: 0.517–1.699 g (light); 1.700–2.672 g (medium); and 2.673–4.997 g (heavy). These shell mass categories were obtained by applying shell length values, <15 mm, 15–18 mm, >18 mm, defined by Gherardi (2006), to our regression equation of shell length and shell mass:

$$y = 3.085x + 9.7561 \qquad (1)$$

where y is shell length (mm) and x is shell mass (g). Since shell morphometric parameters are strongly correlated (Vance, 1972; Mitchell, 1976; Lively, 1988; de Souza *et al.*, 2015), we used shell length to predict shell mass. We also performed a Chi-square test to compare the frequency of survival in crabs that abandoned their shells to those that did not. We tested the shell abandonment behavior among control and treatment groups at each experimental temperature using Chi-square tests and carried out a logistic regression to predict shell abandonment using temperature, depth, and shell mass (continuous) as predictors. Assumptions of linearity, absence of outliers, and multicollinearity were met. Chi-square tests were performed to find the association between shell abandonment and escape from burial, and between temperature treatment and escape behavior. We then carried out a robust regression to analyze the relationship between escape time of the hermit crabs and the potential predictors temperature, depth, and shell mass (continuous). Time to escape (min), shell mass, and crab mass did not meet normality assumptions and were log-transformed (natural log) prior to the multiple

linear regression analysis. Two extreme outliers were excluded from the analysis (n = 61). Assumptions of linearity and absence of multicollinearity were met. Since the assumption of homoscedasticity was violated, a robust regression was performed. In an effort to detect a possible interaction effect between temperature and depth, we added an interaction term (temperature and depth) in the statistical models testing for survival, shell abandonment, and time to escape burial. We used SPSS version 20.0 (IBM Corp., Armonk, NY) and SAS statistical package version 9.4 (SAS Institute, Cary, NC) to perform all statistical analyses. Alpha levels were set at 0.05.

■ Results

The mean size of sand used in the experiment was 591 ± 196 μm, which is considered coarse sand according to the Wentworth grade classification (Buchanan, 1984). Sand used in the experiments was similar to natural sediment at White Point Beach, where hermit crabs were collected. Oxygen monitoring of the sediment showed that crabs faced hypoxic to anoxic conditions during burial events, depending on depth and temperature (Table 1). We used 270 crabs in this experiment, including 90 control animals. The mass of animals ranged from 0.101 to 1.540 g with a mean of 0.617 ± 0.288 g. The shell length of *C. funebralis* inhabited by *P. samuelis* was positively related to, and significantly predicted by, its mass, $F(1, 58) = 249.91$, p$<$0.001. Small shells were lighter than large shells. Also, shell mass explained 81.2% of the variance in shell length. The shell width was positively related to, and significantly predicted by, crab mass, $F_{(1, 48)} = 100.84$, p$<$0.001 (Fig. 3). Crab mass explained 67.7% of the variance in shell width.

One hundred and thirty eight hermit crabs (76.6%) survived following shallow burial events. There was a significant difference in survival between hermit crabs in the experi-

mental group versus the control group at 30°C ($\chi^2_{(1)} = 22.7$, p$<$0.001, Phi $= -0.502$). Survival was higher in the control group than the experimental group (control group $= 96.7\%$, n $= 30$; experimental group $= 45\%$, n $= 60$). The log-binomial regression was statistically significant indicating that temperature was reliable in predicting the survival of hermit crabs, whereas shell mass was a confounder of the relationship between temperature and survival, but was not a significant predictor of survival. Temperature

Table 1. Changes in percent oxygen saturation with time at 0, 3, and 6 cm depths, and the three experimental temperatures (5°C, 20°C, 30°C), as measured by a TPS DO oxygen meter.

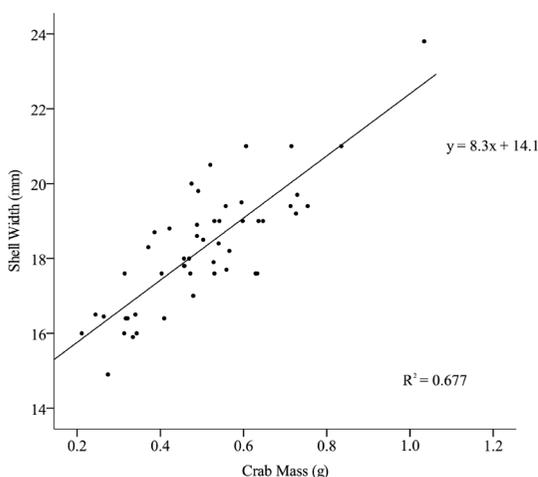| Depth/ cm	Temperature/ °C	Time			
		Start	After 2 hr	After 4 hr	After 6 hr
0	5	31.3	21.6	19.7	15.6
	20	42.0	36.4	35.6	33.6
	30	33.6	30.9	28.4	26.9
3	5	34.3	16.8	15.0	14.1
	20	26.1	9.1	4.2	0.8
	30	29.7	1.6	0.0	0.0
6	5	38.6	22.4	17.5	15.8
	20	32.6	15.0	8.8	2.7
	30	21.0	1.1	0.0	0.0

$$y = 8.3x + 14.1$$

$$R^2 = 0.677$$

Fig. 3. The regression relationship between shell width and crab mass of *P. samuelis* hermit crabs (n $= 50$).

was negatively associated with survival. Overall survival significantly decreased by 50% in 30°C when compared with 20°C (Fig. 4, Table 2). However, hermit crabs had a higher prevalence of surviving (model 1 $= 6\%$; model 2 $= 2\%$) at 5°C compared to 20°C, but this effect was not statistically significant (Table 2). We saw significantly greater survival at 5°C when compared to 30°C (model 1 $= 111\%$; model 2 $= 48\%$). The temperature-depth interaction term was significant for the log-binomial model. The probability of hermit crabs being alive at 30°C and 6 cm was 0.125 times (95% CI: 0.042, 0.371) the probability at 30°C and 3 cm. The same group of hermit crabs (at 30°C and 6 cm) was less likely to survive than all other groups (i.e., 5°C and 6 cm, 5°C and 3 cm, 20°C and 6 cm, and 20°C and 3 cm; Table 3, Fig. 4), and therefore provided the worst conditions for survival during burial. Although, overall burial depth was not a statistically significant predictor of survival, there was a significant association between survival and shell abandonment ($\chi^2_{(1)} = 19.9$, p$<$0.001, Phi $= -0.333$).
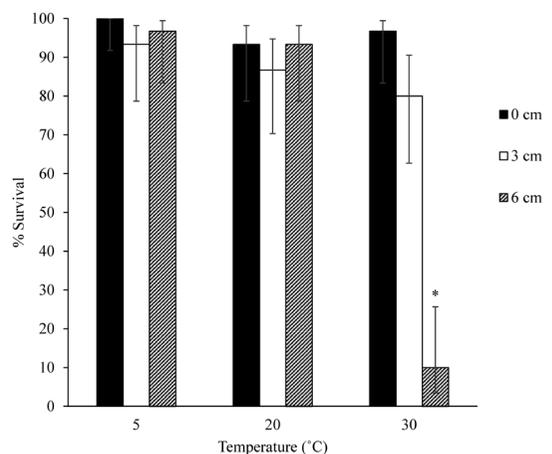

Fig. 4. The percentage of hermit crabs surviving the experimental temperatures (5°C, 20°C and 30°C), at the experimental depths of 3 cm and 6 cm and the surface control. Bars represent live crabs following 6 hours of shallow burial (n $= 270$). Error bars represent 95% CI. * represents a significant difference in the number of crabs surviving at 6 cm in 30°C compared to the other combinations of burial depth and temperature treatments.

Table 2.   Log-binomial regressions of the association of three predictors (temperature, depth, and shell mass) with survival of hermit crabs following shallow burial (n = 180).

| | Bivariate models | | | |
| | 1 Temperature + Depth | | 2 Temperature + Shell mass | |
	Prevalence (CI)	P value	Prevalence (CI)	P value
Temperature				
5°C vs. 20°C	1.055 (0.953–1.169)	0.301	1.024 (0.903–1.160)	0.716
30°C vs. 20°C	0.499 (0.371–0.671)	<0.0001****	0.509 (0.378–0.685)	<0.0001****
5°C vs. 30°C	2.114 (1.580–2.820)	<0.0001****	1.480 (1.214–1.810)	<0.0001****
Depth 6 cm vs. 3 cm	1.002 (0.908–1.107)	0.963		
Shell mass				
Light vs. medium			1.023 (0.911–1.148)	0.698
Heavy vs. medium			0.912 (0.773–1.076)	0.275

**** p<0.0001

Table 3.   Risk ratios for the log-binomial regression after implementing an interaction term between temperature and depth (outcome = survival).

Comparison groups	Risk ratio	95% CI	P value
30°C at 6 cm vs. 30°C at 3 cm	0.125	0.042–0.371	<0.001***
30°C at 6 cm vs. 5°C at 6 cm	0.103	0.035–0.303	<0.0001****
30°C at 6 cm vs. 5°C at 3 cm	0.107	0.036–0.315	<0.0001****
30°C at 6 cm vs. 20°C at 6 cm	0.107	0.036–0.315	<0.0001****
30°C at 6 cm vs. 20°C at 3 cm	0.115	0.039–0.341	<0.0001****

Only significant terms are reported here.
*** p<0.001, **** p<0.0001

Hermit crabs which abandoned their shell during burial had a significantly higher probability of surviving than those which retained their shell (abandoned shell = 95.4%, n = 65; did not abandon shell = 66.1%, n = 115).

Shell abandonment was higher in the experimental group than in the control group at 20°C (experimental group = 53.3%, n = 60; control = 0%, n = 30) and 30°C (experimental group = 46.7%, n = 60; control = 0%, n = 30). These differences were statistically significant (20°C: $\chi^2_{(1)}$ = 24.83, p<0.001, Phi = −0.525 and 30°C: $\chi^2_{(1)}$ = 20.32, p<0.001, Phi = −0.475). Regression results indicated that the overall model of the three predictors (temperature, depth, and shell mass) was statistically reliable in distinguishing between hermit crabs that abandoned their shells and those that did not when sub-jected to shallow burial (overall significance $\chi^2_{(4)}$ = 64.99, p<0.001; −2 Log Likelihood = 170.47; Hosmer and Lemeshow $\chi^2_{(8)}$ = 8.953, p = 0.346). The model correctly classified 79.4% of the cases (abandoned shell = 64.6%, did not abandon shell = 87.8%). Nagelkerke r^2 indicated that the logistic regression model explained 41.5% of the variance in shell abandonment. When comparing temperature treatments of 30°C and 20°C to 5°C, shell abandonment was significantly lower (~94%) at 5°C, after adjusting for depth and shell mass in the logistic regression model (Table 4, Fig. 5). Shell abandonment was negatively associated with burial depth, with hermit crabs buried at 6 cm significantly (85.0%) less likely to abandon their shell than those buried at 3 cm (Fig. 5). Shell mass was also negatively associ-

Table 4.　Logistic regression of the association of three predictors (temperature, depth, and shell mass) with shell abandonment following shallow burial (binary outcome = shell abandonment) (n = 180).

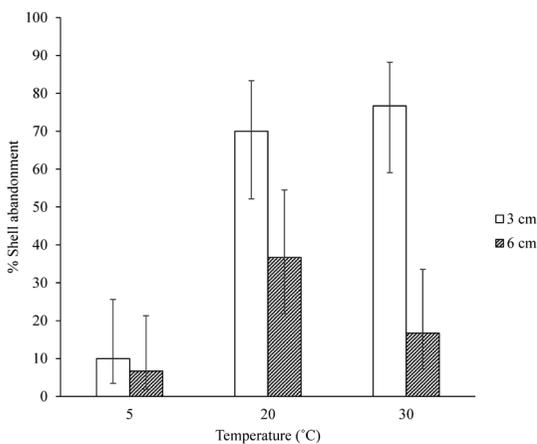| Variable	B	P value	Odds ratio	95% C.I. for odds ratio	
				Lower	Upper
Temperature					
5°C vs. 20°C	−2.930	<0.001***	0.053	0.017	0.167
30°C vs. 20°C	−0.120	0.777	0.887	0.387	2.035
5°C vs. 30°C	−2.809	<0.001***	0.060	0.019	0.193
Depth 6 cm vs. 3 cm	−1.897	<0.001***	0.150	0.069	0.327
Shell mass	−0.466	0.043*	0.627	0.400	0.985
Constant	2.136	0.001	8.462		

* p<0.05, *** p<0.001

Fig. 5.　The percentage of hermit crabs that abandoned their shells at the experimental temperatures (5°C, 20°C and 30°C) and depths (3 cm, 6 cm) (n = 180). Error bars represent 95% CI. No hermit crabs abandoned their shells in the control.
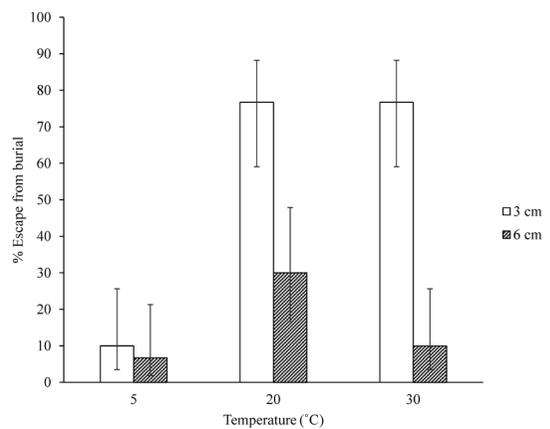

Fig. 6.　The number of hermit crabs that escaped burial when subjected to experimental temperatures (5°C, 20°C and 30°C) and depth (3 cm, 6 cm) (n = 63). Error bars represent 95% CI.

ated with shell abandonment, showing that as shell mass increased by 1 g, shell abandonment significantly decreased by 37.3% (Table 4). No significant interaction effect of temperature and depth was found when examining shell abandonment. Shell abandonment was statistically significant among hermit crabs escaping burial compared to those that did not escape burial ($\chi^2_{(1)}$ = 132.52, p<0.001, Phi = 0.855). Most hermit crabs that escaped burial also abandoned their shells (abandoned shell = 89.2%, n = 65; did not abandon shell = 4.35%, n = 115).

A total of sixty three hermit crabs (35%) escaped burial. The escape time ranged from 1–330 minutes and had a median of 9 minutes. Escaping, irrespective of depth, was statistically affected by temperature ($\chi^2_{(2)}$ = 30.103, p< 0.001, Cramer's V = 0.410), showing that more hermit crabs escaped at 20°C (n = 32) than at either 5°C (n = 5) or 30°C (n = 26) (Fig. 6). The regression of time to escape burial was significant ($F_{(4, 56)}$ = 5.31, p = 0.001). The three variables (temperature, depth, and shell mass) accounted for 22.3% of the explained variability in the time to escape burial. There was a significant difference in escape time for hermit crabs in 30°C compared to 20°C. Time to escape decreased by 55% for those in 30°C compared to 20°C (Table 5). Depth was also a sig-

Table 5. Robust regression of the association of three predictors (temperature, depth, and shell mass) with time to escape shallow burial (outcome = time to escape[a]) (n = 61)

Variable	Unstandardized slope[b]	Std. error	P value
Temperature			
5°C vs. 20°C	0.594	0.530	0.330
30°C vs. 20°C	0.442	0.311	0.011*
5°C vs. 30°C	1.344	0.537	0.585
Depth 6 cm vs. 3 cm	2.658	0.341	0.006*
Shell mass	0.941	0.160	0.704

Intercept antilog = 13.446
Adjusted R^2 = 0.223
[a] Ln transformed
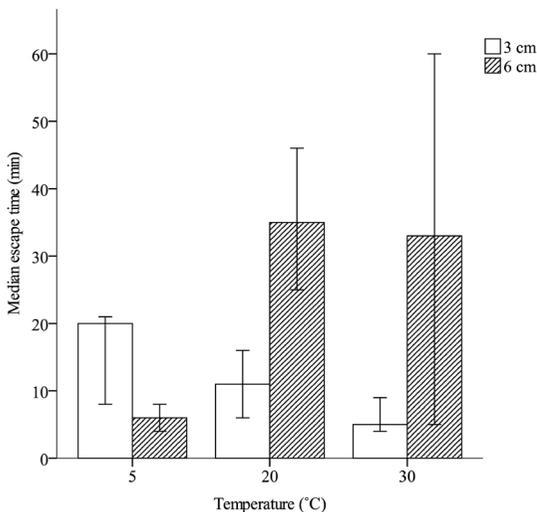[b] EXP(b) = Antilog of slope
* p < 0.05

Fig. 7. The median escape time of hermit crabs exposed to experimental temperatures (5°C, 20°C and 30°C) and depth (3 cm, 6 cm) (n = 63). Error bars represent 95% CI.

nificant predictor of escape time. Overall, hermit crabs buried at 6 cm took 2.7 times longer to escape than those at 3 cm (Fig. 7). The limited number of cases per variable caused us to be conservative in our interpretation of the robust regression results. The temperature-depth interaction term was not significant at 20 °C and 30°C. At 5°C, the interaction could not be tested due to the low number of crabs that escaped at this temperature.

■ Discussion

Most *P. samuelis* in our experiments survived short term exposure (≤6 hr) to hypoxia (<30% air saturation). This is unsurprising, since these intertidal organisms are exposed to frequent sediment deposition and hypoxic tide pool waters. The experimental temperature of 30°C was closer than the other experimental temperatures to the calculated median lethal temperatures (LT50) of 32.4°C and 34.3°C (Taylor, 1977) for *P. samuelis* acclimated at 12°C and 20°C, respectively, thus explaining the higher death rate in this group. Previous investigations of oxygen solubility in sea water at different temperatures (0–40°C) and salinities (0–40 ppt) showed that oxygen solubility decreased with increasing temperature and salinity (Weiss, 1970; Colt, 1984; Boyd, 2000; Dunbar, 2001). The solubility of oxygen at saturation at experimental temperatures 5, 20, and 30°C, and 33.0 ppt salinity are 10.265, 7.469, and 6.289 mg/L, respectively, according to Colt (1984). Paradoxically, as water temperature increases and oxygen solubility decreases, the demand for oxygen in intertidal crustaceans increases (Taylor, 1981). Valverde *et al.* (2012) noted that variations in the critical (24.1 to 53.3%) and lethal (6.8 to 19.3%) oxygen levels for the spider crab, *Maja brachydactyla*, were significantly dependent on water temperature.

In their study, both critical and lethal oxygen concentrations increased with increasing temperature.

In the current study, burial in sediment resulted in hypoxia of the treatment habitat, since diffusion of oxygen is limited to a distance of approximately 2 mm in the absence of sediment mixing or water circulation, according to Hinchey *et al.* (2006). Increased depth of burial presumably resulted in decreased permeability of water and further reduction in available oxygen. Depth was therefore negatively correlated with vertical migration. Movement of the organisms in our experiments may also have been inhibited by compaction at 6 cm that prevented the hermit crabs from escaping burial or abandoning their shells, with an anticipated greater impact on small shells since small gastropod shells are known to withstand less compression force than large shells (Ragagnin *et al.*, 2016). More hermit crabs abandoned small shells because they likely offer less protection from compression, although we did not test this. Marine invertebrates have different abilities to migrate through sediment, which can be related to their morphologies. According to Kranz (1974), mollusks bearing a large cylindrical foot have good escape potential. Bolam (2011) showed that polychaete worms *Tharyx* sp. A. and *Streblospio shrubsolii* had limited ability to migrate up through 6 cm of sediment, while the gastropod *Hydrobia ulvae* demonstrated good migratory abilities through as much as 16 cm of sediment. Chandrasekara and Frid (1998) investigated the migratory abilities of the gastropods *H. ulvae* and *Littorina littorea* at various temperatures, and attributed the greater mortality of gastropods at 20.3°C compared to 7.5°C, to inadequate oxygen supply following increased metabolic activities and reduced oxygen solubility at high temperature. Maurer *et al.* (1981) demonstrated that the mud crab, *Neopanope sayi*, and the amphipod, *Parahaustorius longimerus*, are both good burrowers and had high migratory abilities when buried in up to 30 cm of sand in laboratory conditions.

In the current study, we assumed the reduction in oxygen solubility in water at 30°C limited the oxygen availability for uptake and delivery in the hermit crabs. The critical oxygen pressure was reached faster at 30°C than at 20°C and 5°C, and oxygen was likely insufficient to maintain increased metabolism, resulting in a higher death rate at 30°C than at the other two experimental temperatures. The simultaneous exposure to hypoxia and high temperature may have precipitated the collapse of cardiac and respiratory activities in animals at 30°C, although we did not investigate this aspect of hermit crab physiology. However, in crustaceans, it is known that heart rate increases with increasing temperature up to a certain break point, the Arrhenius break temperature (ABT), after which heart rate decreases and heart beats become arrhythmic (Stillman & Somero, 1996; McGaw & Reiber, 2015). The ABTs of the porcelain crabs *Petrolisthes cinctipes*, inhabiting mid to high intertidal regions, and *P. eriomerus* occupying low intertidal to subtidal regions of the Northeastern Pacific, were found to be 31.5°C and 26.6°C, respectively (Stillman & Somero, 1996). In crustaceans, high temperature also results in a decrease in pH (Truchot, 1992) and cooperative oxygen binding (Torchin, 1994) which decreases oxygen affinity of hemocyanin (Taylor, 1981; Terwilliger, 1998) leading to limited loading of oxygen at the gills, yet increased unloading at the tissues (Frederich & Pörtner, 2000; Bridges, 2001).

In our study, hermit crab metabolism, and therefore oxygen demand, were likely reduced at 5°C since hermit crabs are poikilothermic organisms. Consequently, movement was likely restricted, and this may help explain why most hermit crabs did not escape burial or abandon their shells at low temperature. The higher oxygen content of cold water compared with warmer water may explain the increased num-

ber of surviving hermit crabs at 5°C. This low mortality rate suggests that the critical low temperature for *P. samuelis* is lower than 5°C. However, the very low rate of escape at 5°C is indicative of a severe reduction in metabolism and thus mobility, suggesting that the critical temperature for this species may be close to this temperature. Alternatively, at this temperature hermit crabs may have otherwise not attempted to escape altogether. In *P. longicarpus*, the minimum critical temperature, evidenced by lack of locomotion, was found to be approximately 3°C (Rebach, 1974). Field observations in his study concluded that *P. longicarpus* individuals migrated to deeper waters to bury themselves when water temperatures decreased below 10°C, consequently avoiding predation when locomotory ability decreased (Rebach, 1974).

We found that hermit crabs inhabiting light and small shells abandoned their shells significantly more often than those in heavier and larger shells. Likewise, Gorman *et al.* (2015) observed that *Pagurus criniticornis* abandoned small shells more readily than larger ones. Hermit crabs use their shells as shelters to protect their soft abdomens from predators, abrasion, and desiccation (Reese, 1969; Vance, 1972; Bertness, 1981; Lancaster, 1988; Laidre, 2011) and abandon their shells when facing life-threatening situations, such as asphyxiation (Pretterebner *et al.*, 2012; Turra & Gorman, 2014). Our results support previous findings that shell abandonment increases the survival of hermit crabs when they are buried (Shives & Dunbar, 2010) or trapped (Turra & Gorman, 2014). Shell abandonment is largely dependent on shell adequacy and condition, with hermit crabs inhabiting sub-optimal and damaged shells typically abandoning their shells more rapidly than hermit crabs in optimal and undamaged shells (Gorman *et al.*, 2015). Appel and Elwood (2009) and Elwood and Appel (2009) observed shell abandonment/retention behavior in *P. bernhardus* subjected to electric

shock. They reported that hermit crabs inhabiting the preferred shell species (*Littorina obtusata*) were less likely to abandon their shells than hermit crabs occupying the less preferred shell species (*Gibbula cineraria*). Shell abandonment behavior thus correlates with the perceived value of the shell resource (Gorman *et al.*, 2015), with hermit crabs holding on longer to shells with higher values. In our study, heavier/larger shells were possibly assessed as more valuable resources than lighter shells, since they offer a microhabitat that provides better protection against environmental changes in intertidal regions. Also, hermit crabs inhabiting larger, more-adequate shells, may retain this important resource because gastropods shells in the wild are often a limiting resource (Kellogg, 1976), although in the current study we have not assessed shell resources for *P. samuelis* at the collection location. Hermit crabs can also assess adverse environmental conditions and accordingly choose to abandon their shells or not. Turra and Gorman (2014) found that hermit crabs readily abandon shells of high quality when subjected to life-threatening burial events, yet hold on to their shells when the threat is less severe (such as entrapment). For hermit crabs, surviving life-threatening situations superseded retention of the highest quality shells. However, according to Jackson and Elwood (1989), when the potential gain or loss is negligible, a hermit crab will take longer to make a decision. The motivation to hold or abandon a shell can also be influenced by the physical state of the hermit crab as demonstrated by Billock and Dunbar (2009). Moreover, when hermit crabs are buried with their aperture up, as in our study, sediment may infiltrate the shells as hermit crabs endeavor to escape, making the shells heavier and the hermit crabs more likely to abandon the shell as it becomes energetically costly to retain (Shives & Dunbar, 2010). According to these authors, shell abandonment may also facilitate mobility (maneuverability) of the crabs through the sed-

iment. Alternatively, shell retention can be beneficial, as the shell protects the soft abdomen of the hermit crab against abrasion while moving through sand. In the rocky intertidal environment, where the risk of predation is high, shell retention may be a better strategy than shell abandonment. Gorman *et al.* (2015) found that the hermit crabs *P. criniticornis* and *Pagurus brevidactylus*, which inhabit low predation risk intertidal mud zones, had a greater tendency to abandon their shells compared with *Clibanarius antillensis*, which is found in rocky intertidal zones where the risk of predation is higher. The search for a new shell is easier in low predation environments than in more risky environments, such as rocky intertidal zones, leading to hermit crabs inhabiting low risk regions abandoning their shells more readily. Waiting for waves or wind to shift the overload of sediment may be a better strategy than escaping burial by shell abandonment for rocky intertidal organisms, as long as oxygen is available. This may however, be dependent on the water temperature and depth of burial, being more favorable at low temperatures and shallow burial depths. The movement of waves may also increase the diffusion of oxygen and nutrients through the sediment during the burial period.

Intertidal organisms are sensitive to changes in environmental conditions since they have a reduced capacity for further thermal acclimatization and are at risk of increasing extreme temperature events and hydrodynamic disturbances. Hopkin *et al.* (2006) investigated the seasonal critical thermal maxima (CTMax) of eight crustaceans (*Cancer pagurus*, *Carcinus maenas*, *Hyas araneus*, *Liocarcinus depurator*, *Munida rugosa*, *Necora puber*, *Nephrops norvegicus* and *Pagurus bernhardus*) in the United Kingdom, and found the temperature at which these crustaceans lost the ability to right themselves after being turned over, to range between 20°C and 34°C, with summer caught organisms (14°C–17°C) having significantly

higher upper thermal tolerance values than winter caught organisms (9°C). McGaw (2003) found that the purple shore crab, *Hemigrapsus nudus*, had a high CTMax, which ranged between 31 and 34°C. However, decapods with higher CTMax values had poorer acclimatization capacity than decapods with lower CTMax (Hopkin *et al.*, 2006). Organisms with higher CTMax are more susceptible to an increase in temperature since they already live at or close to their maximum thermal tolerance capacities (Stillman, 2003; Somero, 2011).

In conclusion, increasing temperature and depth have negative effects on the survival of hermit crabs and their ability to escape burial. Despite shells being an important source of protection for hermit crabs, these organisms may resort to abandoning their shells when facing burial. Hermit crabs which abandoned their shells had a higher survival rate than those which kept their shells. Shell characteristics, such as shell size, shape, depth, and width may affect shell abandonment behaviors. The fact that less than half of crabs escaped burial within 6 hours may have potentially serious consequences for the subsequent distribution of intertidal organisms following sedimentation events. Human-related processes, such as urban development, dredging, and industrial and domestic discharge, enhance the input of sediments into coastal zones and represent a relatively immediate threat to marine diversity, potentially altering trophic interactions and driving changes in species composition and distribution. Intertidal zones are also valuable warning systems of more long-term climate change. More studies are required to better understand how intertidal organisms will respond to changes in climate, and whether they will be able to acclimatize thermal tolerances to warmer conditions. Moreover, high winds and waves from more intense storms may result in higher rates of sedimentation which, combined with acute temperature changes, may result in increasing mortality risk among buried animals.

Our study focused on the synergistic effect of two environmental parameters (sedimentation and acute temperature change) on the survivability of intertidal hermit crabs during burial. Future studies accounting for more factors, such as high concentrations of carbon dioxide and low pH, will provide additional understanding of how intertidal organisms may respond to abiotic factors related to climate change.

■ Acknowledgements

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