



Behavioral responses to burial in the hermit crab, *Pagurus samuelis*: Implications for the fossil record

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ABSTRACT

The intertidal hermit crab, *Pagurus samuelis*, was subjected to various treatments analyzed to determine behavioral responses to the ecological stress of burial. Hermit crabs were buried at varying depths (2, 4, and 6 cm), and in two orientations (shell aperture up and aperture down). Hermit crab weight, shell weight, shell shape, aperture orientation, and depth of burial were analyzed to determine their influence on shell abandonment and survival. We found a significant number of hermit crabs that abandoned their shells when compared with the control group. Aperture orientation strongly influenced shell abandonment, with 73.2% of hermit crabs that abandoned their shells doing so from an aperture up position. None of the other variables significantly affected shell abandonment behavior. However, shell weight, shell abandonment, aperture orientation, and depth of burial were all found to be significant factors in the survival of *P. samuelis* when buried. Although abandoning the shell significantly increases the chances of surviving a sedimentation event, such as flooding, this behavior likely puts the crab at increased risk of both predation and being buried in a subsequent event if flooding persists in the short term. Hermit crabs are underrepresented in the fossil record. Especially rare are *in situ* specimens. We suggest one possible reason for this paucity is that, whether the hermit crab survives the burial event or not, if it abandons the shell, the body and shell are less likely to be found fossilized together.

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1. Introduction

1.1. Burial of extant marine invertebrates

Hermit crabs are common intertidal, lower trophic invertebrates. Because of their physiological responses to fluctuating conditions in the intertidal zone they can be used as ecological indicators of freshwater inundation (Dunbar et al., 2003). Flooding is a common event in the intertidal zone, and a substantial amount of sediment is often carried by this freshwater. The term “sediment” includes a broad range of materials such as silt, sand, and gravel from both terrestrial and marine sources (Schiel et al., 2006). Burial with sediment occurs by both natural and anthropogenic means, and is a periodic stress that near shore animals must face. Sediments are physically displaced by a wide variety of mechanisms such as storms (McCall, 1978), tidal sand movements (Grant, 1983), deposition from rivers (McKnight, 1969), terrestrial runoff (Edgar and Barrett, 2000), dredging (Messieh et al., 1991; Essink, 1999; Schratzberger et al., 2000), bait collecting (Jackson and James, 1979), fishing (Hall et al., 1990), bioturbation (Thayer, 1983; François et al., 2001) and trampling (Chandrasekara and Frid, 1996). Disturbed

sediment can vary in depth from 1 mm (Niedoroda et al., 1989) to 5 m (Maurer et al., 1981) depending on the strength of the disrupting force. Thus, even in one location there can be high spatial and temporal variability in the amount of sediment movement.

Other studies have investigated marine invertebrates after burial with sediment both *in situ* and in the laboratory. Nichols et al. (1978) carried out an *in situ* study involving the burial of a pelecypod–polychaete assemblage. They found that within 4 h of burial with 10 cm of sediment, individuals of large size (>0.42 mm) had moved upward at least 5 cm, whereas smaller individuals (0.30–0.42 mm) had not. However, when the experiment was repeated with a 24 h duration the results showed both sizes being distributed equally throughout the 10 cm of sediment. They concluded that *in situ* burial with 10 cm or less did not significantly affect the survival of the pelecypod–polychaete infaunal community as a whole, even though many individuals remained buried.

However, other taxa may have a more difficult time surviving a burial event. Chandrasekara and Frid (1998) assessed the survival of two epibenthic gastropod species, *Hydrobia ulvae* and *Littorina littorea*, after burial with sediment, and in different temperatures. They found the number of *H. ulvae* surviving burial with 5 cm of sediment decreased with increased burial duration and temperature. *Littorina littorea* did not survive the 5 cm burial up to 24 h at any temperature. In addition, increasing burial depth in 1 cm increments up to 5 cm

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significantly reduced the ability of *L. littorea* to escape out of the sediment.

Studies have investigated the responses of hermit crabs to life in the often disrupted intertidal zone with respect to salinity (Dunbar et al., 2003), temperature (Burggren and McMahon, 1981; Dunbar, 2001) and industrial and agricultural runoff (Lyla et al., 1998). Although hermit crabs are very common along the sediment–water interface, we are aware of no previous studies that have investigated the effects of burial on this taxon.

1.2. Hermit crabs and the fossil record

When an intertidal organism is buried immediately *in situ*, that organism has a higher likelihood of becoming part of the lithosphere (fossilization), instead of being recycled into the biosphere (decomposition, scavenging), than those organisms remaining exposed, or transported at death (Behrensmeier et al., 2000). Although hermit crabs live in habitats that are conducive to fossilization, they are nevertheless underrepresented in the fossil record (Gordan, 1956; Dunbar and Nyborg, 2003; Jagt et al., 2006). Of the hermit crab fossils that have been found, disarticulated chelipeds are most common (Walker, 1988). Records of fossil hermit crabs articulated with the gastropod shells they once inhabited are especially rare (Hyden and Forest, 1980). Only a handful of *in situ* specimens have been described worldwide (Dunbar and Nyborg, 2003; Fraaije, 2003; Jagt et al., 2006). Fossilized, unoccupied gastropod shells that hermit crabs once inhabited also provide indirect evidence of hermit crabs in the fossil record (Boekschoten, 1967; Muller, 1979; Walker and Carlton, 1995). Thus, both the hermit crab body and the shell are fossilizable. This begs the question why hermit crabs are not found more often fossilized within their gastropod shells after burial.

Hermit crabs provide an appropriate model for testing behavioral strategies to escape burial since they require gastropod shells to protect their soft abdomens but, unlike gastropods, are able to abandon the shell when necessary. The purpose of this study was to analyze the behavioral responses of the intertidal hermit crab, *Pagurus samuelis*, to the environmental stress of burial, and to investigate factors influencing shell abandonment and survival of buried hermit crabs.

2. Materials and methods

2.1. Collection and care of hermit crabs

Individuals of the hermit crab, *Pagurus samuelis* (Stimpson 1857) were collected by hand from tide pools at Shaw's Cove (33° 32' 43" N, 117° 47' 57" W) and Little Corona del Mar (33° 35' 21" N, 117° 52' 05" W) in Southern California from February 2005 to February 2006. We selected individuals of all sizes, with hermit crab body weights from 0.018 to 0.629 g. Animals were not sexed because other studies have found no effect of sex on behavioral response of hermit crabs (Bertness, 1980; Hazlett, 1996; Briffa et al., 2008). No gravid females were used in treatments or controls. Hermit crabs were transported to the laboratory within 2 h of collection, and subsequently kept in aquaria. Salinity was maintained at 36 ± 3 ppK and temperature at 24 ± 2 °C with ambient light. Diet consisted of frozen, commercial salad shrimp once a week, and water was changed every three weeks.

2.2. Pre-burial methods

To test the hypotheses that animal size and shell size affects survivability and shell abandonment, morphometric measurements were recorded for each *P. samuelis* before burial. Hermit crabs were randomly selected from the aquarium for experimentation, shaken gently and blotted with paper towel to remove excess water. The shape of the shell was categorized and recorded as either "round" (i.e.

Tegula funebralis) or "elongate" (i.e. *Acanthina spirata*). Length and width for both the shell and the aperture were measured using Vernier calipers (± 0.25 mm). Total wet weight of each crab inside the gastropod shell was measured and recorded to ± 0.001 g.

2.3. Burial methods

Hermit crabs were placed into plastic containers previously filled with 3 cm of sand of preselected grain size (>0.3 mm– <0.5 mm) in one of two aperture orientations. This sediment size range is considered "medium" (Wentworth, 1922; Alexander et al., 1993). In order to test the effect of aperture orientation on shell abandonment and survivability, 45 hermit crabs were placed with apertures up and 45 down. Aperture orientation of the replicates was decided ahead of time, but hermit crabs were selected randomly from the aquarium. Individuals were held in place while they were slowly buried with water saturated sand, until the desired depth of sand covered the crab, and there was 1 cm of standing water. We tested hermit crabs at three burial depths: 2, 4, and 6 cm of sand. At 8 h intervals hermit crabs were checked and, if applicable, we recorded escape time and shell association. Treatments were ended after 24 h, at which time hermit crabs that had not escaped were excavated. Depths at which the crab and shell were found during excavation were recorded. A control group ($n = 10$) underwent the same pre-burial and burial methods, short of being buried.

2.4. Post-burial methods

After each treatment, forceps were used to gently pull dead hermit crabs from their shells. If a live crab remained in its shell, the crab was separated from its shell by placing the animal into a labeled paper bag and cracking the shell open with a bench vise. The paper bag enabled all shell fragments to be weighed. Once disarticulated from the shell, wet weights were obtained for the crab and the shell separately.

These methods were repeated until 30 data sets were obtained for each of the 3 sand depths. After each treatment, water inside each burial container was changed, and the sand rinsed to reoxygenate the sediment and removed any metabolic wastes, or traces of previous hermit crabs.

2.5. Statistical analyses

To determine the relationship between the weight of the hermit crab and the weight and size of the shell, a 2-tailed Pearson correlation was done for each pair of variables. To test the hypothesis that more hermit crabs abandoned their shells among the treatment group than the control group, a one-tailed Fisher exact test was used because the data violated assumptions for a chi-square test (Wheater and Cook, 2000). The independent variables shell weight, crab weight, weight ratio, shell shape, aperture orientation, and burial depth were analyzed using two step-wise logistic regressions ($\alpha = 0.05$) to test their affect on the dependant variables; shell abandonment and survival. All statistical tests were performed with the program Statistical Package for the Social Sciences (SPSS) 14.0.

3. Results

3.1. Preliminary tests

Preliminary tests with a TPS 90-D oxygen meter and Clark-type oxygen electrode were used to determine the extent to which conditions within the sediment became hypoxic. Results of the oxygen saturation tests showed a decline in the percent saturation with time. Oxygen saturation dropped to a mean of $26.6 \pm 4.4\%$ within 15 min of burial. An oxygen concentration of less than 10% was

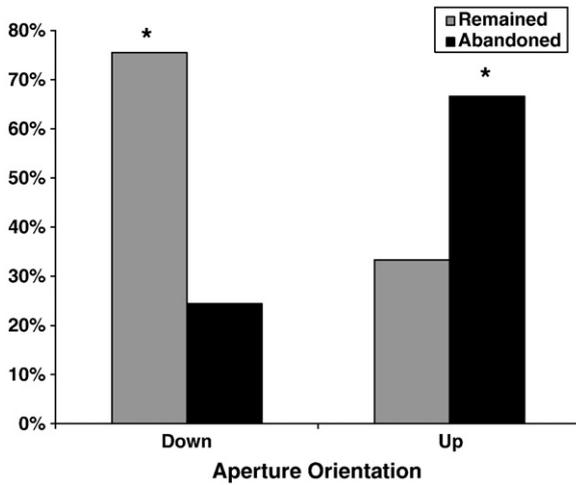


Fig. 1. The percent of individuals that remained in or abandoned the shell at each shell aperture orientation after burial with sediment. Logistic regression $B = -1.822$, S.E. = 0.469, Wald = 15.061, $df = 1$, $p < 0.001$, odds ratio = 0.162. An asterisk represents $p < 0.05$.

reached within 7.5 h after burial and continued to decline to a mean of $1.8 \pm 0.7\%$ at 24 h.

We found that hermit crab weight correlated significantly with both shell weight and shell aperture width (shell weight: $r = 0.855$, $p < 0.001$; shell aperture width: $r = 0.852$, $p < 0.001$).

3.2. Factors affecting shell abandonment

The total number of hermit crabs that abandoned their shells after burial in the treatment group was found to be significantly higher than individuals that abandoned the shells in the control group (treatment = 46%, $n = 90$; control = 0%, $n = 10$; Fisher exact test, $p = 0.004$).

A forward, step-wise logistic regression was conducted to determine which independent variables (shell weight, crab weight, shell shape, aperture orientation, and burial depth) were predictors of shell abandonment. Regression results indicated the overall model of one predictor (aperture orientation) was statistically reliable in distinguishing between hermit crabs abandoning their shells or remaining inside (2 Log Likelihood = 107.340, $\chi^2_{(1)} = 16.715$, $p < 0.001$). The model correctly classified 71.1% of the cases. Regression coefficients were $B = -1.822$, S.E. = 0.469, Wald = 15.061, $df = 1$, $p < 0.001$, Odds ratio = 0.162. Aperture orientation strongly influenced shell abandonment so that 66.7% of crabs buried aperture up abandoned the shell, while only 24.4% of crabs that were buried aperture down abandoned (Fig. 1). Of the total number of hermit crabs that abandoned the shell 73.2% did so from an aperture up orientation. None of the other variables significantly affected shell abandonment behavior.

Table 1
The number of hermit crabs that remained in the shell or abandoned the shell for each state.

	Number of individuals	In shell	Abandoned
Escaped (survived)	69	30	39*
Remained buried (died)	21	19 ^a	2
<i>n</i>	90	49	41

*Logistic regression $B = 4.223$, S.E. = 1.109, Wald = 14.505, $df = 1$, $p = < 0.001$, odds ratio = 68.257.

^a One individual remained buried, but was alive.

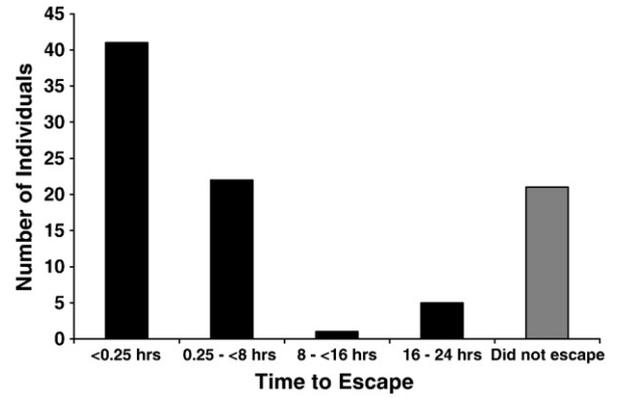


Fig. 2. The number of hermit crabs that escaped the sediment for each time interval.

3.3. Factors affecting survival

Over all treatment depths 76.7% of the hermit crabs escaped the sediment (Table 1). Hermit crabs that escaped the sediment ($n = 69$) remained alive until the trial was ended. Conversely, all crabs (except one) that remained buried in the sediment ($n = 21$), were dead at the end of the trials (Table 1). When comparing the amount of time hermit crabs took to escape, most crabs (91.3%) did so within the first 8 h of the trial, and only 5.6% escaped the sediment at the 24 h point (Fig. 2).

Regression results indicated the overall model of four predictors (shell weight, shell abandonment, aperture orientation, and burial depth) was statistically reliable in distinguishing between survival and death of the hermit crabs when buried (-2 Log Likelihood = 50.344; $\chi^2_{(5)} = 45.003$, $p < 0.001$). The model correctly classified 87.8% of the cases. Shell weight was a significant predictor of survival (logistic regression $B = 1.239$, S.E. = 0.632, Wald = 3.840, $df = 1$, $p = 0.05$). Hermit crabs that survived the burials irrespective of aperture orientation had a smaller mean shell weight (Fig. 3).

There was an obvious interaction between the factors shell abandonment (logistic regression $B = 4.223$, S.E. = 1.109, Wald = 14.505, $df = 1$, $p < 0.001$, odds ratio = 68.257) and aperture orientation (logistic regression $B = -1.968$, S.E. = 0.897, Wald = 4.817, $df = 1$, $p = 0.028$, odds ratio = 0.140). While survival rate for crabs that remained in the shell was 63.3%, survival for those that abandoned their shells was significantly higher (95.1%) (Table 1). This becomes more evident when taking aperture orientation into account. Fig. 4 shows the percentage of crabs that survived from the two different aperture orientations, and whether or not they used shell abandonment as the primary method of survival. Hermit crabs buried with the aperture

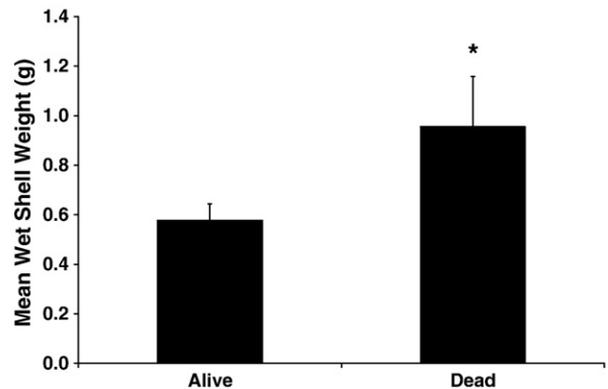


Fig. 3. The mean shell wet weights of hermit crabs that survived the burial and those that died. Error bars represent ± 1 S.E. Logistic regression: $B = 1.239$, S.E. = 0.632, Wald = 3.840, $df = 1$, $p = 0.05$. An asterisk represents significance at the $\alpha = 0.05$ level.

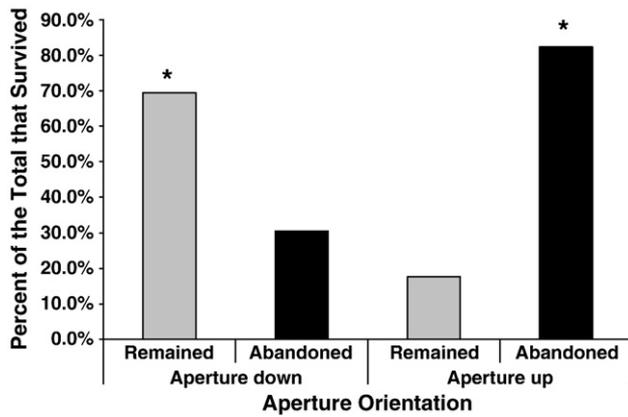


Fig. 4. The percentage of crabs that survived the experiment by either remaining in the shell (gray bars) or abandoning the shell (black bars) and in which aperture orientation they were buried. Logistic regression $B = -1.968$, $S.E. = 0.897$, $Wald = 4.817$, $df = 1$, $p = 0.028$, odds ratio = 0.140. An asterisk represents $p < 0.05$.

down primarily survived by remaining in their shells (69.4%), and secondarily survived by abandoning. Conversely, those crabs buried with the aperture up primarily survived by abandoning shells (82.4%) and secondarily survived by remaining in shells.

Depth of burial was also a significant factor in determining the survival of *P. samuelis* (logistic regression $Wald = 10.734$, $df = 2$, $p = 0.005$). We found that depth and survival were inversely related. At depths of 2, 4, and 6 cm, 96.7%, 73.3%, and 63.3% of the crabs survived the trials, respectively (Fig. 5).

4. Discussion

We found that a significant number of hermit crabs abandoned their shells when buried with sediment, and that the only factor influencing this behavior was the orientation of the shell aperture at the time of burial. Hermit crabs that were buried with shell apertures facing upwards abandoned the shells significantly more often than hermit crabs buried with shell apertures downward. We suggest two reasons for this. First, it was more difficult for hermit crabs to pull the shell upwards through the sediment compared to the aperture down orientation in which crabs could push their shells from underneath towards the surface. This may be because when the shell is in an aperture down position, its external architecture may provide a substrate over which sediments above can flow (McNair et al., 1981; Holomuzki and Biggs, 2006). Secondly, as hermit crabs buried aperture up emerged from shells to pull themselves and their shells

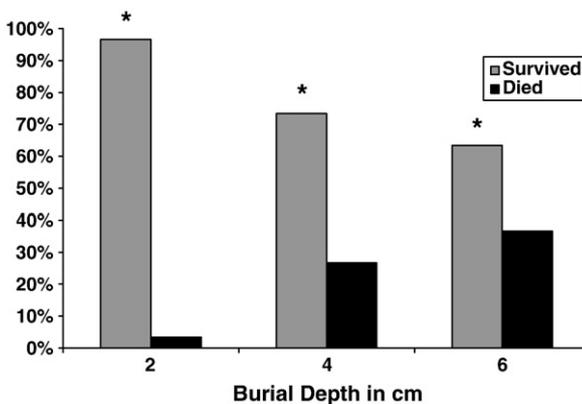


Fig. 5. The proportion of hermit crabs that survived the burial based on burial depth. Logistic regression $B = -1.968$, $S.E. = 0.897$, $Wald = 4.817$, $df = 1$, $p = 0.028$, odds ratio = 0.140. An asterisk represents $p < 0.05$.

to the surface, sediment likely began to fill the shell. The further out of the shell the hermit crab emerged, the more the shell would fill with sand. This would, in all likelihood, cause the hermit crab to leave the sediment filled shell.

Although gastropod shell type has been shown to influence hermit crab fitness (Bertness, 1981), and probability of being oviparous (Bach et al., 1976; Fotheringham, 1980), we did not find it to be a predictor of shell abandonment or survival. Bertness (1981) found that shell species with a higher internal volume and a lower weight were optimal for increasing hermit crab growth and clutch size. Not only does shell species affect hermit crab fitness, but so also does weight variations within a given shell species. Childress (1972) calculated weight ratios for hermit crab shell weight to body weight and discovered optimum ratios for growth and fecundity. Côté et al. (1998) found that when faced with the stress of hypoxia hermit crabs will choose to abandon larger, heavier shells in favor of smaller, lighter ones. Therefore, it is likely that a hermit crab in a shell that is either lighter or heavier than preferred, and faced with the additional stress of a shallow burial event, such as those presented here, would abandon that shell. However, we found no effect of weight ratios on shell abandonment or survival. This may be because vacant shells in a wide range of sizes were available in the aquaria, so it is unlikely hermit crabs inhabited inadequate shells. The highly significant correlation between hermit crab weight and shell aperture size supports this conclusion.

We found shell weight, shell abandonment, aperture orientation, and depth of burial were all significant factors in survival of buried hermit crabs. Shell weight, among other factors, significantly influences hermit crab shell choice (Reese, 1963). Studies have found that a moderately large (and likely also moderately heavy) shell is beneficial for protection from predation (Vance, 1972; Vermeij, 1974), growth rate (Markham, 1968), and fecundity (Childress, 1972). However, an increase in shell weight beyond optimum can cause hermit crab growth rate (Bertness, 1981) and clutch size (Childress, 1972) to decrease. Moreover, our study suggests that crabs with heavier shells are less likely to survive a burial event, independent of orientation or depth. One possible explanation for this is that a heavier shell may be more difficult to maneuver through the sand. Fotheringham (1976) concluded that an increase in shell weight would increase the energy a hermit crab must expend carrying it, and could reach a point at which the weight may impede mobility. In addition we found that shell weight and aperture size correlated directly with hermit crab weight, so crabs having large shells are themselves large.

Another hypothesis is that the larger crabs were more likely to remain tucked inside the shell to wait out the stress. We observed instances in which some large crabs made no effort to escape the burial (J.S., personal observation). Fink (1941) found that larger *Pagurus longicarpus* once startled into retraction, took longer to reemerge from the shell than smaller hermit crabs. However, a more recent study found no correlation between startle response and weight of *Pagurus bernhardus* (Briffa et al., 2008). In the current study, individual hermit crabs were prevented from crawling up the sediment until the determined burial depth was reached, but Hinchey et al. (2006) observed some amphipod individuals swimming upward through the sediment as it was being deposited. They concluded that, among species, motility was the most important survival factor, rather than whether the species was naturally infaunal or epibenthic. We suggest that this is true within *P. samuelis* as well, and those individuals that exhibited greater motility were more likely to survive our treatments.

Shell abandonment behavior also played a significant role in whether or not crabs survived burial. In both groups (crabs that escaped and those that remained buried) some individuals abandoned their shells. However, the majority of hermit crabs that abandoned their shells escaped out of the sediment and survived

the burial event. This was verified by the high odds ratio (68.3) for shell abandonment indicating that if the hermit crab abandoned the shell instead of remaining inside, it was very likely to switch survival categories as well. Herreid and Full (1986) showed that it was energetically costly for hermit crabs to carry shells while running on a treadmill when compared to hermit crabs without shells. To expend less energy is most likely an important motivation for hermit crabs in the present study to abandon shells and therefore survive the burial event.

Our data suggest that abandoning the shell may facilitate easier mobility and maneuvering through the sediment to emerge at the surface, however not all crabs did so. When faced with multiple stressors, hermit crabs may actually evaluate each situation and choose to fulfill the most urgent need, whether metabolic or behavioral. Côté et al. (1998) demonstrated that hermit crabs facing hypoxia will choose shells in which they must expend less energy to carry. Additionally, Billock and Dunbar (2009) found that hermit crabs can prioritize information depending on what they decide is their most immediate need, and that they are more motivated to find a protective shell than feed when both needs are present. Although abandoning the shell may help the crab survive a burial event, it may also increase susceptibility to other threats upon reaching the surface. Without the shell, the soft abdomen of the hermit crab is exposed and vulnerable to predation (Reese, 1969; Vance, 1972; Angel, 2000), desiccation (Reese, 1968) and osmotic stress (Shumway, 1978). The overarching need to have the protection of the gastropod shell may be a reason some hermit crabs in the current study remained in the shell even in hypoxic conditions.

Aperture orientation was also a significant indicator of survival. We demonstrated that crabs buried with shell apertures down were more likely to survive while remaining in their shells. In contrast, crabs buried in the aperture up position were more likely to survive by abandoning their shells. Thus, we suggest that being buried aperture up may increase the potential for surviving a shallow burial event such as those simulated by our experiments.

With respect to burial depth, our results demonstrated that depth was strongly and negatively correlated with survival. Therefore, if a hermit crab is buried during a sedimentation event in the intertidal zone, the deeper the sedimentation the more likely the crab will be unable to escape, making it a candidate for *in situ* fossilization. The converse is also true; that the more shallow the hermit crab is buried, the more likely it will survive the sedimentation event, and will not be fossilized at that time.

However, different burial depths affect various taxa in diverse ways. A study involving polychaetes found that survival of both juvenile and adult *Streblospio benedicti* exponentially declined with deeper burial depth (Hinchey et al., 2006). The same study also investigated burial in the clam, *Macoma balthica*, and juveniles of the oyster, *Crassostrea virginica*. Depths used in treatments were considered “high” based on the greatest sedimentation amount found by the authors in the natural environment of each species. *Macoma balthica*, which is a natural burrower, showed no decrease in survival or growth with an increase in burial depth. *Crassostrea virginica*, which is typically anchored to a substrate, was also able to survive six days of the highest burial depth used in the study. However, the highest mean depth of 0.5 cm of sediment for *C. virginica* was not at all high when compared to the highest depth used for *M. balthica* (24.6 cm). Moreover, one could hypothesize that *C. virginica* would not survive any burial in which the sediment was not removed by the researcher, water, wind, or some other force. Additionally, Hinchey et al. (2006) investigated the amphipod, *Leptocheirus plumulosus* and found survival of this species declined exponentially with increasing burial depth, but not nearly as sharply as the polychaete, *S. benedicti*. Despite this decline, the authors still demonstrated that even at high depths (5.9–20.2 cm) *L. plumulosus* and *M. balthica* had greater survival than other species studied, and

that one reason for this was the greater motility exhibited by amphipods and clams. Nichols et al. (1978) found that with a burial depth of 30 cm, no polychaetes or pelecypods moved upward at all in the sediment column. They suggested that 30 cm was a critical burial depth in which some event, such as compaction, inhibited any movement. In our study, the deepest burial depth of 6 cm was not a critical depth, because some individuals escaped.

We suggest that shell abandonment behavior is a possible reason for the paucity of *in situ* fossilized hermit crabs. Although shell abandonment occurred in either aperture orientation, it is more likely that hermit crabs will leave their shells behind if buried aperture up. This empty, buried shell, with evidence of hermit crab inhabitation, could then be fossilized. If the hermit crab abandons the shell but is unable to reach the surface (as two crabs did in this study) the crab may also become disarticulated and fossilized away from its shell. Therefore, *in situ* fossilization may be less likely for crabs buried with the shell aperture upward.

Finding possible reasons for the lack of *in situ* fossilized hermit crabs has implications for geology, biology, and ecology. Understanding a possible taphonomic bias can improve interpretations of paleoenvironments. Successful escape from burial decreases the probability of being fossilized and biases the resulting fossil assemblage (Nichols et al., 1978).

Ecology and biology are impacted by determining the adaptations of marine invertebrates to rapid sedimentation and physiological responses. A catastrophic burial may selectively kill certain organisms that cannot crawl up through the sediment, thus creating vacant patches (Hall, 1994) in which other organisms can become established. Several factors determine which organisms survive a burial event including mobility (Hinchey et al., 2006; current study), being a naturally burrowing species (Hinchey et al., 2006), and ability to provide for the body's energy needs by undergoing anaerobic respiration (Henry et al., 1994). While further investigations into the physiological responses of buried hermit crabs are needed, the current study has shown that some behaviors demonstrated by hermit crabs during shallow burial events may increase their chances of survival.

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