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

Janelle A. Shives [a,b], Stephen G. Dunbar [a,b,*]

[a] *Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92350, USA*
[b] *Marine Research Group, LLU, USA*

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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.

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

* Corresponding author. Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92350, USA. Tel.: +1 909 558 4530; fax: +1 909 558 0259.
E-mail address: sdunbar@llu.edu (S.G. Dunbar).

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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 (Behrensmeyer 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