

The Confounded Feeding Biology of Trypetesid Burrowing Barnacles and Their Impacts on Hermit Crab Hosts

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Darwin on his “beloved” and “confounded” barnacles¹:

“I could spend another month on it, and daily see some more beautiful structure.” to Robert Fitzroy (Commander of the H.M.S. Beagle) in 1846.

“I hate a Barnacle as no man ever did before, not even a Sailor in a slow-sailing ship.” to William Fox (Darwin’s second cousin) in 1852.

Abstract

The burrowing barnacle family Trypetesidae is composed of seven living species that are exclusively associated with hermit crab hosts. These barnacles exhibit sexual dimorphism and the larger females are typically found in burrows associated with the columella of gastropod shells inhabited by hermit crabs. Although trypetesids were known since before Darwin’s multi-volume work on barnacles, their feeding biology has remained a mystery. I have found that at least three species of trypetesids are egg predators of hermit crabs, as evidenced by their gut contents. It appears that several unique aspects of their morphology (including lack of anus, reduced feeding structures [cirri], and

¹From: Darwin Correspondence Database, (<http://www.darwinproject.ac.uk>) accessed May 2, 2012

cushions on the cirri) can be explained by their evolution as egg predators. Future research on the natural history of trypetesid barnacles is discussed.

Introduction

Charles Darwin spent many productive years of his life studying barnacles and these fascinating marine invertebrates served as a taxonomic training ground for him. However, it is not commonly conveyed how enamored of marine invertebrates he was and how he developed into a great marine biologist (Rainbow, 2011). In fact, Darwin devoted over 8 years to the study of the barnacles (living and extinct species), ultimately producing four monographs on the group (Darwin, 1851, 1852, 1854, 1855). It was a burrowing barnacle found in a gastropod shell on the coast of Chile that initially inspired his interest in barnacles. Although his excitement and enjoyment in the study of these marine creatures was apparently replaced by a sense of dread that he would never complete his work, he persevered and became an authority on this ecologically and commercially important group (Crisp, 1983; van Wyhe, 2007).

Darwin delved into both the thoracican barnacles (filter feeding barnacles, commonly recognized as fouling species attached to rocks and docks) and the acrothoracican barnacles (the burrowing barnacles, not often encountered unless one finds the small slits left by the barnacles in shells). The acrothoracican barnacles are known to bore into a wide range of substrates, including commercially important molluscs, corals, and rocks. One additional group of barnacles (the parasitic rhizocephalans) are currently recognized (see Boyko & Williams, 2009; McDermott et al., 2010) but were not covered by Darwin. Darwin's work on barnacles has been chronicled in numerous scientific (e.g., Crisp, 1983; Newman, 1993; van Wyhe, 2007; Deutsch, 2009, 2010) and popular (Stott, 2003) texts.

Among the burrowing barnacles, Darwin examined a member of the genus *Trypetesa*. The species *T. lampas* was originally described by Hancock (1849), but Darwin more completely described some interesting aspects of its life history. This research required him to think deeply about the evolutionary relationships of barnacles (and other crustaceans), although he was not always correct in his conclusions about the features he observed in barnacles (see Crisp, 1983; Deutsch, 2009, 2010). His struggle with species

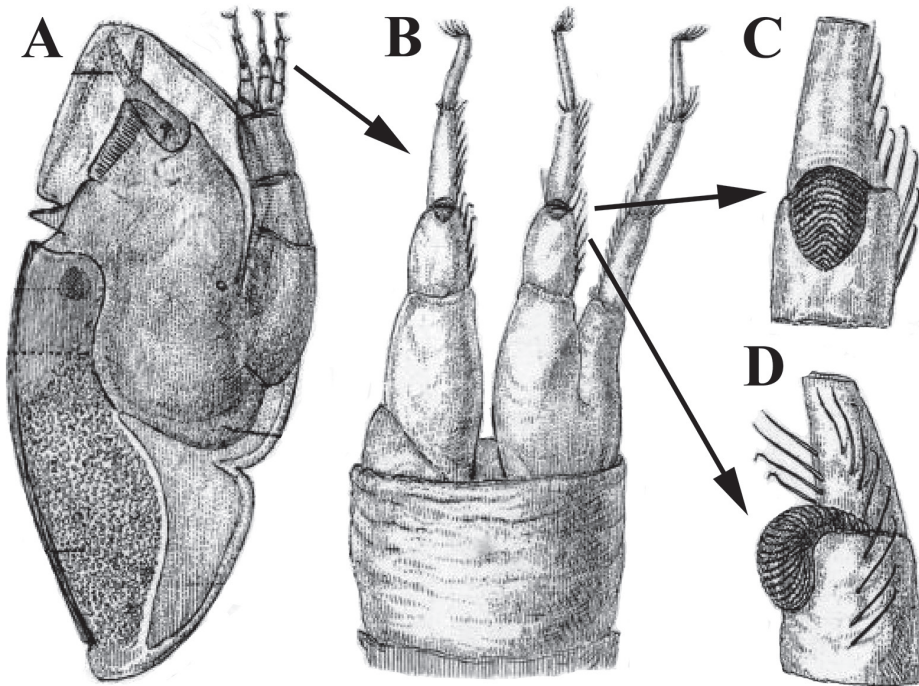


Figure 1. The burrowing barnacle *Trypetesa lampas* as figured by Darwin (1854). **A)** Overview of *T. lampas* with thoracic cirri on right side. **B)** Magnified view of three cirri. **C)** Cirral cushion, frontal view. **D)** Cirral cushion, lateral view. Not to scale, typical adult barnacles as in (A) approximately 4mm in length. (A–D, modified from Darwin, 1854; Plate 22.)

boundaries, classification and morphology of barnacles certainly influenced and supported his work on the *Origin of Species*. Specifically for the trypetesid barnacles, Darwin observed some puzzling and unique characteristics, such as the lack of an anus, very reduced cirri (feeding structures), and possession of cushions on the cirri (**Figure 1**). Whereas female trypetesid barnacles are relatively large (up to 5mm or longer) and conform to the shell they reside in (**Figures 2A, 4A–E**), male trypetesid barnacles are dwarfs and consist of little more than a penis and bag of sperm (**Figures 2B, 4D, F**); the males lack all feeding structures and are sometimes labeled as “parasitic”—reflecting their obligate attachment to the surface of female barnacles (Gotelli & Spivey, 1992).

A total of seven living species of barnacles have been described in the family Trypetesidae, and all burrow only in empty gastropod shells inhabited

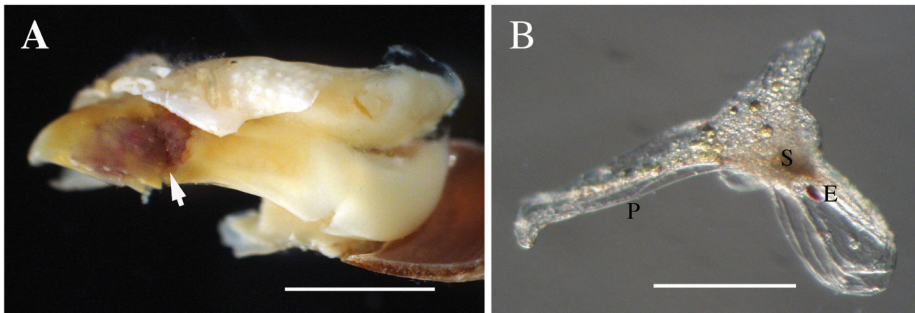


Figure 2. The burrowing barnacle *Trypetesa lampas* collected from the Mediterranean. **A)** Female of *T. lampas* partially removed from gastropod shell, with distended gut containing eggs of host hermit crab (arrow). **B)** Male *T. lampas* with penis (P), sperm (S) and eyespot (E). Scale bars: A = 2.0mm; B = 250 μ m. (Modified from Williams et al., 2011, **Figure 5.**)

by hermit crabs (Williams & Boyko, 2006). The family contains five species in the genus *Trypetesa* and two species in the genus *Tomlinsonia*; the two genera are distinguished by the fact that *Trypetesa* has cirral cushions on only two pairs of cirri whereas *Tomlinsonia* has cushions on all three pairs of cirri (**Figures 4G, 5A–C**; Turquier & Carton, 1976; Williams & Boyko, 2006; Kolbasov, 2009). Darwin was not able to study the feeding biology or ecology of these barnacles in detail but did suspect that the cushions on the pads of the barnacles served some role in feeding. For over 150 years the feeding biology of these barnacles and the function of the cirral cushions remained poorly known. The purpose of this review is to describe the studies completed in my laboratory that have shown at least some of these barnacle species to be egg predators of their hermit crab hosts.

Hermit crabs and their associates

Hermit crabs are common members of marine habitats, ranging from the intertidal to deep sea. Although probably most familiar to non-biologists, terrestrial hermit crabs are relatively rare (representing only ~1.5% of the 1100+ species presently known; McLaughlin et al., 2010) and are restricted to the tropics. However, like all hermit crabs, they must return to the sea in order to reproduce, releasing their larvae into the water where they develop for a period prior to settling. After metamorphosis, most hermit crabs occupy

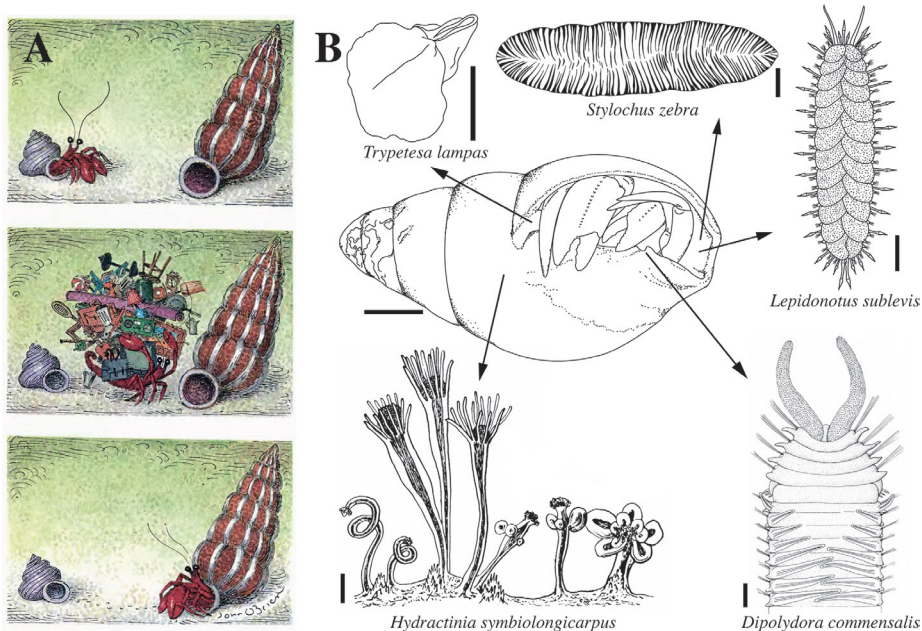


Figure 3. Hermit crab symbiont communities. **A)** Cartoon of the baggage that hermit crabs carry, an analogy for the symbionts (commensal, mutualistic and parasitic) that are hosted by hermit crabs. **B)** Symbionts of the hermit crab *Pagurus longicarpus* (shown occupying an empty shell of the eastern mudsnail *Ilyanassa obsoleta* in center) that have been documented to act as egg predators (clockwise from top left to bottom left: the burrowing barnacle *Trypetesa lampas*, the flatworm *Stylochus zebra*, the free-living polychaete worm *Lepidonotus sublevis*, the boring polychaete worm *Dipolydora commensalis*, and the colonial hydroid *Hydractinia symbiolongicarpus*). Scale bars: B, horizontal scale for center figure = 2.5 mm; vertical scales to left of symbionts = 0.5 mm; vertical scales to right of symbionts = 5 mm. (A, modified from *The New Yorker*, May, 9, 1994, with permission from the Cartoon Bank of the New Yorker; B, modified from Williams & McDermott, 2004, Figure 3.)

empty gastropod shells to protect their soft abdomens from predators, which include fish, birds and other crabs (McGuire & Williams, 2010). Partly due to their use of gastropod shells as protective and portable “homes,” hermit crabs act as hosts to a wide range of symbionts, including commensal, mutualistic and parasitic species (Figure 3).

Many of the associates of hermit crabs live with them due to their use of empty gastropod shells and other substrates. In fact, over 550 species of invertebrates have been found to live with hermit crabs, either living attached

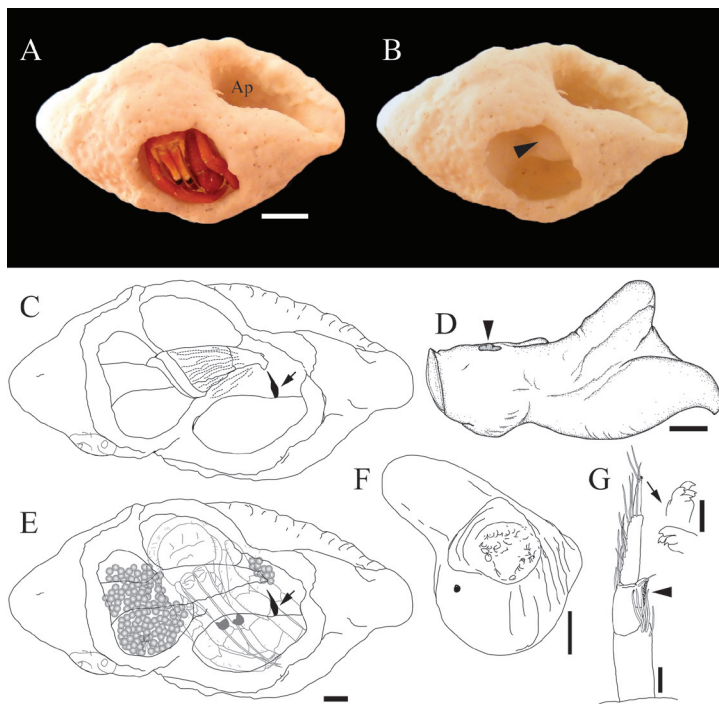


Figure 4. The burrowing barnacle *Tomlinsonia mclaughlinae*. **A)** Shell of the gastropod *Drupella cornus* inhabited by the hermit crab *Calcinus gaimardii* shown withdrawn into shell through a cut away section in the shell; in life the legs of the hermit crab body would be positioned out of the shell aperture (Ap) for movement; minute holes on surface of the shell are made by a burrowing polychaete worm. **B)** Same gastropod shell as in part (A) but hermit crab has been removed to show columella of the shell (arrowhead) where the body of the burrowing barnacle would be positioned. **C)** Empty shell of the gastropod *Drupella cornus* cut away to show position of barnacle aperture (arrow) on the columella; the position of the body of the barnacle within the shell is shown by the striations (weakened area of the shell due to burrowing activity of the barnacle). **D)** Female *T. mclaughlinae* removed from shell, male barnacle attached to female shown by arrowhead. **E)** Same gastropod shell as in part (C) but here a semi-transparent ovigerous hermit crab (*Calcinus gaimardii*) is shown withdrawn in the shell as it would be positioned in life. The eggs (shown as grey spheres) are attached to the abdomen of the hermit crab and would be positioned over the barnacle aperture (arrow) when the hermit crab is extended from the shell and mobile. **F)** Boot-shaped male of *T. mclaughlinae*. **G)** Lateral view of single terminal cirrus of *T. mclaughlinae*, showing two magnified views of terminal hooks on cirrus and cirral cushion (arrowhead). Scale bars: A, B = 3mm; C, E = 2mm; D = 1mm; F = 125 μ m; G = 50 μ m, inset = 6.25 μ m. (C–G, modified from Williams & Boyko, 2006; Figures 1, 2, 5.)

to their shells, free living within the shells, or boring into the shells (**Figure 3B**). In this way, hermit crabs can support a whole community of species and for this reason hermit crabs are labeled as ecosystem engineers (analogous to beavers that support a range of species due to their modification of the environment; Williams & McDermott, 2004). Hermit crabs also harbor over 150 species of strict parasites that live on or within the hosts, often deriving all their energy requirements from the hosts (McDermott et al., 2010). The impacts to hosts are clear for many parasites, some of which shut down reproduction of their hosts or cause parasitic castration (Boyko & Williams, 2009).

In contrast, the impacts of most hermit crab associates are not completely known or can change based on environmental conditions. Thus, the nature of their symbiotic relationship can be frustratingly nebulous. For example, burrowing polychaete worms and hydroids are typically categorized as commensal species (i.e., they live with the host and gain benefits but do not harm the hosts in the process). However, these species are known to weaken the shells inhabited by hermit crabs and thus can expose the hosts to increased predation (Buckley & Ebersole, 1994). In addition, they have been shown to be egg predators of hosts, removing eggs or developing embryos of the hermit crabs. For these reasons, they cannot be defined as commensal species (perhaps no symbionts can be defined narrowly as commensal species; see Zapalksi, 2011) and categorizing them as transient egg predators better conveys their parasitic tendencies. Egg predation is found in other marine systems (e.g., Shields et al., 1990; Järnægren et al., 2005) and egg predators are not uncommon among hermit crabs, with at least 14 species presently documented (**Figure 3B**; Williams & McDermott, 2004; Williams et al., 2011; Williams, unpubl.). Among these are the trypetesid barnacles, another example of hermit crab symbionts that were not previously known to negatively impact hermit crabs.

The natural history and feeding biology of trypetesid barnacles

The fact that trypetesid barnacles were classified for 150+ years as commensals largely reflects ignorance of their dietary habits. Although the unique morphological features pertaining to their feeding biology (lack of anus, reduced cirri, and cirral cushions) were noted in the original description of *T. lampas*, the food preferences of the barnacles remained a mystery.

Hancock speculated that the modified feeding structures of the barnacles were used to capture prey items, stating "...the arms or feet indeed appear to be merely prehensile organs laying hold of prey by the aid of the cushion-like swellings before described as attached to their inner margins" (Hancock, 1849, pg. 311). In contrast, Darwin was not convinced of this as being their function and noted "I at first thought, with Mr. Hancock, that these buttons served to catch the prey; but, reflecting on their convexity and hardness, they appear very badly adapted for this purpose; it would, in fact, be a marvelous feat to secure, in the dark, any moving object between four balls. On the other hand, this very convexity, the hardness, and especially the crenated ridges, and the powerful muscles (which from the first surprised me), are all well explained, if we suppose the prey, being secured by the terminal segments, to be triturated between these four balls..." (Darwin, 1854, pg. 544). Neither author was able to observe the movements during feeding; such observations were not made until the work of Tomlinson (1969) who concluded that the cirri were not extended from the burrows of the barnacles. Tomlinson (1969) and Kamens (1981) proposed that the barnacles fed by a pumping action of the mantle, allowing them to draw in small food particles. The barnacles were suspected to be restricted in their diet, being microphagous and feeding on small particles in the plankton or perhaps the fecal material of host hermit crabs, but these hypotheses have not been experimentally tested.

Field studies and research in my lab over the past decade have shown that trypetesid barnacles are able to engage in a macrophagous mode of feeding and can ingest eggs and developing embryos attached to the pleopods of hermit crab hosts. I first observed hermit crab eggs within the gut of a trypetesid barnacle (*Trypetesa spinulosa*) that I collected in the Philippines. At the time, I was already studying egg predation by another group of hermit crab symbionts: polychaete worms of the family Spionidae (Williams, 2000, 2002). In spite of my familiarity with egg predation by the worms, the extremely distended gut of the barnacles, displaying a deep purple color, the same color as the eggs of the host hermit crab, was still a surprise (**Figure 2A**). My students and I have sampled thousands of hermit crabs and observed the eggs within the guts of 3 trypetesid species from the Philippines, Jamaica, and the Mediterranean (Williams et al., 2011; Murphy & Williams, 2013). Egg predation has been directly observed in the field (through the presence of egg

and/or egg membranes in the gut) and by histological examination of fixed specimens. Prevalence of the barnacles with host hermit crabs ranges from approximately 1.5 to 8%.

To have a better understanding of how the barnacles are able to ingest the eggs, one must understand the position of the barnacles within the shells. Most trypetesid barnacles are positioned on the columella of the gastropod shells and the opening, or aperture of the barnacle, is positioned inside the shell such that the cirri are located adjacent to where the clutch of eggs are attached on ovigerous females (**Figure 4A–C, E**). Normally this would be a well-protected space for the brood of the hermit crab but, for those harboring the barnacles and other egg predators, the eggs are vulnerable.

Discussion and future directions

Hermit crab use of gastropod shells beginning in the early Jurassic, circa 175–200 million years ago, provided a new habitat for trypetesid barnacles, and through their long shared evolutionary history with hermit crabs they have evolved many unique morphological and behavioral features in terms of their feeding biology. It appears possible that all trypetesids are egg predators of hermit crab hosts. Although we now know more about their mode of feeding and can further define their symbiotic relationship with their hosts, there are still many questions that remain to be answered regarding their natural history. Among these is the question of how hermit crab eggs are captured. In other words, although we know the eggs are ingested, we do not know the mechanics of egg capture itself. Are the reduced cirri and their cushions used to “lay hold of prey” as predicted by Hancock (1849)? Based on the formation of the cirri, the cushions do appear to be positioned such that they could act in the capture of host eggs (**Figure 5A**). In addition, scanning electron microscopic examination shows these cushions have a surface covered with rows of minute blade-like denticles (spines) that are oriented downward (**Figure 5B, C**) and the cirri terminate in minute terminal hooks (**Figure 4G**).

Unfortunately, this hypothesis on the mode of capture is very difficult to test because the barnacles reside within an opaque shell, blocking observations of their feeding appendage movements. It may be possible to drill “windows” into shells and make observations with a dissecting scope or, alternatively, an endoscope may be used to observe their activity as has been done on the

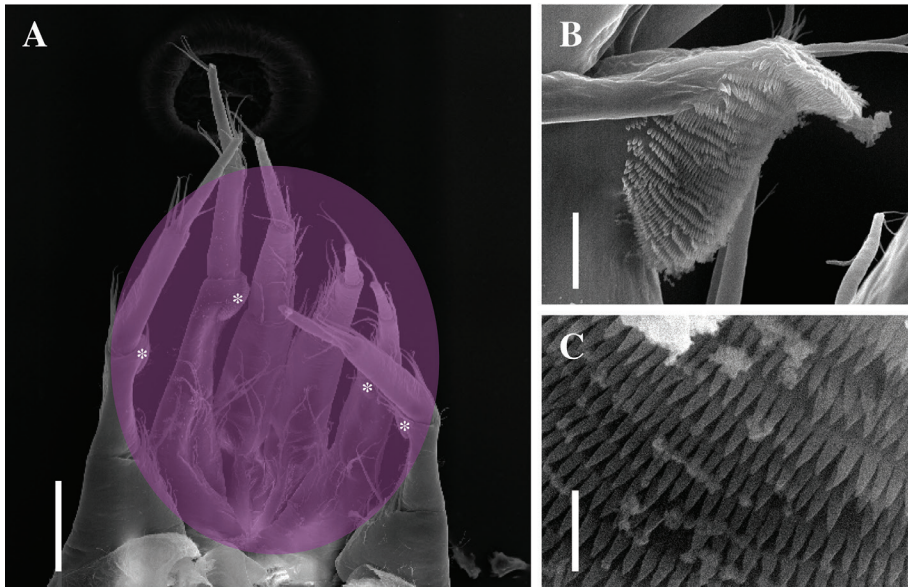


Figure 5. The burrowing barnacle *Trypetesa lampas*, SEM micrographs. **A)** Three pairs of terminal cirri (with cirral cushions denoted by white asterisks). Purple oval shows size of host hermit crab egg in relation to three pairs of cirri. **B)** Lateral view of single cirral cushion; **C)** rows of denticles on cirral cushion. Scale bars: A = 100 μ m; B = 10 μ m; C = 2.5 μ m. (Modified from Murphy & Williams, 2013)

feeding biology of bivalves (e.g., Ward et al., 1993). Glass or plastic shells, which have proved useful in other studies with hermit crabs (e.g., Lytwyn & McDermott 1976), do not work for trypetesids because the barnacles will not bore into these substrates.

The timing of egg predation is not completely known. We have documented that the barnacles can feed on eggs or embryos once these are attached to the pleopods (Williams et al. 2011; Murphy & Williams, 2013). It is possible that some of the eggs are also ingested prior to this as they are extruded from the gonopores of the female hermit crab. In addition, loss of developing embryos from the brood is common in hermit crabs and some of the embryos that are ingested may have been naturally dislodged, as opposed to being removed from the pleopods by the cirri.

All trypetesids we have studied to date were found significantly more often with female hermit crab hosts (Williams & Boyko, 2006; Williams et al., 2011, Murphy & Williams, 2013). This finding is perplexing given the fact

that hermit crabs actively seek out new shells regularly and will switch shells based on a variety of factors including the presence of symbionts (Williams & McDermott, 2004). If female hermit crabs were able to sense the presence of the trypetesids and/or the loss of embryos, then why would they remain in shells harboring the barnacles? This may reflect the fact that empty shells, especially those of optimal size and condition, are limited in most hermit crab populations. Therefore, females may remain in shells with trypetesids because avoidance of barnacles would expose them to predators while they move into new shells. The impacts of the barnacles on hermit crabs at the population level may be minimal since the hosts produce many more eggs than ultimately develop to adulthood, even in the absence of egg predators.

Although predominately found with female hermit crabs, the barnacles will occupy shells inhabited by male hosts. What do barnacles feed on while in shells occupied by male hermit crab hosts or non-ovigerous females? Do they forgo feeding during this time or do they switch to another food source? Stable isotope analysis has been used to investigate the diets of a wide range of marine species; in these studies the relative concentrations of Carbon, Nitrogen and Sulfur atom isotopes (e.g., ^{13}C versus ^{12}C , the latter of which has one less neutron in its nucleus) found in potential food items are used to infer the diet of consumers. These methods could be used to determine the relative contribution of hermit crab eggs compared to other potential food sources (e.g., plankton) of the barnacles, as has been done for other egg predators (Järnegen et al., 2005). Such future studies will help to more completely disentangle the confounded nature of trypetesid feeding biology and natural history.

Acknowledgements

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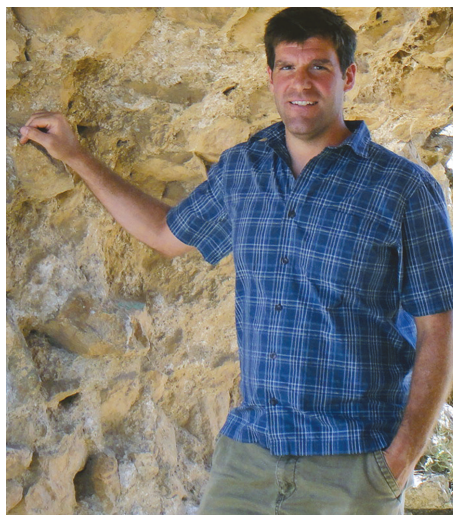
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About the author

Jason Williams received his B.A. in biology from Franklin & Marshall College in 1995, where he began research on hermit crabs and their associates. Williams then went to the University of Rhode Island, earning an M.S. in zoology and a Ph.D. in biological sciences in 1997 and 2000, respectively. He is currently an associate professor at Hofstra University where he teaches courses such as Invertebrate Zoology and Parasitology. For his studies he



has been awarded the Douglas Nolan Award for academic achievement in the sciences (University of Rhode Island) and the Lawrence A. Stessin Prize for outstanding scholarly publication (Hofstra University). His work has been funded by the National Science Foundation, the Sigma-Xi Scientific Society, and the Lerner-Gray Fund for Marine Research. He has published more than 35 peer-reviewed publications.

Effect of F&M education on my career

At Franklin & Marshall College my interests in biology were inspired by the many faculty members who displayed infectious enthusiasm in their courses. In particular, Professor McDermott's marine biology course (including field trips and research) allowed me to begin exploring the biology of invertebrates, especially those with weird and wonderful lifestyles. From that point forward I was hooked, and I hope to impart this passion to my students in both the classroom and research.