The Not So Lonely Lives of Hermit Crabs: Studies on Hermit Crab Symbionts

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The common name "hermit crab" is applied to decapod crustaceans that occupy empty gastropod (snail) shells for protection of their soft abdomens. The name has been in use since the early part of the 18th century and at first glance seems appropriate, based on the apparent solitary lifestyle of these crabs. Since the first description of a hermit crab, more than 800 species have been described from terrestrial to deep-sea habitats worldwide. While the common name has stuck, hermit crabs certainly do not live in seclusion. In fact, due to their use of gastropod shells, whole communities are found associated with hermit crabs. The communities include species that attach to the shells (inside and outside), bore into the shells, live within the lumen of the shells, and attach to the hermit crabs themselves (either as commensals or parasitic species). The behavior of hermit crabs in tidepools has often caught the attention and imagination of children (who are often quick to recognize interesting associates such as "snail fur" or colonial hydroids), yet investigations on the symbiotic relationships among the species in these communities are lacking.

Hermit crabs are some of the most conspicuous and ecologically important members of intertidal and subtidal marine habitats. As scavengers, they compose an important link in the food chains of these habitats and they often attain large populations. They act as food for other crustaceans and some fishes, often when they have been unsuccessful in procuring an adequate shell home. Thus, the attributes of inhabited shells (including the type, weight, size and condition) have been shown to affect predator avoidance, reproduction and development of hermit crabs. In spite of the extensive behavioral studies completed on shell choice by hermit crabs, few researchers have cataloged the biocoenoses or communities of hermit crab symbionts found living on (epibiotic), within (free-living) and boring (endolithic) into occupied shells.

Review of the literature has shown that there presently more than 500 invertebrate species, representing 15 phyla, found associated with hermit crabs (Fig. 1). More than 100 of these symbionts exhibit an obligate relationship with host hermit crabs (i.e., they are found associated only with hermit crab hosts) while the rest of the symbionts are facultative (may or may not occur with hermit crabs) or incidental (found only occasionally with hermit crabs).

Arthropods, flatworms and polychaetes are mostly found free-living within the lumen of inhabited shells. Almost all cnidarians, bryozoans and sponges are found attached externally. Some of these species benefit hermit crabs by alleviating the need of the host to switch into new shells as they grow because the epibionts grow with them. The protozoans are unique in containing mostly species that live on the hermit crab hosts. Endolithic species are most prevalent in the polychaetes but are also found in the arthropods, sponges and bryozoans. Boring species negatively impact hosts by reducing shell strength and thus making hosts more susceptible to predation by shell crushing predators such as crabs. Even land hermit crabs har-

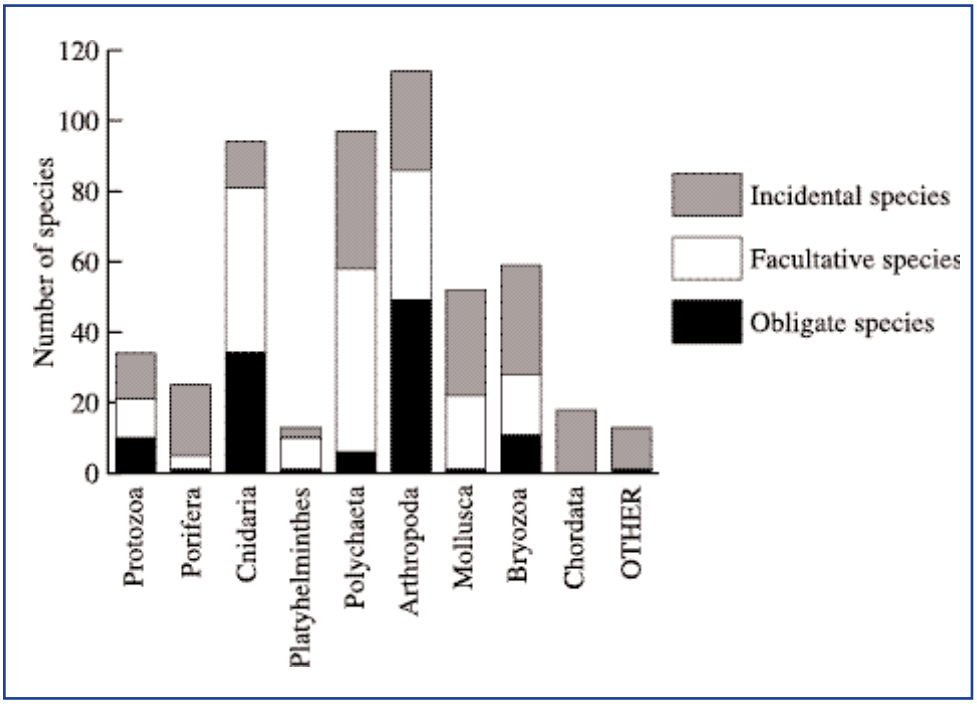

Fig. 1. Number of species of hermit crab associates per major taxonomic grouping, showing the type of symbiotic relationship (obligate, facultative or incidental).

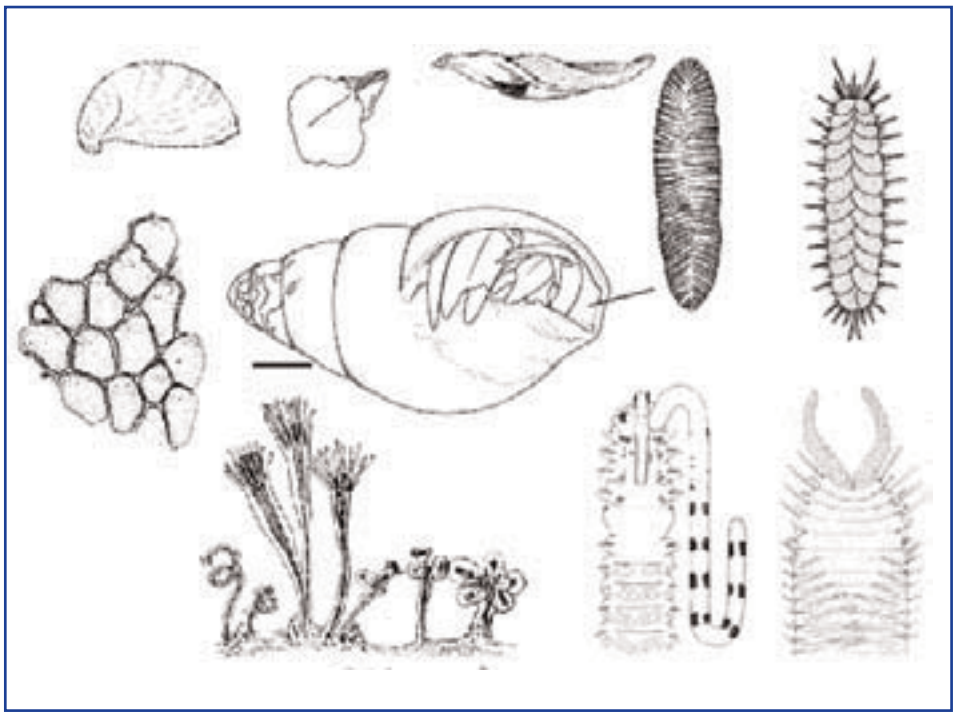

Fig. 2. Symbionts associated with the long wrist hermit crab, *Pagurus longicarpus,* from the east coast of the United States. Scale = 5 mm, for center figure; rest not to scale.

bor symbionts; nine species of mites are found attached to the gills of *Coenobita* species.

The number of symbionts associated with individual hermit crabs can reach 120 species in the best-studied cases. Along the east coast of the United States the long wrist hermit crab, *Pagurus longicarpus*, is known to harbor more than 40 symbionts (Fig. 2). Species commonly associated with *P. longicarpus* include the colonial hydroid (*Hydractinia symbiolongicarpus*), the boring worm (*Dipolydora commensalis*), and the free-living scale-worm (*Lepidonotus sublevis*); typically, 25 to 50 percent of hermit crab shells contain these symbionts in areas of Long Island.

The diversity of communities associated with hermit crabs remains poorly studied for most host species. As a result, the differences in number of species associated with hermit crabs most likely represent a disparity in sampling efforts rather than a real difference in the diversity patterns among geographic regions. For example, while the temperate species, *Pagurus bernhardus*, is associated with more than 80 symbionts, most Indo-West Pacific species have been found with fewer than 10 species; these findings run counter to expectations based on biodiversity of these regions.

Polychaete Worms Associated With Hermit Crabs

Approximately 100 species of polychaetes are associated with hermit crabs, 26 of which are endolithic. I have focused my work on the family Spionidae, particularly *Polydora* and related genera (termed polydorids) that bore into shells and other calcareous substrates. The genera *Dipolydora* and *Polydora* contain more than 70 species, of which 14 are known to bore into gastropod shells occupied by hermit crabs and are considered facultative commensals. Three polydorids (*Dipolydora commensalis*, *Polydora biocipitalis,* and *P. robi*) are obligate commensals, found only in hermit crab shells.

My research in the Indo-West Pacific led to the identification of eight polydorid species among five genera all of which were first records for the Philippines and three were new to science. In addition, two of these species (*Polydora robi* and *P. umangivora)* were found to prey on host hermit crab eggs. Previously polydorids had been considered commensals, but these investigations showed a need to re-examine their symbiotic relationships with hosts and indicated a shift from commensalism to parasitism based on negative impacts on reproductive success of hermit crabs.

Polydora robi creates unique burrows in hermit crab shells (Fig. 3), extending from a hole at the apex to the inside of the shell. Up to 35 percent of shells inhabited by hermit crabs from the Philippines may contain one adult female worm in such burrows. The worms are able to reverse direction in their tubes, thereby allowing access to eggs attached to the abdominal appendages of hermit crabs. *Polydora robi* feeds with a pair of feeding appendages (palps) containing a median ciliated groove. The worms extend from their burrow and remove eggs from host hermit crabs through a combination of muscular movement and ciliary action of the palps (Fig. 4). Field investigations showed that *P. robi* and *P. umangivora* preyed upon the eggs of multiple hermit

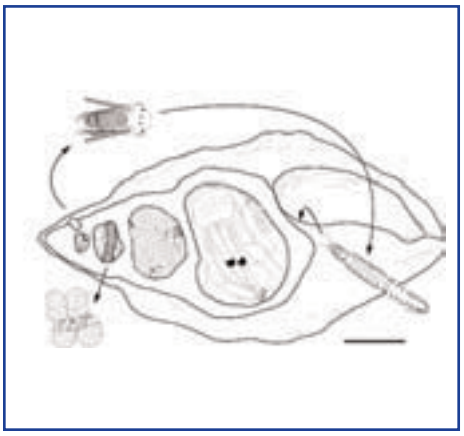

Fig. 3. Burrow morphology and life cycle of *Polydora robi*. Center of figure shows gastropod shell inhabited by an ovigerous hermit crab. A large female specimen of *P. robi* occupies a burrow in the apex; note feeding appendages among eggs of host. Egg capsules (bottom left), three-segment larvae (top right) and juveniles (bottom right) of *P. robi* are shown. After development of larvae to the three-segment stage, developing *P. robi* are released into the water column where they will grow to the juvenile stage before settling on a new hermit crab shell and bore in. Scale = 5 mm, for center figure; rest not to scale.

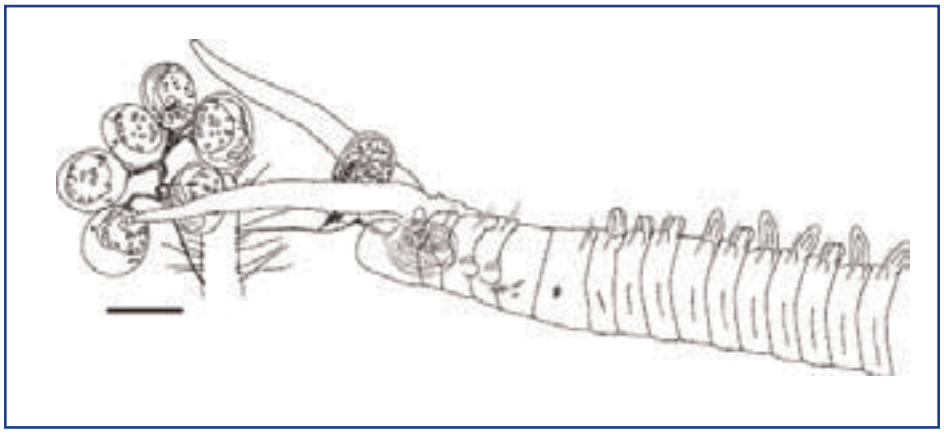

Fig. 4. Lateral view of *Polydora robi* ingesting an embryo of the hermit crab, *Calcinus latens*. The embryo has been engulfed by the worm but is still attached to the appendage (endopod) of the hermit crab by a stalk. Scale = 0.5 mm.

crab species. In laboratory experiments, *P. robi* was able to ingest a maximum of 70 embryos over a six-hour period. For hermit crab species that produce small broods of eggs (e.g., *Paguristes runyanae* with typically less than 300 eggs), the worms can have large impacts on reproductive success.

Ten other invertebrates are known egg predators of hermit crabs. Egg predators include cnidarians (anemones and hydroids), flatworms, polychaetes and crustaceans. However, besides work on polydorids, the only species to have been studied in detail is the flatworm, *Stylochus zebra*. Along the east coast of the United States, two polychaete species (*Dipolydora commensalis* and *Lepidonotus sublevis*) are found commonly with *Pagurus longicarpus* and are suspected to ingest eggs of hosts.

Parasitic Isopods of Hermit Crabs

Hermit crabs also host a variety of true parasites. For example, more than 185 species of parasitic isopods (family Bopyridae) infest hermit crabs worldwide. These species attach to the abdomens (subfamily Athelginae) or inside of the branchial cavities (subfamily Pseudioninae) of hermit crabs. My investigations have concentrated on the systematics and biology of parasitic isopods from the Indo-West Pacific.

Due to limited sampling, athelgine isopods remain largely underrepresented from the Indo-West Pacific. For example, only 13 species among five genera are known from the Philippines and surrounding waters. This number of bopyrids is suspected to be far lower than the number that actually occurrs in this region and my investigations in the Indo-West Pacific support this prediction. Nine genera of bopyrids have been identified from hermit crabs examined from the Philippines; in these samples, six species have been provisionally identified as new to science. This work has also led to the revision of two genera and the description of a new species of *Pseudostegias* from Bali, Indonesia. Scanning electron microscopy is being used to examine the fine structure of new *Asymmetrione* and *Pseudione* species from hermit crabs collected in Palau Ubin, Singapore.

Due to their parasitic existence, female bopyrids are highly modified from the typical isopod form (think of the "pill bugs" under rocks in the backyard), exhibiting non-motile legs used to clutch onto the host. In addition, the females possess a large marsupium devoted to the brooding of eggs. The eggs are fertilized by dwarf males that have a more typical isopod form. The eggs give rise to the first larval stage that will be released into the water column and parasitize a secondary crustacean

Fig. 5. Lateral view of the hermit crab, *Pagurus minutus*, with the abdominal parasitic isopod, *Atheleges takanoshimensis*, attached. White arrow indicates female parasite attached to the abdomen of the hermit crab, black arrowhead indicates the dwarf male on the posterior end of the female. Scale = 2.5 mm.

host (copepods). The larvae feed on the copepods and metamorphose into a second larval stage. The life cycle is complete after these larvae attach to the final host and develop into adults. After piercing the cuticle of hermit crabs, the female isopods feed on haemolymph and are known to castrate hosts due to the resulting energy burden.

While the life cycle of representative bopyrids are known, the fecundity and larval development have not been studied in detail for many species. Along these lines, I have begun fieldwork and scanning electron microscopy investigations on *Athelges takanoshimensis*, an abdominal parasite of hermit crabs from Hong Kong (Fig. 5). Approximately, 2.5 percent of hermit crabs from Hong Kong are infected by *A. takanoshimensis*. Large females of this species can produce up to 4,000 eggs per brood. Additional field research will examine the behavior of *A. takanoshimensis* and its impacts on hosts.

Future Research

Hermit crabs and the communities of species they support can act as excellent models to examine diversity patterns among geographic regions at a variety of scales. Future research will utilize quantitative sampling at collection sites in the Indo-West Pacific, Jamaica (Hofstra University Marine Lab) and along the east coast of the United States to investigate hypotheses on trends in the diversity of hermit crab symbiont communities. It is predicted that these studies will show the communities of invertebrates associated with hermit crabs follow the global biodiversity patterns found among free-living species. Specifically, it is hypothesized that: 1) diversity of hermit crab biocoenoses will be higher in Indo-West Pacific than the Atlantic, 2) diversity of hermit crab biocoenoses will decrease with increasing latitude, and 3) variability in assemblages will be greater between larger spatial scales (e.g., greater variability between regions than localities).

While addressing these big picture questions will expand our understanding of the role of hermit crabs as ecosystem engineers, it is my hope to also foster the many remaining questions on the natural history of hermit crabs and their symbionts in students who still look with wonder among the creatures of tide pools.

The review of hermit crab symbionts described above was completed in collaboration with Dr. John J. McDermott of Franklin & Marshall College. Research on bopyrid parasites of hermit crabs was conducted in collaboration with Dr. Christopher B. Boyko of the American Museum of Natural History and Ms. Lauren Scheurlein, an undergraduate biology major at Hofstra University. The research on polychaete worms is supported in part through a grant from the National Science Foundation.

Jason D. Williams joined Hofstra University in 2001 as an assistant professor in the Department of Biology. Prior to this appointment, he was an instructor at the University of Rhode Island where he earned a Ph.D. in biological sciences in 2000 and an M.S. in zoology in 1997. For his work at the University of Rhode Island, he was awarded the Douglas Nolan Award for academic achievement in the sciences. He completed a B.A. in biology in 1995 at Franklin & Marshall College, where he began investigations of hermit crab symbionts under the guidance of Dr. John J. McDermott. He is pleased to be able to continue collaboration with his undergraduate mentor on the research presented herein.

Dr. Williams' research interests encompass the biology of marine invertebrates. Specifically, he has focused on the systematics, ecology, feeding biology, and reproduction of polychaete worms and crustaceans. In addition to completing research on the associates of local hermit crab species, he has conducted extensive field studies on these organisms from Hong Kong, Indonesia, the Philippines and Singapore. His investigations in these regions have led to the description of 10 new species. His work has been supported by the Lerner-Gray Fund for Marine Research, the Sigma-Xi Scientific Research Society and the National Science Foundation (NSF). Currently he is collaborating with Dr. James A. Blake of the University of Massachusetts, Boston, on an NSF-funded project to train a new generation of polychaete taxonomists. This grant will continue to support the research of Hofstra undergraduates in the laboratory of Dr. Williams through 2005.

Dr. Williams has authored or co-authored 14 peer-reviewed papers for journals such as the *Bulletin of Marine Science*, *Journal of Crustacean Biology*, *Journal of Natural History*, *Journal of Zoology*, and *Zoological Journal of the Linnean Society*, among others. His chapter titled "Annelida — The Segmented Worms" was included in *Life on Earth: An Encyclopedia of Biodiversity, Ecology, and Evolution* edited by Dr. Niles Eldredge. He is the recipient of numerous awards and honors, including induction as an honorary member in the Golden Key International Honour Society for which he now serves as an adviser in the Hofstra Chapter.