FACULTATIVE PARASITISM BY THE BIVALVE *KURTIELLA PEDROANA* IN THE MOLE CRAB *EMERITA ANALOGA*

R. N. Bhaduri, P. Valentich-Scott*, M. S. Hilgers, R. Singh, M. E. Hickman, and K. D. Lafferty†

Department of Biological Sciences, California State University-Stanislaus, One University Circle, Turlock, California 95382. Correspondence should be sent to R. N. Bhaduri at: *rbhaduri@csustan.edu*

ABSTRACT: Evolutionary transitions to parasitism are rare. In this study, we documented a potential step toward parasitism in the commensal clam *Kurtiella pedroana* (Bivalvia: Galeommatoidea). Galeommatoideans are known commensals of various invertebrates, including crustaceans. *Emerita analoga* (Decapoda: Hippidae) is an abundant intertidal mole crab inhabiting Pacific coast beaches in North and South America. Mole crabs collected from Monterey Bay, California, were measured and examined externally and internally for associated molluscs. Out of the 520 mole crabs, 37 large female individuals harbored 49 clams (prevalence of 7.11% and mean intensity of 1.3). Forty-one ectocommensal clams were attached by their byssal threads to the inside of the gill chambers or to the lateroventral surfaces. However, our key finding was 8 clams that lacked byssal threads and were living in the hemocoel of 6 crabs. These internal clams were smaller than the ectocommensals. Because these internal clams lacked access to their normal food, we hypothesize they might have fed on hemolymph as would a parasite. Clam larvae have no obvious exit from the hemocoel, implying that endoparasitism is a dead-end for *K. pedroana*. Regardless, facultative parasitism in a free-living or an ectocommensal is uncommon and suggests a pathway to parasitism.

Parasitism has evolved about 223 times in just 15 phyla (Weinstein and Kuris, 2016). One way to transition from a free-living to a parasitic lifestyle is to first develop an intimate association with the host through commensalism. Commensal associations between bivalves and other invertebrates are common. For instance, sessile benthic organisms often compete for limited natural attachment space in coastal marine environments (Connell and Keough, 1985), leading some larval invertebrates, including bivalves, to settle on other organisms (Wahl, 1989). Here, we describe how an ectocommensal clam can sometimes occur inside the host's body as if it was an endoparasite.

Bivalve molluscs sometimes settle on crustaceans. Poulter et al. (2017), reported multiple instances of the free-living blue mussel, *Mytilus edulis*, living inside the gill chamber of the shore crab *Carcinus maenas*. The rock mussel *Semimytilus algosus* has been seen attached to *Emerita analoga* (Villegas et al., 2006), and we observed the California mussel *Mytilus californianus* attached to *E. analoga*'s lateroventral surface (Bhaduri et al., 2017). These reports likely represent accidental settlement, but facultative commensalism is exemplified by the bivalve *Mimachlamys varia*, which settles on a crustacean host rather than a soft substratum but can release its byssus, swim, and settle elsewhere (Albano and Favero, 2011). Of the 121 recorded Galeommatoidean clam species, 64 are obligate or facultative commensals associated with diverse invertebrate groups (Li et al., 2012) including sponges (Tsubaki and Kato, 2012), the brachiopod *Lingula* (Goto et al., 2014), holothurians (Kato, 1998), heart urchins (Valentich-Scott et al., 2013), a polychaete sea mouse (Li and Foighil, 2012), a mud shrimp (Li and Foighil, 2012), thalassinidean burrowing shrimps (Kato and Itani, 2000), and other decapods (Boss, 1965) that live in soft-sediment habitats. Some Galeommatoidean clams associate with hosts to avoid being buried in soft sediment (Goto et al., 2007), but none are endoparasitic.

The Galeommatoidean we studied, *Kurtiella pedroana* (formerly *Mysella pedroana* Dall, 1898), can be free living or commensal (Scott, 1987; Coan and Valentich-Scott, 2012). This clam is commensal on the spiny sand crab *Blepharipoda occidentalis* (Lafferty, 1993), the mole crab (also called sand crab) *E. analoga* (Lafferty and Torchin, 1997), and the hermit crab *Isocheles pilosus* (Carpenter, 2005), indicating that it is not host specific.

Lafferty (1993) described *K. pedroana*'s natural history in relation to its predominate crustacean host, the spiny sand crab, *B. occidentalis*. Clams either find a spiny sand crab or settle as larvae on the crab's exoskeleton, attach with byssus, and some then move into the gill chamber. Those in the gill chamber attach to gill filaments with their byssal threads, where they cause some necrosis. They are much larger and less abundant than those found on the exoskeleton. However, oxygen consumption in respiratory chambers does not vary with the clam intensity inside the gill chamber nor is there evidence that clams feed on spiny sand crab tissue. Rather, the gill chamber seems to provide a safe and oxygenated habitat. When spiny sand crabs molt their exoskeleton, some clams are able to transfer back to their host, but most remain attached to the shed exuvium and presumably then perish or live in the sand until they find another crab. Because mole crabs co-occur with spiny sand crabs, and large mole crabs are the size of small spiny sand crabs, we suspect *K. pedroana* life history on mole crabs is similar to its life history on spiny sand crabs after controlling for crab size.

The mole crab, *E. analoga,* is common in sandy-beach swash zones along the temperate North and South American Pacific coasts (Contreras et al., 1999) and often hosts commensals and parasites (Lafferty and Torchin, 1997; Villegas et al., 2006; Smith, 2007; Bhaduri et al., 2017). As part of an 11-beach parasitological survey, Lafferty and Torchin (1997) sampled 24 large mole crabs at Pismo Beach, finding 11 individuals of *K. pedroana*: 1 external clam (shell width < 3 mm) and 10 gill-chamber clams (shell widths: 3, <3 mm; 6, 3–6 mm shell width) on 7 females (28–31 mm crab carapace length), but did not find clams within the hemocoel.

TABLE I. The number of crab hosts sampled and inhabited by crab size class. This includes the number of *Kurtiella pedroana* per size class range and the proportion of the clam sample found in each host size class.

| | Host crab | | Bivalve | |
| | *Emerita analoga* | | *K. pedroana* | |
Size range (mm)	No. sampled	No. inhabited	No. individuals	Proportion
10.1–14	169	0	0	0
14.1–18	108	3	3	0.03
18.1–22	164	17	20	0.12
22.1–26	71	15	22	0.31
26.1–30	8	2	4	0.50
Total	520	37	49	

In our study, we investigated the distribution and abundance of *K. pedroana* on mole crabs and documented what appears to be simultaneous commensal and facultative (but dead-end) endoparasitism.

MATERIALS AND METHODS

Field sampling was conducted in the swash zone at Del Monte Beach in Monterey Bay, California (36.80°N, 121.90°W) between August 2014 and November 2015. Mole crabs were collected by perturbing the sandy surface with a shovel until liquefaction occurred. The collected material was sieved through a 1-mm mesh, ~12″ in diameter, and mole crabs were captured as they emerged from the sediments with the receding waves. Specimens were transferred by hand into an iced cooler, transported to the laboratory, and frozen for future analysis.

Each mole crab was measured using Vernier calipers (total carapace length, in millimeters). To examine the relationship between mole crab size and clam abundance, crabs were subdivided into 5 (4-mm size) groups: 11.1–14, 14.1–18, 18.1–22, 22.1–26, and 26.1–30 mm. Each mole crab was sexed; for females, non-gravid vs. gravid conditions were noted. The mole crab's external body surface was examined for ectocommensals and their positions recorded. Using a small pair of scissors, an incision along the mid-dorsal line was cut and the carapace removed. A binocular stereomicroscope (Olympus 10× dissecting microscope; Olympus, Philadelphia, Pennsylvania) was used to examine endosymbionts. Bivalve specimens were identified using taxonomic keys (Coan and Valentich-Scott, 2012). When *K. pedroana* was observed, it was photographed, measured (in millimeters), and its microhabitat noted. The latter included the mole crab's external surface, the gill chamber, and the hemocoel. Several *K. pedroana* were preserved with 70% ethanol and deposited as voucher specimens in the Santa Barbara Museum of Natural History, California, under the accession number 2014–024 and catalogued as SBMNH 453415 and 462475.

We looked for patterns to better understand how internal and external clams were distributed amongst the mole crab population. Prevalence (proportion colonized by clams) and mean intensity (number of clams per colonized mole crabs) were calculated (Bush et al., 1997). Prevalence and its relationship with mole crab sex were analyzed using the Fisher's exact test. Chi-square (χ^2) tests were employed to compare mole crab sex ratio
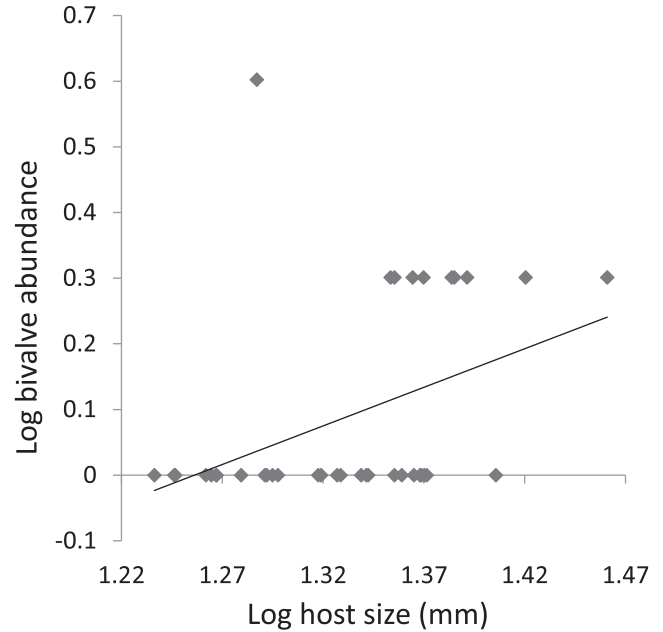

FIGURE 1. Relationship between *Emerita analoga* size and *Kurtiella pedroana* abundance.

and to compare clam distributions among different locations on or in the mole crab. To assess size differences between males and females, as well as gravid and non-gravid individuals, unpaired *t*-tests were used. Fisher's exact test was also used to compare the clam distribution on gravid and non-gravid females. Mole crab size and clam abundance were log-transformed to meet assumptions of normality and homoscedasticity. A linear regression was used to determine whether the clam abundance differed with respect to carapace length. A one-way ANOVA was applied to test differences between the sizes of clams that were found on an external surface, within the gill chamber, and inside the hemocoel. *P*-values < 0.05 were considered statistically significant.

RESULTS

In total, 520 mole crabs were examined. Most (77.1%) were females ($\chi^2 = 152.93$, $P < 0.001$). Mole crabs were 10.1–29.6 mm (avg. 17.3 mm) in length, with smaller 10.1–17.1 mm (avg. 12.8 mm) males and significantly larger females (11.2–29.6 mm; avg. 18.6 mm; $t = 22.1$, $P < 0.001$). Of the 401 females, 100 (24.9%) were gravid and were significantly larger (avg. 20.0 mm) than were non-gravid females (18.2 mm; $t = -5.1$, $P < 0.001$). Table I summarizes clam abundances per 5 (4-mm) mole crab size groups. Of the 520 mole crabs examined, 37 harbored 49 clam individuals (7.1% prevalence, with a 1.3 mean intensity). There was a significant difference in prevalence between sexes; only females had clams (Fisher's exact test: $P < 0.0001$). Of these 37 females with clams, 20 (54%) were gravid. There was no significant difference in clam counts between gravid and non-gravid females (Fisher's exact test, $P > 0.05$).

Clam counts increased with carapace length. Although the average length was 17.3 mm, only adult crabs measuring >17.2 mm had clams. There was a positive correlation between carapace length and clam abundance (Fig. 1; $F = 6.76$, $R^2 = 0.162$, $P = 0.01$). Spatial distribution patterns revealed significant differences

in attachment sites, with 62% of clams documented as ectocommensals, 21% within the gill chamber, and 17% inside the hemocoel ($\chi^2 = 17.15$, $P < 0.001$).

Ectocommensal clams were attached by byssal threads to lateroventral surfaces (size range = 0.6–5.6 mm; mean size = 3.3 mm) or inside the gill chambers (size range = 1.6–4.8 mm; mean size = 3.1 mm; Fig. 2A–D). The mean intensity for the ectocommensal clams was 1.26 (max = 5). We found 8 clams (size range = 0.6–4.4 mm; mean size = 2.4 mm; Fig. 2E–F) inside the hemocoel of 6 mole crabs, with a mean intensity of 1.3 (max = 2). The clams inside the hemocoel were not attached via byssus. One crab had 2 clams in the hemocoel around the mid/hind gut junction. Veliger larvae consistent with clam larvae were sometimes found inside the hemocoel as well.

There was a significant difference in clam sizes in the 3 microhabitats ($F_{2,44} = 3.61$, $P = 0.03$; Fig. 3). Post hoc comparisons using the Tukey HSD test indicated that external clams did not differ significantly from those found within the gill chamber ($Q = 0.51$, $P > 0.05$), but external and gill-chamber clams were significantly larger than those found inside the hemocoel ($Q = 3.78$, $P = 0.03$).

DISCUSSION

The most remarkable finding in our study was the several clams inside the mole crab's hemocoel. Larval stages of trematodes, tapeworms, acanthocephalans, and nematodes have been reported from the hemocoel inside the mole crab (Smith, 2007). However, a bivalve has never been documented as endoparasitic in the hemocoel of crustaceans or in any other host. The closest that clams come to endoparasitism is as veligers attached to fish gills or as adults in crab gill chambers or holothurian brachial pockets (Kato, 1998; Lützen, 2011). Also, *Entovalva* spp. occupy a unique niche amongst the bivalves, being the only known endosymbiotic bivalves to be found in the esophagi of either synaptid or holothurid holothurians (Bristow et al., 2010). The presence of diatoms on this clams' gills may indicate active straining of planktonic organisms from sea water; yet, whether it is a parasite or a commensal is not clear (Bristow et al., 2010). Regardless of the novelty, we consider the hemocoel to be an accidental infection site for *K. pedroana*.

We are unaware of how a clam gets into the hemocoel, what it feeds on, how it obtains oxygen, if it can reproduce, and whether its larvae can leave the hemocoel. Given the veliger larvae we saw in the hemocoel, the infective stage could be the veliger. The latter might enter through the gut after being ingested by filter-feeding. Or clams might penetrate the gill. Or mole crabs might become infected when the exoskeleton is soft during or after molting. The veliger might land on a freshly molted mole crab and the spat, while looking to attach, might burrow through the soft exoskeleton and come to rest inside the hemocoel. Alternatively, the veligers in the hemocoel were the offspring of endoparasitic clams. Oliver and Lützen (2010) documented an ectoparasitic galeommatid clam that was fluid-feeding, and it is possible that endoparasitic individuals of *K. pedroana* fed on hemolymph. Although we suspect that *K. pedroana* can feed and grow within the mole crab, it is unlikely that veligers can exit the hemocoel, suggesting that endoparasitism is likely a dead-end for the clam, as happens for many parasites when they infect an accidental host, but a challenge that other parasites, such as schistosomes

and various arthropod-transmitted nematodes, have managed to overcome.

No pathology was associated with clams in the hemocoel. Although crabs will respond to larval parasites in the hemocoel with melanization, we did not find any melanization around the clam, including the attachment area, suggesting the immune system did not react to clams in the hemocoel. However, if clams do feed on hemolymph, they might compete with the mole crab for nutrients.

Mole crab size probably affects where the clams attach and how fast they grow. The clams in the hemocoel were significantly smaller than the ectocommensals; most likely, the clams faced space constraints inside the hemocoel that restricted their growth. In addition, the higher clam intensity on the exoskeleton might reflect limited space within the gill chambers. Similar observations were reported for *K. pedroana* on *B. occidentalis* (Lafferty, 1993; Boyko and Mikkelsen, 2002) and on *I. pilosus* (Carpenter, 2005). *Kurtiella pedroana* is often prevalent on *B. occidentalis*; for instance, 51 of 85 spiny sand crabs (60%) harbored *K. pedroana*, with a mean intensity of 1.89 and up to 22 juveniles per spiny sand crab (Boyko and Mikkelsen, 2002). Furthermore, Lafferty and Torchin (1997) found that clams in the spiny sand crab gill chamber (shell widths: 6 [<3 mm], 20 [3–6 mm], 31 [>6 mm]) are larger than clams in the gill chamber (shell widths: 3 [<3 mm], 6 [3–6 mm] shell width). Contrary to our observations that *K. pedroana* occurs only on large-sized and female mole crabs, this clam showed no preference for size or sex in spiny sand crabs. This disparity among crab species probably occurs because mole crabs (and especially males) are small compared to spiny sand crabs, which can grow up to 80 mm (Faulkes and Paul, 1997).

Examples of the fluctuating nature of symbiotic relationships among marine organisms are rare. In 1 nemertean-bivalve association, questions have been raised on whether the ribbon worm is commensalistic or parasitic on the mollusk. The worm *Malacobdella arrokeana* attaches to the bivalve's mantle and the vacuum force generated by the sucker stretches the host's epithelial cells; moreover, this worm is capable of independent existence, which led to its categorization as a commensal (Vázquez et al., 2009). This particular relationship was also tested by Alfaya et al. (2015) who reported that, based on stomach content analysis, the nemertean should be considered a commensal, not parasitic. In another bivalve-crab association, the blue mussel, *M. edulis*, was documented to inhabit the branchial chamber of the shore crab *C. maenas*, and could act as a facultative commensal or parasite of *C. maenas*, although it appeared more likely to be a case of accidental colonization with negative outcomes for the colonizer (Poulter et al., 2017). Towanda and Thuesen (2006) found a transitioning relationship between the crab *Cancer gracilis* and its host jellyfish *Phacellophora camtschatica*; in this association, the crab juveniles eat host tissue. As they grow, they feed mostly on an amphipod *Hyperia medusarum*, a harmful parasitoid of their scyphozoan host. Thus, the status of *C. gracilis* changes from being a parasite to a defensive mutualist. In certain gastropod families, the path between a free-living lifestyle and parasitism has been postulated. For example, young individuals of families Epitoniidae and Coralliophilidae are free-living, but as they grow they attach to soft corals and feed on their host tissue or the mucus that the corals secrete (Robertson, 1981). Some eulimidaean snails cause
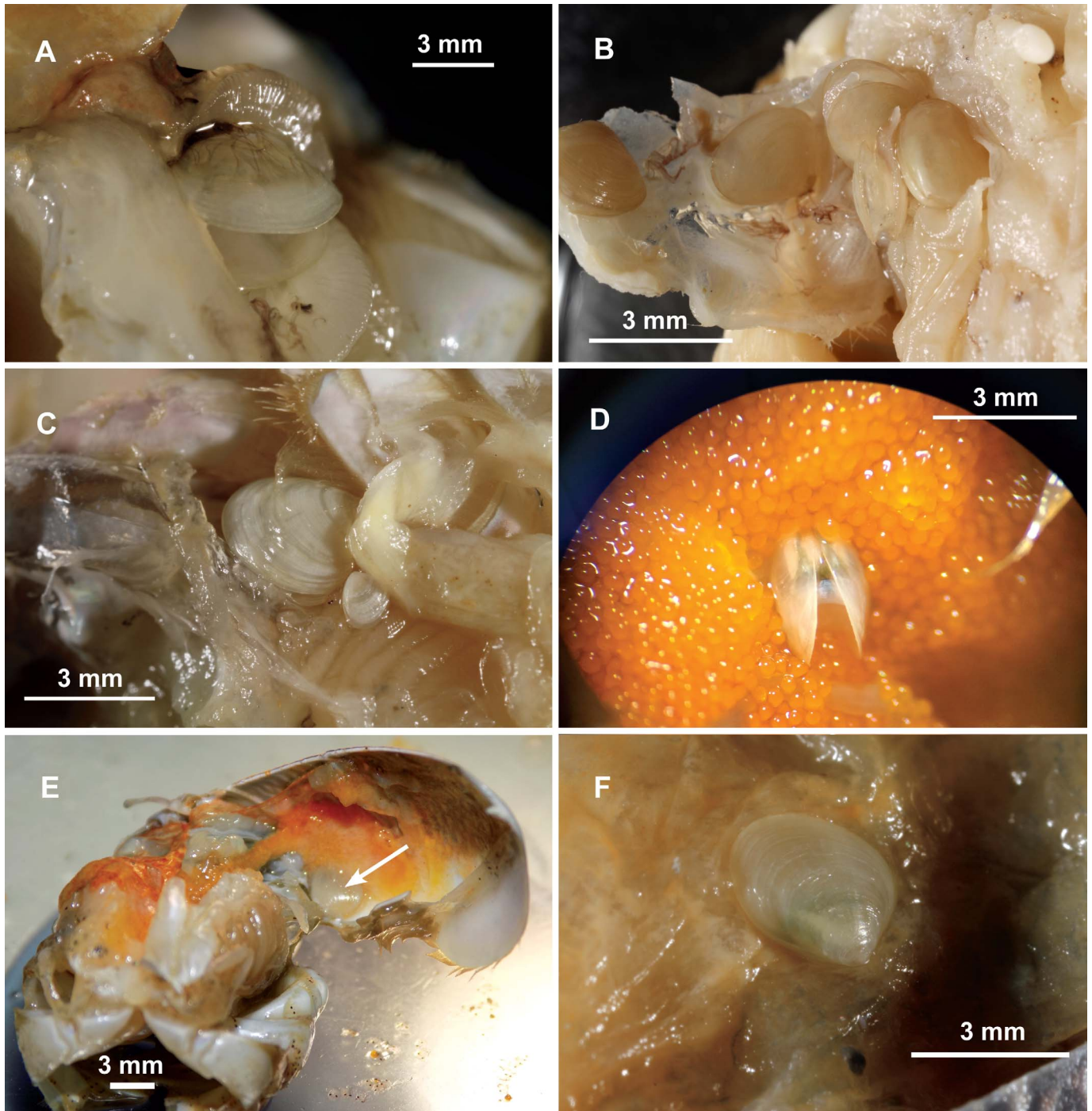
FIGURE 2.   *Kurtiella pedroana* associated with the mole crab *Emerita analoga* (scale bar = 3 mm): (**A**) A clam on the mole crab, attached with byssal threads; (**B**) 5 clams inside the gill chamber of a mole crab; (**C**) 2 clams inside the gill chamber; (**D**) 1 clam attached to the ventral surface of a female mole crab, amidst egg mass; (**E**) clam inside the mole crab's hemocoel (see arrow); (**F**) a close-up of a clam inside the hemocoel. Color version available online.
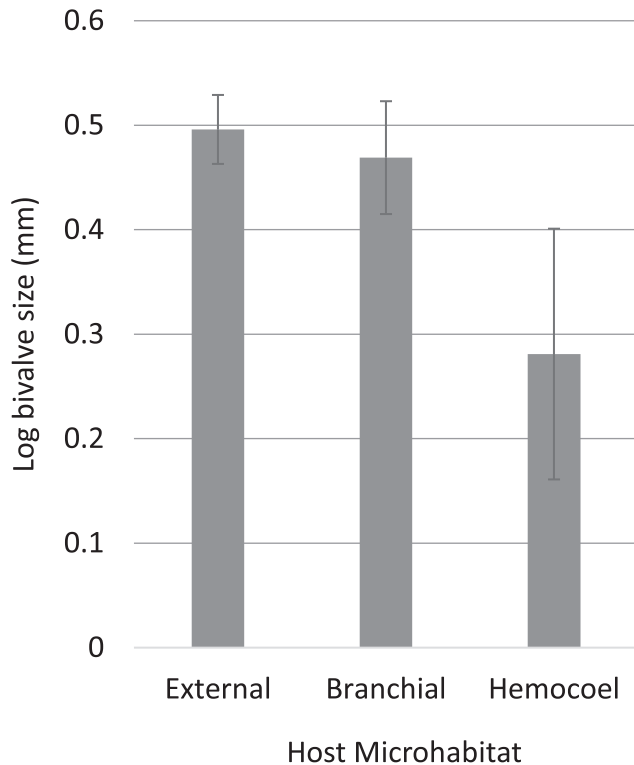
FIGURE 3. Comparison of mean clam size in relation to their location on the mole crab. Error bars represent the standard error.

gall formations on their echinoderm hosts and transition from ectoparasitism to endoparasitism (Warén, 1983).

The transition of *K. pedroana* from a free-living to a commensal to a possible parasitic lifestyle is an opportunity to study morphological and physiological features of symbioses. Moreover, the unusual occurrence of *K. pedroana* inside the mole crab, which we presume to be a dead-end host, could be a step toward evolving an endoparasitic life style for the clam. The road to parasitism is likely filled with many such dead ends; only rarely does a species find an on-ramp to parasitism.

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