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BODY SIZE OF THE ENDOSYMBIOTIC PEA CRAB *TUMIDOTHERES MACULATUS*: LARGER HOSTS HOLD LARGER CRABS

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ABSTRACT The endosymbiotic pea crab, *Tumidotheres maculatus*, uses a broad range of host taxa, including several bivalve species, in the northern Gulf of Mexico. Because shelter size affects the size of other, free-living crab species, we hypothesized that pea crabs living in larger bivalve hosts should attain larger sizes. Crabs and hosts collected from 3 field sites in northern Florida show this trend. We examined crabs living in a large host, the pen shell *Atrina rigida*, and found them to be larger than pea crabs living in a small host, the bay scallop *Argopecten irradians*. Moreover, this trend was only apparent among female pea crabs, which are lifelong endosymbionts, but not among males, which are free-ranging and move among hosts. Our data support the broader conclusion that shelter size influences adult crab size in brachyuran crabs.

INTRODUCTION

The pea crab (*Tumidotheres maculatus*) is an endosymbiont that has been found in many different species of hosts. At least half of these hosts are bivalves (Derby and Atema 1980, Bierbaum and Ferson 1986). The pea crab (reassigned from the genus *Pinnotheres* by Campos (1989) for morphological reasons) has "dwarf" males that rarely exceed 6 mm across the carapace, move freely from host to host, and are able to feed independently of the host (Sastry and Menzel 1962, Bierbaum and Ferson 1986). Female pea crabs grow much larger, pass through 7 distinct developmental stages (Pearce 1964, Campos 1989), and live their entire adult lives within a host (Bierbaum and Ferson 1986). By clinging to the gills of the host with their legs, they use their chelae to pick up mucous food strands aggregated by the host (Bierbaum and Ferson 1986, Bierbaum and Shumway 1988). This symbiotic relationship is believed to be either commensal or parasitic (Bologna and Heck 2000). Common bivalve hosts in the northeastern Gulf of Mexico include the bay scallop (*Argopecten irradians*), the pen shell (*Atrina rigida*), and the mussel (*Modiolus americanus*).

The prevalence of pea crabs in bivalve populations appears to vary widely. Sastry and Menzel (1962), working in Florida, found that infestation rates of pea crabs ranged from 20% to more than 47% in bay scallops collected between October 1957 and November 1958. Pearce (1964) reported that 97.6% of mussels, *Mytilus edulis*, in Quicks Hole, Massachusetts, were infested with pea crabs. Bierbaum and Shumway (1988) found that 69% of mussels from a bed in Martha's Vineyard, Massachusetts, were infested with pea crabs. In St. Joseph Bay, Florida, Bologna and Heck (2000) found that the infestation rate of bay scallops by pea crabs ranged from 0% to more than 20% from 1994 to 1996. In none of these studies did variations in pea-crab infestation rates appear to be seasonal.

Within an individual host bivalve, endosymbiont infestation may vary in 2 ways: 1) variation in the number of pea crabs per host and 2) variation in the size of female crabs. Crab size can be influenced by environmental factors, such as shelter size, among non-symbiotic brachyuran crabs. Kuhlmann and Walker (1999) found strong and significant size differences between 2 populations of the spineback hairy crab, *Pilumnus sayi*, in the northeastern Gulf of Mexico, and they showed that the difference in crab sizes between the 2 populations was due to differences in the sizes of available shelter at the 2 locations. Likewise, Beck (1995) showed that in populations of the stone crab, *Menippe adina*, crabs molted and spawned more often when large PVC pipe shelters were provided. However, a relationship between host size and symbiont size has not yet been demonstrated for symbiotic crabs such as the pea crab, despite the fact that potential bivalve hosts for this crab vary greatly in size.

We hypothesized that pea crabs living in larger host species might grow to larger sizes than pea crabs in smaller bivalve hosts. Mussels and bay scallops are roughly similar in size, ranging from 45–55 mm in length when mature, while pen shells can achieve lengths greater than 200 mm (data from this study). Here, we show that pea crabs occur more frequently in large pen-shell hosts than in 2 species of smaller hosts, and that crabs in pen-shell hosts are larger than crabs found in smaller bay scallops. Mussels, the third host in our study area, appeared to host pea crabs infrequently, and crabs resident in mussels were smaller than in any other host.

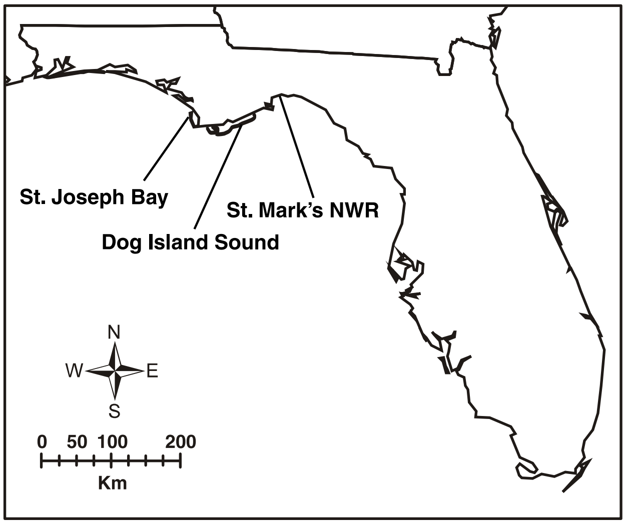

Figure 1. Collection sites in northwest Florida. Map Credit: The Florida Center for Instructional Technology, University of South Florida.

METHODS AND MATERIALS

During the summer of 2002, we collected the bivalves *Modiolus americanus*, *Argopecten irradians*, and *Atrina rigida* from 3 sites off the coast of northwest Florida (Figure 1): Dog Island Sound, immediately adjacent to the Florida State University Marine Laboratory; St. Mark's National Wildlife Refuge to the east; and St. Joseph Bay to the west.

We collected 100 mussels from St. Joseph Bay, 100 from St. Mark's NWR, and 93 from Dog Island Sound. Mussels were not abundant in Dog Island Sound, and we found only 93 individuals during the study period.

From St. Joseph Bay, we collected 50 pen shells, and 48 from St. Mark's NWR. We found no pen shells in Dog Island Sound during the study, despite extensive searches.

We also obtained 100 bay scallops each from Dog Island Sound and St. Mark's NWR. Weather conditions, principally hurricanes, and the short duration of this study precluded us from collecting bay scallops from St. Joseph Bay. All bivalves were collected by hand, using snorkel gear, in water up to 2 m deep.

We measured and recorded each bivalve's length (anterior/posterior), height (dorsal/ventral) and width (left/right valves) to the nearest 0.05 mm. We then opened every bivalve and examined it for the presence of pea crabs. If a crab was present, we recorded its sex and carapace width. When analysis at field sites was not practical, we transported the bivalves to the Florida State University Marine Lab in St. Teresa, Florida. At the lab, animals were maintained in seawater tables with constant water flow at a temperature of 25–28° C.

To compare mussel sizes from different sites, we executed a one-way analysis of variance using mussel length as the dependent variable and the collection site as the independent variable. Because we only had scallops from 2 sites, and pen shells from 2 sites, we compared bay scallop lengths from St. Mark's NWR and Dog Island Sound using a Student's *t*-test, and we compared pen-shell lengths from St. Mark's NWR and St. Joseph Bay using a separate Student's *t*-test.

To compare infestation rates within a host species between 2 collection sites, we used *G*-tests for independence (Sokal and Rohlf 1981). Additionally, we used Student's *t*-tests to compare carapace widths of pea crabs found in pen shells and pea crabs found in bay scallops. In one comparison (the comparison of pea crab carapace widths from pen shell and bay scallop hosts at St. Mark's NWR), the assumption of equal sample sizes was violated. Finally, among pea crabs found in a single host species, we sought relationships between pea crab carapace width and host size using linear regression analyses. We used bivalve length, height, and width as independent variables in separate regression analyses; pea crab carapace width was always used as the dependent variable.

RESULTS

Bivalve sizes, infestation rates, and pea crab sizes from different sites

Modiolus americanus. Mean length of collected mussels did not vary from site to site: mussels were 44.7 ± 6.8 mm (mean ± 1 standard deviation) in St. Joseph Bay; 45.4 ± 7.9 mm in Dog Island Sound, and 45.8 ± 10.6 mm in St. Mark's NWR. These values are not significantly different (ANOVA, $F = 0.415$, $P = 0.66$, df = 292).

Pea crabs rarely used mussels as a host. None of the 100 mussels collected from St. Joseph Bay contained pea crabs. One of the 100 mussels collected from St. Mark's NWR contained a small immature female pea crab with a carapace width of 5.5 mm. Similarly, one of the 93 mussels collected from Dog Island Sound also contained a female with a carapace width of 6.5 mm (Table 1).

Argopecten irradians. Bay scallops varied in size between the 2 collection sites. Scallops obtained from Dog Island Sound were significantly larger (longer in length) than those obtained from St. Mark's NWR (Student's *t*-test, $t = 16.798$, $P = 0.0001$, df = 196; Figure 2).

The infestation rate in bay scallop hosts was more than four times higher in St. Mark's NWR (Table 1). Only 4% of the bay scallops collected from Dog Island Sound contained pea crabs; all 4 of the crabs collected were female. In contrast, 17% of the bay scallops from St.

TABLE 1

Bivalves collected at each of 3 field sites and rates of infestation by the pea crab.

Bivalve	Location	*N*	Infected	% Infected
Modiolus americanus	St. Joseph Bay	100	0	0.0
Modiolus americanus	Dog Island Sound	93	1	1.1
Modiolus americanus	St. Mark’s NWR	100	1	1.0
Argopecten irradians	Dog Island Sound	100	4	4.0
Argopecten irradians	St. Mark’s NWR	100	17	17.0
Atrina rigida	St. Joseph Bay	48	33	68.8
Atrina rigida	St. Mark’s NWR	50	37	74.0

Mark's NWR were infested; at this site, 13 (76.5%) of collected pea crabs were female, and 4 were male (23.5%). The difference between infestation rates at the 2 sites was significant (*G*-test for independence, *G* = 9.381, *P* = 0.0022, df = 1). All pea crabs occupying bay scallops were found living singly, irrespective of collection site.

Larger bay scallops in Dog Island Sound hosted larger pea crabs (Figure 2). The mean carapace width of female pea crabs found in bay scallops at St. Mark's NWR was 8.3 mm. The mean size of the female pea crabs found in bay scallops from Dog Island Sound was 9.5 mm. Because only 2 female pea crabs were found in the 100 bay scallops collected from Dog Island Sound, the mean carapace width was calculated using 2 additional female pea crabs found in other bay scallops from that site (G. Farley, unpublished data). The difference in mean female pea crab size from the 2 locations was not significant (Student's *t*-test, *t* = 1.239, *P* = 0.2344, df = 15). The mean size of the male pea crabs found in bay scallops at St. Mark's NWR was 5.7 mm.

Atrina rigida. Pen shells in St. Joseph Bay were significantly larger than pen shells from St. Mark’s NWR, (Student's *t*-test, *t* = 5.910, *P* = 0.001, df = 96; Figure 3). Pen shells from the 2 sites were infested with pea crabs at a similar rate (*G*-test for independence, *G* = 0.3244, *P* = 0.569, df = 1). Pea crabs were found in 68.8% of pen shells from St. Joseph Bay, while 74.0% of pen shells from St. Mark's NWR were infested with pea crabs (Table 1). Most of the infested pen shells from both sites contained female pea crabs: 83.8% at St. Mark's NWR and 81.8% in St. Joseph Bay. Male-only infestation accounted for 16.2% of infested pen shells from St. Mark's NWR and 18.2 % of those infested from St. Joseph Bay.

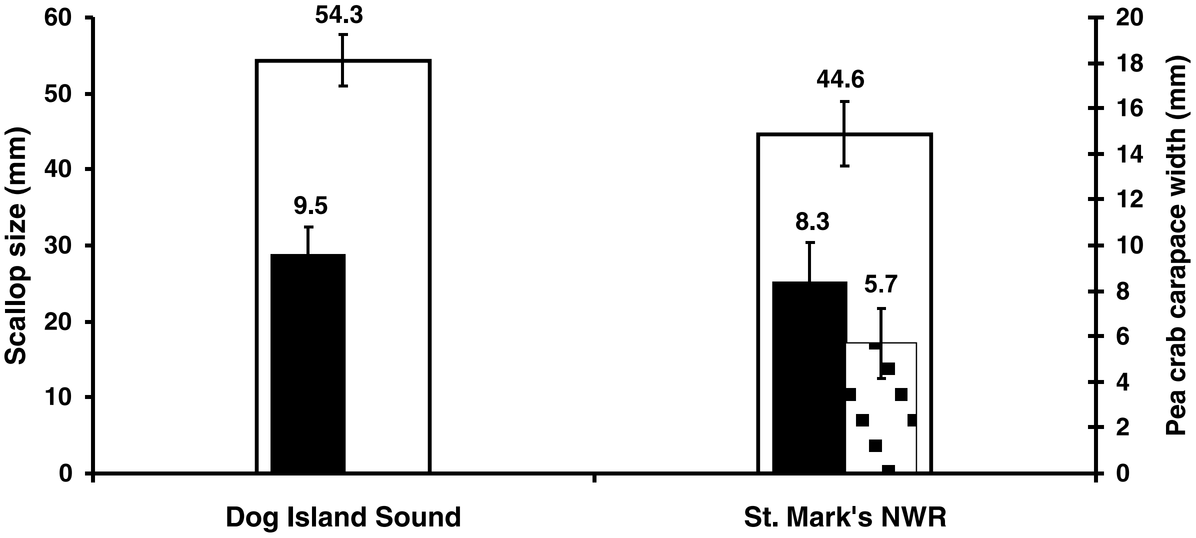

Figure 2. Mean lengths (mm, ± 1 SD) of bay scallops and mean carapace widths (mm, ± 1 SD) of male and female pea crabs at 2 sites. Large white bars are bay scallop lengths; small black bars are female pea crab carapace width; small striped bars are male pea crab carapace width. Bay scallops from Dog Island Sound were significantly larger than bay scallops from St. Mark’s NWR. Female pea crabs were larger, although not significantly so, in bay scallops from Dog Island Sound; low numbers of crabs in Dog Island Sound may be obscuring a true difference in crab carapace widths.

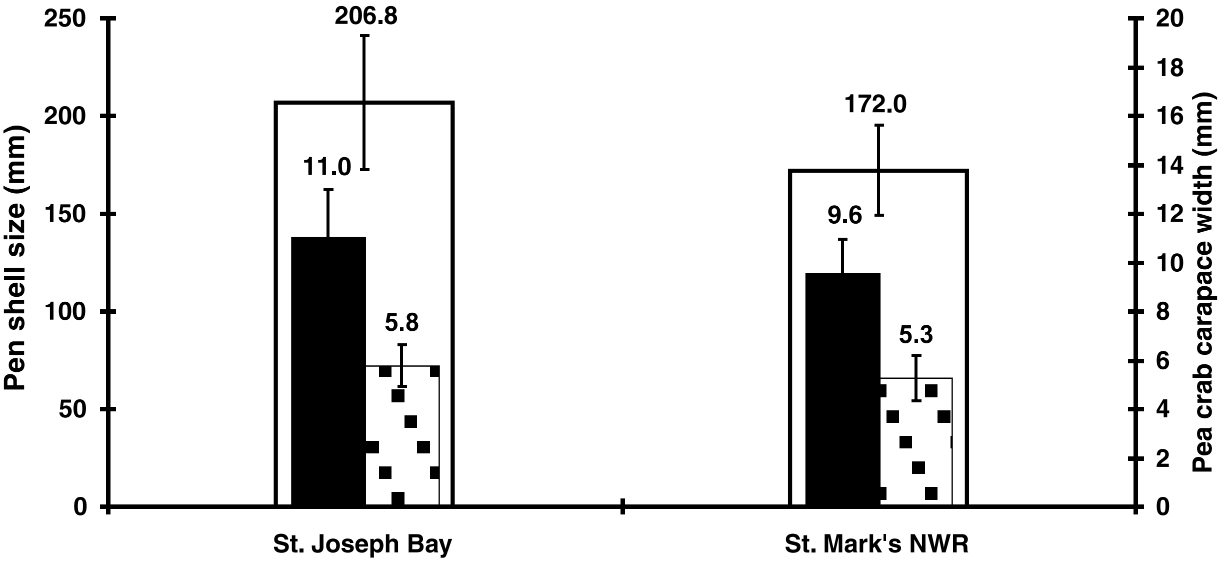

Figure 3. Mean lengths (mm, ± 1 SD) of pen shells and mean carapace widths (mm, ± 1 SD) of male and female pea crabs at 2 sites. Large white bars are pen shell lengths; small black bars are female pea crab carapace width; small striped bars are male pea crab carapace width. Pen shells from St. Joseph Bay were significantly larger than pen shells from St. Mark's NWR. Larger pen shells in St. Joseph Bay were host to larger female pea crabs, but male crabs were similar in size in all pen shell hosts.

Larger pen shells in St. Joseph Bay were hosts to significantly larger female pea crabs (Student's *t*-test, $t = 3.188$, $P = 0.0023$, df = 56; Figure 3). Mean carapace width for female pea crabs from St. Joseph Bay pen shells was 11.0 mm. At St. Mark's NWR, the mean carapace width of female pea crabs was 9.6 mm.

Male pea crabs from pen shell hosts were similar in size at both sites (Figure 3). Mean carapace width among male pea crabs at St. Joseph Bay was 5.8 mm, and pea crabs averaged 5.3 mm carapace width at St. Mark's NWR. This was not a significant difference (Student's *t*-test, $t = 2.064$, $P = 0.7388$, df = 24).

Pen shells were the only host in this study to harbor more than one pea crab per bivalve. Most multiple infestations consisted of one female pea crab and at least one male. Of pen shells containing female pea crabs, 14.8 % (4 of 48) from St. Joseph Bay and 8.1% (3 of 50) from St. Mark's NWR also contained one male. One pen shell from St. Joseph Bay contained 2 males. One pen shell at St. Mark's NWR contained a female and 2 males, and one pen shell from St. Joseph Bay contained one female and 3 male pea crabs.

Smaller pen shells had higher infestation rates. When pen shells from both collection sites were pooled, the percentage of pen shells hosting pea crabs declined with increasing host size (Figure 4). This pattern was not evident among scallop hosts.

Pea crabs were larger in a larger host bivalve. The only site at which we found both large and small host bivalves in abundance was St. Mark's NWR. At this site, larger bivalves, pen shells, hosted larger female pea crabs than bay scallops (Figure 5). The mean carapace width of female pea crabs found in pen shells was 9.6 mm ($n = 31$), whereas the mean carapace width of females found in scallops was 8.3 mm ($n = 13$). This was a significant difference (Student's *t*-test, $t = 2.470$, $P = 0.0177$, df = 42), although the assumption of equal sample sizes has been violated in this test.

For male pea crabs, this trend was not significant. Mean carapace width of male pea crabs living in pen shells was 5.3 mm ($n = 11$), which did not differ significantly from the mean carapace width of those found in scallops, 5.7 mm ($n = 4$) (Student's *t*-test, $t = 0.699$, $P = 0.497$, df = 13). Again, the assumption of equal sample sizes is violated in this test.

Female pea crab size was not strongly correlated with bivalve size within a host species. There was a notable correspondence between the larger host species and larger size of female pea crabs. However, even though this trend was significant between the different bivalves, relationships between host size and pea crab size within host species are weak for pen shell hosts. Variation in pen shell length, the shell dimension with the greatest explanatory power of any we measured, explains only 9.5% of the variation in pea crab carapace width using linear regression ($r^2 = 0.095$, $P = 0.019$; Figure 5).

All other linear regression analyses, including regressions of pea crab carapace size on pen shell width and

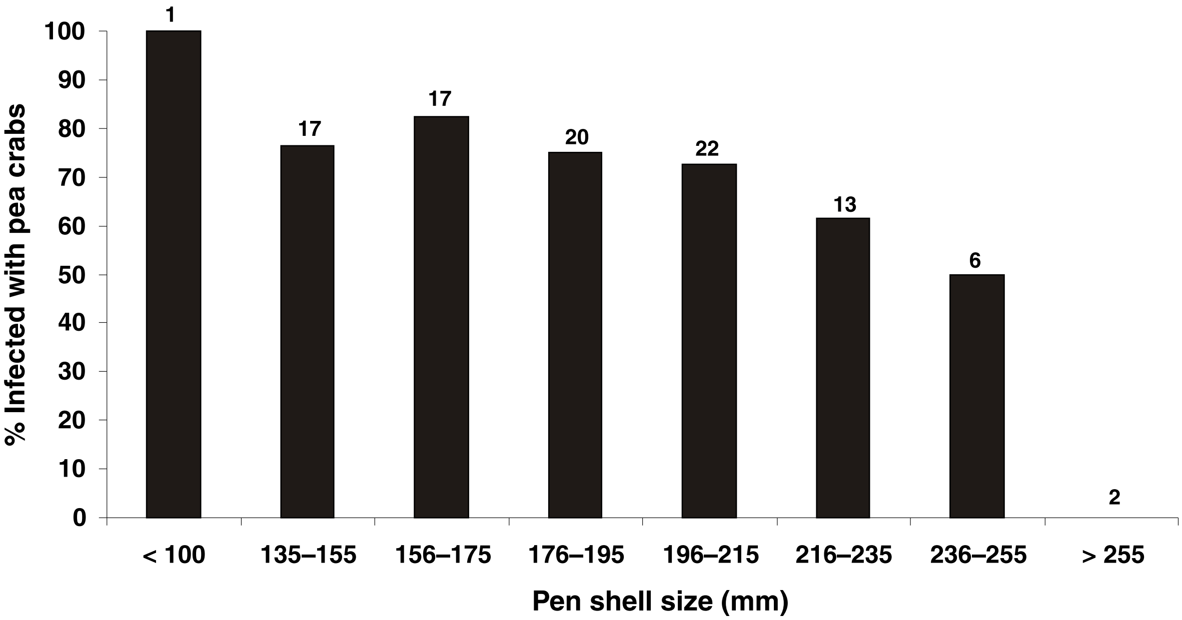

Figure 4. The proportion of pen shells infested with pea crabs, as a function of pen shell length. Data have been pooled from both collection sites, and the number above each bar indicates the number of pen shells in that grouping. Smaller pen shells host greater numbers of pea crabs.

height, were not significant. Linear-regression relationships between pea crab carapace width and scallop length, width, and height were all nonsignificant, although a regression of pea crab carapace width against scallop length did show a positive slope.

DISCUSSION

Mussels from the 3 different geographic areas we sampled did not host pea crabs very frequently. Out of 300 mussels collected, only 2 pea crabs were found; both pea crabs were small females. However, this may be a limitation of our one-time study, and not an accurate reflection of the biology of pea crabs. In casual observations of mussels from Dog Island Sound prior to the study, we found an infestation rate of about 10%. Pearce (1969) and Campos (1989) state that individual pea crabs use multiple hosts at different stages in their life history, and Bierbaum and Ferson (1986) found that small (< 6 mm), immature females are able to move from host to host. Kruczynski (1974) found that another species of mussel, *M. edulis*, was more likely to be infested with pea crabs in deeper water than we surveyed (> 10 ft in his study). A study of greater duration than ours, and covering a greater depth range than ours, is needed to fully investigate the relationship between mussels and pea crabs in the northern Gulf of Mexico.

Bay scallops hosted fewer pea crabs than pen shells. The percentage of scallops hosting pea crabs varied strongly among collection sites, from 4% in Dog Island Sound to 17% at St. Mark's NWR. This may reflect differences in larval recruitment of pea crabs to hosts between the 2 sites, a hypothesis that our data do not address. Alternatively, because scallops in Dog Island Sound were larger than scallops at St. Mark's NWR, it remains possible that larger scallops are able to resist infestation by pea crabs. However, bivalve anatomy offers no ready mechanism for resistance, and to the best of our knowledge, no such resistance has been reported in the literature.

Pen shells were frequent hosts of pea crabs, regardless of collection site: about 70% of pen shells collected were host to at least one pea crab. Pen shells are large, sessile bivalves that can not draw their valves together tightly; even when its adductor muscles are contracted, there is a gap between the shells as they protrude from the sea bed. This unique facet of pen-shell anatomy may make them vulnerable to infestation by symbionts, although in our survey, the only endosymbiont we ever encountered in pen shells was the pea crab. While the outsides of pen shells are heavily fouled by a wide variety of invertebrates, we found only pea crabs inside the mantle cavities. This suggests that pen shells tolerate pea crabs, or that pea crabs defend their hosts against other invading species. However, to date, no studies have explored either of these hypotheses.

It is not clear why there was such a large difference in the infestation rates of 2 common hosts. Pea crabs may show a preference for a certain host, but the literature is contradictory on this point. Derby and Atema (1980) test-

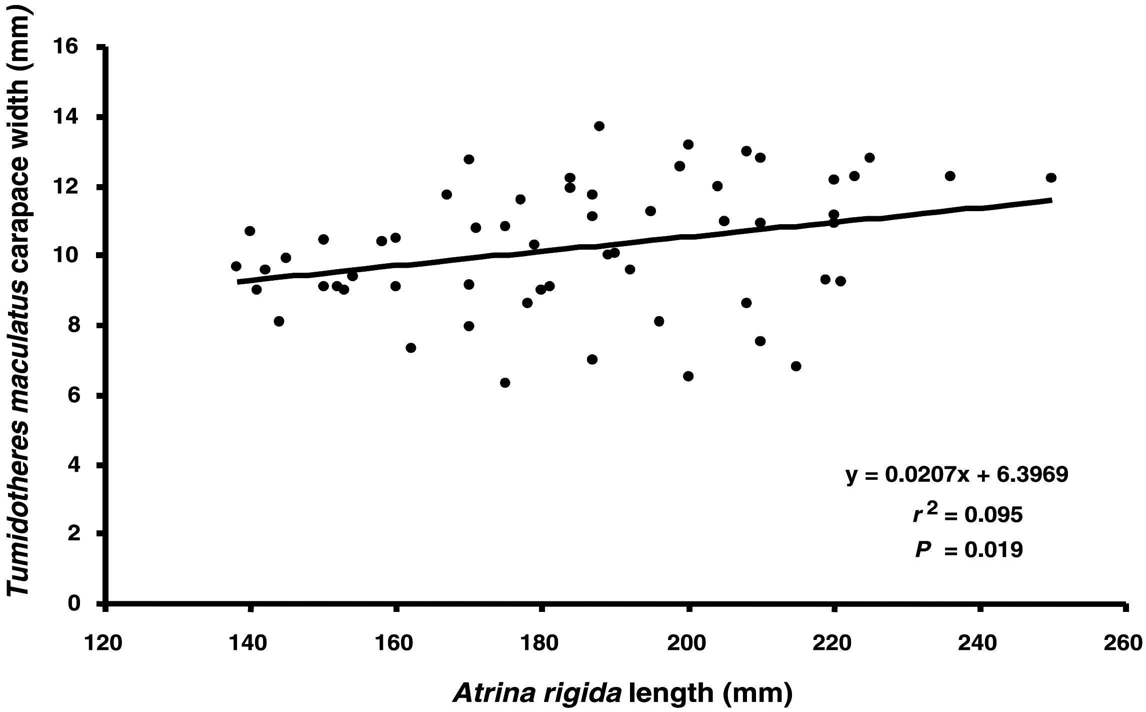

Figure 5. Pea crab carapace width (mm) as a function of pen shell length (mm). A weak but significant trend indicates that larger pen shells host larger pea crabs.

ed pea crabs taken from mussels, *M. edulis*, for attraction to 4 different bivalves and found that pea crabs exhibited a strong preference for *M. edulis*. However, Sastry and Menzel (1962), working in the same region that we studied, performed host recognition experiments with pea crabs taken from bay scallops; in their experiment, pea crabs showed no preference for scallops over pen shells. Whether the pea crab discriminates among host species remains unresolved.

Pen shells may harbor more pea crabs than scallops because pen shells are a year-round occupant of seagrass beds in northern Florida. Bay scallops are mobile, and populations in shallow seagrass beds wane in the winter months. Pen shells, by contrast, are infaunal, and can be found year-round at our study sites (pers. obs.). Stationary, persistent shelters might gradually accumulate pea crabs over time, so it is possible that the long-term persistence of pen shells contributes to the larger numbers of endosymbionts we found. However, our data show that smaller, presumably younger pen shells have higher endosymbiont loads, and extremely large pen shells—those greater than 255 mm in length—have the fewest endosymbionts of any size class. Therefore, our data appear to contradict the hypothesis that older, stationary pen shells may gradually accrue more endosymbiotic pea crabs.

The only host bivalves that ever housed multiple pea crabs in our study were pen shells, the largest host species we collected. While one of us (GSF) has seen photographs, taken in the lab, of multiple pea crabs in a single bay scallop, we never found this condition in the field. Infestations involving multiple pea crabs were rare during our study period, occuring in only 10 of 200 hosts, and all multiple infestations except one were single-female, multiple-male assemblages. The single exception was a pen shell that hosted 2 male pea crabs.

Data from other crab species (Beck 1995, Kuhlmann and Walker 1999) led us to expect that larger host bivalves should hold larger pea crabs. Our data support that hypothesis: at St. Mark's NWR, female crabs living in pen shells were significantly larger than female pea crabs living in scallops. The same trend is apparent within host bivalve species; larger pen shells in St. Joseph Bay hosted significantly larger pea crabs than the smaller pen shells in St. Mark's NWR. Likewise, pea crabs living in larger bay scallops in Dog Island Sound were larger than pea crabs living in smaller bay scallops in St. Mark's NWR, although small numbers of pea crabs in Dog Island Sound preclude adequate statistical support for this trend. Our data, taken as a whole, indicate that the pea crab, a symbiotic pinnotherid crab, conforms to patterns found in free-living xanthid crabs (Beck 1995, Kuhlmann and Walker 1999). Growth in shelter-dwelling brachyuran crabs seems limited by shelter size, whether shelter is biotic or abiotic.

Data from male pea crabs supports this conclusion, albeit in a roundabout fashion. Male pea crabs were strikingly uniform in size in our study, regardless of host species, host size, or collection site. One possible explanation for this trend is that dwarf male pea crabs have terminal growth and reach a well-defined size at maturity that is consistent across populations. Alternatively, male pea crabs may all reach a similar size because male pea crabs move from host to host, and do not rely on host organisms for food (Sastry and Menzel 1962, Bierbaum and Ferson 1986). Crabs that do not spend long periods in a single shelter may not be constrained in their growth. Further data from free-living crab species, such as portunid swimming crabs, is needed to test this hypothesis.

It is possible that we have documented not simply a difference in host size, but also a difference in host quality that could drive differences in pea crab size and frequency among hosts. In pen shell hosts, pea crabs occur more frequently, attain larger sizes, and more often occur in groups. Because pea crabs feed on the gills of bivalve hosts (Bierbaum and Ferson 1986, Bierbaum and Shumway 1988), it is possible that the larger size of pen shells provides pea crabs with more gill surface area and therefore more food than the smaller gills of smaller bivalve hosts. Our data do not address this hypothesis directly, and this hypothesis does not exclude the possibility that shelter size also contributes to pea crab size and frequency.

The possibility that the pea crab uses multiple hosts at different life-history stages (Pearce 1964, Campos 1989) also confounds our conclusions. Whether more mature pea crabs prefer pen shell hosts, specifically, or whether the pea crab chooses among hosts, is unclear in the literature. However, it seems likely that life history, along with host quality and host size, contributes to the patterns we witnessed.

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