

Population dynamics and reproduction of *Dissodactylus mellitae* (Brachyura: Pinnotheridae) on its sand dollar host *Mellita quinquiesperforata* (Echinodermata)

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ABSTRACT: Population dynamics of the symbiotic crab *Dissodactylus mellitae* Rathbun were studied by monthly collections from their sand dollar host *Mellita quinquiesperforata* (Leske) in North Inlet, South Carolina, USA. Size frequency analysis of carapace widths indicated a 12 to 15 mo life cycle for *D. mellitae*. Larvae were released during summer, grew to produce one or more clutches of eggs the next summer, and died shortly thereafter. Sex ratio was 1:1 throughout the year; females attained a slightly larger maximum size. Fecundity did not vary over the reproductive season (April through September) and mean egg number was 206 ± 62 (s. d.) eggs per clutch. Most recruitment occurred from May through September. *D. mellitae* differs from other species in the family Pinnotheridae in that males and females are more similar in size and longevity, there are no soft carapace stages, clutch size is relatively small and the entire clutch is completely covered by the abdomen. Accessibility of sand dollars to settling *D. mellitae* and protection provided to post-metamorphic individuals may decrease mortality enough to balance the small clutches produced by this crab.

INTRODUCTION

The influences of the biotic environment of a host on its symbionts are not well understood. Symbionts must adapt to the physical constraints, physiological characteristics and movements of their hosts. They may modify not only their own morphology, physiology, reproduction and behavior, but also that of the host to make a space to live (e. g. Patton, 1967).

Because of the tight coupling between symbionts and their hosts, comparative investigations of symbionts within the same taxonomic group should reveal diverse adaptive patterns. Life history components should be particularly varied because a symbiont must contend with the constraints of the host in addition to those of the habitat in which the host lives. In marine waters, for instance, egg numbers of symbiotic copepods seemed to vary with the abundance, accessibility, mobility, and chemical cues of the host, as well

as with the host habitat (Gotto, 1962). Although chemical cues followed by symbionts are discernible to investigators only by experimentation (e. g. Johnson, 1952; Davenport et al., 1960; Gray et al., 1968; Castro, 1978; Derby and Atema, 1980), host abundance, mobility, and habitat are relatively easily observed and could explain much of the variability in life histories of closely related symbionts.

Groups which inhabit a wide variety of hosts should provide an excellent opportunity for comparative study and elucidation of host effects on symbiont life history patterns. One such group is the brachyuran family Pinnotheridae, whose members may live with bivalves, polychaetes, burrowing shrimp, gastropods, holothurians, tunicates or echinoids. They may be endo- or ectocommensal, have one or many possible hosts, be confined to the host or have some free-living stage, and share their host or live alone. Although several investigators have studied the life cycles of pinnotherids, most of those studied (*Pinnotheres maculatus* – Pearce, 1964; *P. novaezelandiae* – Jones, 1977a, b; *P. ostreum* – Christensen and McDermott, 1958; *P. pisum* – Atkins, 1926, 1955, 1958; *Fabia subquadrata* –

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Pearce, 1966a) live in bivalve hosts and exhibit similar life cycles. A tendency to generalize to the whole family Pinnotheridae on the basis of these studies has begun (e. g. Jones, 1977a), but should be viewed with caution. Crabs which inhabit non-bivalve hosts or several different hosts may have very different life history patterns. There may be trends within the family, such as evolution from a free-living existence to obligatory symbiosis, or from a single host to a multiple host life cycle (Pearce, 1966a), which comparative studies on non-bivalve-inhabiting species could clarify.

One such species is the symbiotic pinnotherid *Dissodactylus mellitae* Rathbun. This tiny crab ranges from Massachusetts to Florida; it clings to the spines of sand dollars, including *Mellita quinquesperforata*, *Echinarachnius parma* and *Encope michelini* (Williams, 1965). *D. mellitae* has a purplish-brown and white mottled carapace which matches the underside of *M. quinquesperforata*, and bifid dactyls on the first 3 pairs of walking legs to help it maintain a position among the spines. Several crabs are often found on 1 host (Gray et al., 1968) and mean densities range from 0.4 to 2.7 crabs per sand dollar (Bell, 1981). However, they do not appear to do physical damage such as Dexter (1977) found on Panamanian echinoids. Although sand dollar tissue may be consumed by the crabs (T. S. Hopkins, pers. comm.; Telford, 1982), whether the tissue is dead or alive, and whether the crabs subsist mainly on such tissue or on material secreted or captured by the host, such as mucus, diatoms and detritus, is unclear. In the present study, age structure, growth, sex ratio, sexual dimorphism, recruitment, larval release and fecundity of a population of *D. mellitae* on its sand dollar host, *M. quinquesperforata*, were studied in North Inlet, South Carolina, to allow comparisons with other members in the genus and in the family Pinnotheridae.

MATERIALS AND METHODS

Between April 1979 and March 1980, 10 field collections were made at approximately monthly intervals from Debidue Shoal, a sandy, well-sorted, subtidal shoal near the mouth of North Inlet Estuary, Georgetown County, South Carolina (33°20'N, 79°19'W). *Mellita quinquesperforata* were collected by hand using SCUBA in 0.5 to 2.0 m of water during slack low tide. Immediately after removal from the sand, sand dollars were placed in individual 15 cm plastic Petri dishes to allow discrete observation and measurement of the crabs on each sand dollar. Hand collection and placement in Petri dishes reduced loss of crabs caused by other collection methods such as dredging. Petri dishes were placed in a PVC collecting

tube and transferred to coolers in the boat. Coolers were filled with ice and transported to the Belle W. Baruch laboratory in Columbia, where samples were kept cool until examination (within 7 d).

In the laboratory, a fine stream of seawater was used to wash sand from each sand dollar into the Petri dish. Filling the interstices of the spines of the sand dollar with water aided in the detection of small crabs (0.7 to 1.6 mm). Crabs were found in the sand and water in the Petri dish also. Carapace width (CW) was measured with an ocular micrometer. Sex was determined by inspection of the pleopods (Atkins, 1926; Stauber, 1945; Jones, 1977a). Crabs with CW less than 1.4 mm bore pleopods not yet sexually differentiated and were classed as juveniles.

Ovigerous females were stored in 10% buffered formalin. Later their eggs were removed, counted, and the diameters of 15 randomly selected eggs were measured with an ocular micrometer. Dark eyespots in an egg indicate that it is close to hatching, so a female with such eggs may have already released part of her clutch. However, comparisons showed that females with eyed embryos ($n = 10$) did not have significantly fewer eggs (196.4 ± 50.6 ; one-sided t -test, $P > 0.05$) or smaller clutch volumes ($2.21 \pm 0.67 \text{ mm}^3$; one-sided t -test, $P > 0.05$) than other gravid females (208.5 ± 65.1 eggs and $2.42 \pm 0.95 \text{ mm}^3$; $n = 38$). All values are given as mean \pm standard deviation. Mean egg volume was also the same for both types of females (t -test, $P > 0.05$); consequently, all ovigerous females were pooled.

RESULTS

Size structure and growth

Fig. 1 shows the proportions of juveniles, males, females and ovigerous females in the *Dissodactylus mellitae* population from April 14, 1979 to March 15, 1980. A total of 1,215 crabs was collected from 1,257 sand dollars. Ovigerous females, which were always larger than 2.8 mm CW, were found only in collections between April and September 30, 1979, although collections were made in both March 1979 and March 1980. Water temperature had risen to 22°C by April 14, 1979, but was only 12°C in March. Only 2 of the 14 ovigerous females in April had eyed ova (indicating a near-hatching condition), so the first zoeal releases probably occurred in late April/early May. Length of larval life is thus probably less than 6 wk (unless the juveniles in the June sample came from another population). Juveniles were present in all collections except April, but the major settlement was from June to October with peaks in June, July, and August. When the smallest crabs (0.7 to 1.0 mm) were removed from

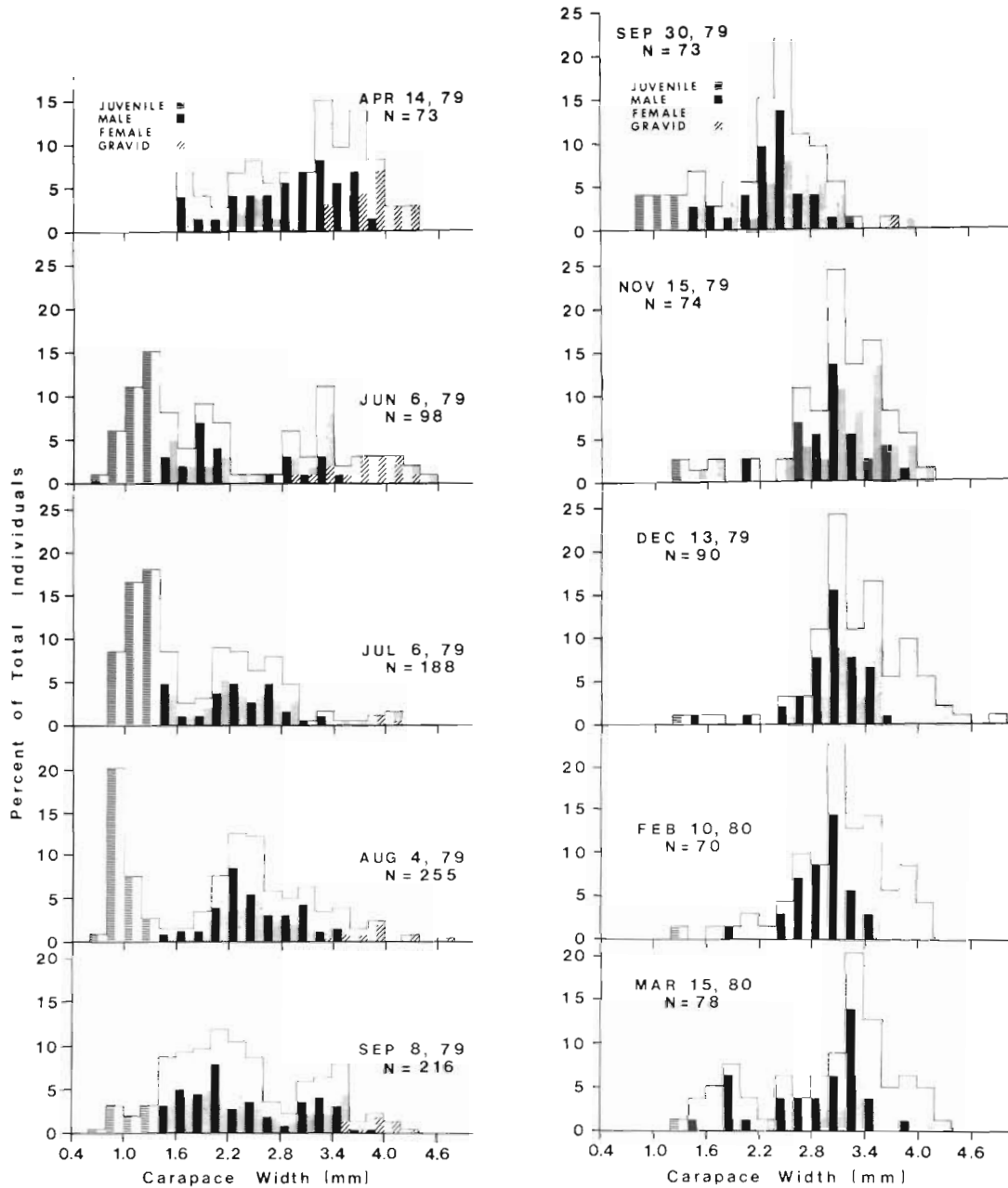


Fig. 1. *Dissodactylus mellitae*. Monthly size-frequency histograms of carapace width April 1979 to March 1980. Total individuals in each 0.2 mm size class are represented by the enveloping bar graph

their hosts and placed in seawater they swam by rapid movements of the abdomen. Although swimming ability usually characterizes megalopae of other crab species, these *D. mellitae* had no other megalopal characteristics (J. Christy, pers. comm.) and were therefore classified as first stage crabs.

Two classes of sexable individuals were present in April, presumably after surviving the winter season (Fig. 1). The first, including all crabs larger than 2.0 mm CW in April, made up a smaller proportion of the population in June. By July, this group, which

displayed little growth during the previous three months, had nearly disappeared. By August, only a small proportion of the original cohort of large crabs remained, and they were all ovigerous females greater than 4.2 mm CW.

The second class of overwintering crabs was about 1.6 to 2.0 mm CW in April, 1.8 to 2.2 mm in June, and 2.6 to 3.0 mm in July. By August, some individuals had grown as large as 4.0 mm CW and ovigerous females as small as 3.2 mm were present. All members of this group were larger than 3.0 mm in September, and most

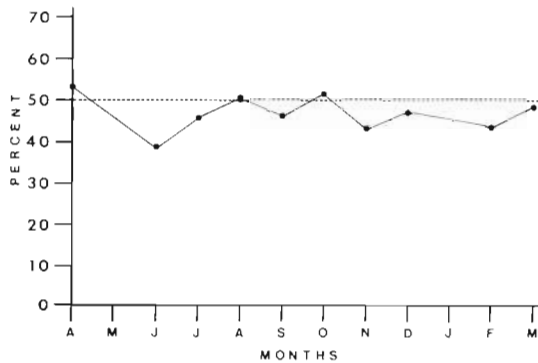


Fig. 2. *Dissodactylus mellitae*. Monthly percentages of males in collections, April 1979 to March 1980

females over 3.4 mm were ovigerous. By September 30, nearly all of the animals which had survived the previous winter were gone.

Newly-settled juveniles first appeared in the June collection (water temperature: 28°C), and probably began to settle in May. Recruitment remained high through August, resulting in a broad peak of crabs between 0.6 and 3.0 mm which had settled in 1979, but with a notable absence of individuals in the 1.4 to 2.0 mm size range in both July and August. By September 30, these crabs had grown to a narrower size range between 1.8 and 3.4 mm; they continued to grow through November, when the size class ranged from 2.4 to 4.2 mm. A few crabs which settled in June may have oviposited in 1979, but the majority appears to have overwintered without growing or producing young, as evidenced by the stationary peak between

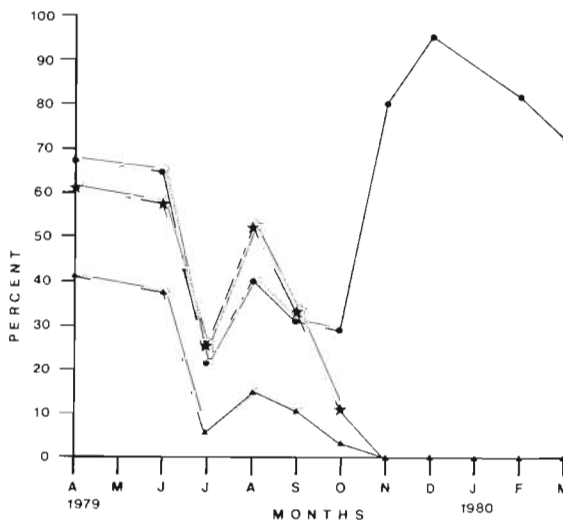


Fig. 3. *Dissodactylus mellitae*. Ovigerous females April 1979 to March 1980. ▲ percent ovigerous of the female population; ● percent of adult females (> 2.8 mm carapace width) in the female population; ★ percent of ovigerous females in the adult female group

2.4 and 4.2 mm from November 15, 1979 to March 15, 1980. If the pattern seen in 1979 were to be repeated, these crabs would have been the first to reproduce when temperatures rose in April 1980.

The fall recruits (CW about 0.8 to 1.8 mm on September 30, 1979) made up a very small, but consistent, proportion of the population throughout the winter. They grew little, remaining between 1.2 and 2.4 mm CW from November 1979 to March 1980. There was a 70% reduction in the number of crabs per sand dollar between September 8 and September 30, only 35% of which can be accounted for by loss of the oldest, largest individuals (Bell, 1981). Since the low number of crabs per sand dollar (0.5) resulted in small sample sizes even when over 200 sand dollars were collected, this smallest group may be underrepresented in the winter collections. As water temperatures rose again in the spring, these crabs would be expected to resume growth and reach maturity in early summer, 1980.

Sex ratio and size dimorphism

Although sex ratio (Fig. 2) was not significantly different from 1:1 in any month (G-test with Yates correction for continuity, $P > 0.05$; Sokal and Rohlf, 1969), females outnumbered males in all but 2 collections (April, October 1979). The largest difference (June 1979) may have been due to inexperience at sexing smaller crabs. June crabs were used for other experiments and were not available for later reanalysis. Sex ratio did not differ among months either, according to a 2×10 test for independence (G-test, $P > 0.50$).

Males and females were present throughout the year and appeared to have similar growth patterns. However, females attained a larger maximum size (4.82 mm CW) than males (3.96 mm). This difference was particularly evident between November 1979 and March 1980 (Fig. 1), when the female modal size was shifted 0.4 to 0.8 mm to the right of that of males. Because modal sizes coincided on September 30, 1979, males apparently ceased growing some time between then and November, or grew more slowly than females.

Egg production

All oviposition appeared to take place during the warmer parts of the year, between late April and late September. Fig. 3 shows monthly percentages of total females which were ovigerous, as well as the proportion of adult females in the population and the percentage of adult females which were ovigerous. Adult size was determined by the smallest ovigerous female

found in any collection (2.8 mm CW; June 1979). Abundance of ovigerous females peaked in spring (April to June), with a smaller peak in August. The July sample contained fewer adult females, and fewer of these were ovigerous, than in any other month; consequently, the percent of total females which were ovigerous declined in this month. No ovigerous females were found after September 30, 1979.

At the end of September, only 30% of the females were of adult size (Figs. 1 and 3), but by the middle of November, 95% had attained this size. This growth pattern would allow most overwintering females to develop a clutch as soon as water temperatures warmed in the spring. In fact, several females taken into the laboratory on February 10, 1980, and maintained without males at 15°C on a 12:12 light-dark cycle produced viable clutches within four weeks.

Clutch size

Fifty-six ovigerous females with a mean carapace width of 3.81 ± 0.32 mm were collected throughout the year; 48 were analyzed in the laboratory and the remainder, all from the June sample, were used in hatching experiments. Clutches had an overall mean egg number of 206.0 ± 62.1 eggs (female)⁻¹, a mean egg volume of $1.16 \pm 0.26 \times 10^{-2}$ mm³ (mean egg diameter: 279 ± 21 μm), and a mean clutch volume of 2.38 ± 0.90 mm³. Among months when ovigerous females were present, no variations were observed for egg number ($P > 0.50$), mean egg volume ($P > 0.10$), or clutch volume ($P > 0.50$; ANOVA; Sokal and Rohlf, 1969).

Several regression models (linear, exponential, power and log) were calculated to test the relationship among crab size, egg number and clutch volume. For all variables, linear models gave the highest correlation coefficients and lowest residuals. Clutch volume and carapace area (length \times width) yielded a correlation coefficient (r) of 0.54; egg number and carapace area had an r of 0.70. Egg number was less closely correlated with carapace length ($r = 0.44$) than with carapace width ($r = 0.74$; Fig. 4), and a multiple correlation among these three variables did not improve the correlation ($r = 0.74$). Thus, variability in egg number can best be explained by differences in carapace width (slope significant at $P < 0.001$; Fig. 4). However, variability in the relationship was substantial; for instance, the female with the most eggs (373) was 0.6 mm (13%) smaller than the largest ovigerous female, and egg number among females of similar size varied as much as 64% (Fig. 4).

Several females with eyed ova were maintained in the laboratory to examine patterns of larval release.

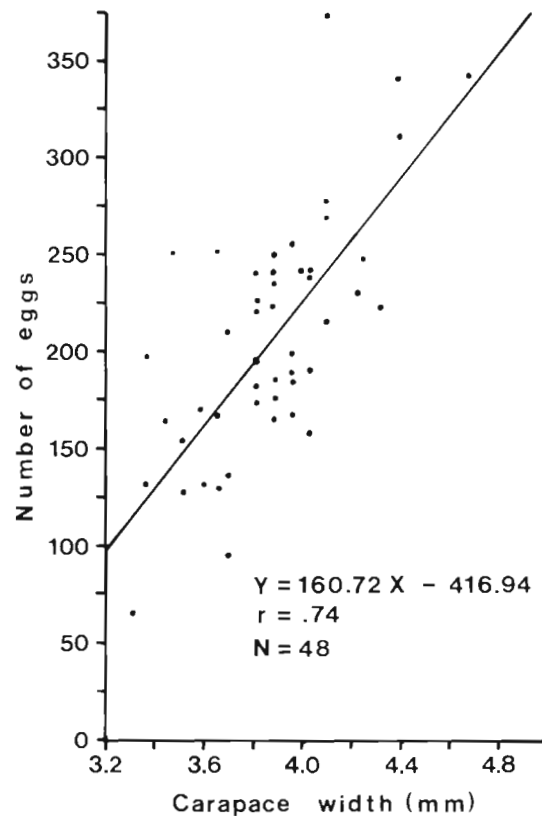


Fig. 4. *Dissodactylus mellitae*. Linear regression of egg number on carapace width of ovigerous females. April to November 1979

Two females collected April 29, 1979, released large portions of their clutches (234 and 262 zoeae) 6 d after collection. In June, 5 crabs released partial clutches (188, 182, 172, 143, and 156 zoeae) after 5 to 8 d in the laboratory. Four days after the initial release, the crab which released 156 young released 39 more zoeae, and still retained some eggs; the remaining crabs died before releasing additional young. The number of young liberated in initial releases was always well over half of the clutch; when a second release was observed, the initial release was 80% of the two. Although all females which released clutches in the laboratory liberated partial clutches, whether this also occurred in the field was not determined. Additionally, the total number of clutches a single female could produce was not resolved.

DISCUSSION

Although *Dissodactylus mellitae*, like other pinnotherids, is symbiotic, its life history characteristics are quite different from those of the more well-

studied pinnotherids (e. g. *Pinnotheres pisum* – Atkins, 1926; Christensen, 1958; *P. ostreum* – Christensen and McDermott, 1958; *Fabia subquadrata* – Pearce, 1966a), which typically inhabit bivalves but are occasionally found with other sessile invertebrates. For instance, *F. subquadrata* lives 2 y and *P. ostreum* may live 3 y. This study shows that *D. mellitae* in North Inlet have only a 12 to 15 mo life cycle, and the population can be divided roughly into 2 groups. The first group includes crabs which settled during the first part of summer 1979 (May to early August). Although some of the earliest-settling or fastest-growing individuals may have grown large enough to reproduce in late fall 1979, most probably overwintered as large adults, to spawn early the following year and then die. These crabs probably mated in the fall or winter. All had attained adult size and had well-developed secondary sexual characteristics by then. Females brought into the laboratory during the winter produced clutches, indicating that they were already fertilized. Many of the first-group crabs disappeared between September and October 1979, when their density dropped from 1.63 to 0.65 individuals (sand dollar)⁻¹ (Bell, 1981). This reduction could have been due to increased competition between larger adults, leading to mortality or emigration. Male and female crabs usually share a host with a member of the opposite sex rather than with a conspecific, a tendency which was significant ($P < 0.005$) all year, but was particularly marked during the fall and winter (Bell, 1981). The second group, crabs which settled later in the summer and in the fall, overwintered at small or intermediate sizes and resumed growth when temperatures rose in the spring. Their small size in March 1980 suggests that they would mate sometime in midsummer and release young which would settle in September and October 1980.

Growth and morphological characteristics of *Dissodactylus* also differ from many other pinnotherids. *D. mellitae* did not appear to change carapace texture or shape appreciably, although mature females of many pinnotherids often attain an enlarged abdomen (Patton, 1967) and a spherical shape (own obs.) uncommon in other brachyurans. Telford (1978) found no change in the length-width ratio of the carapace of *D. crinitichelis* or *D. primitivus* throughout post-larval life, and also concluded that these species did not change carapace shape. The small number of *D. mellitae* in the 1.6 to 2.0 mm size range in July and August (Fig. 1) was unexpected, but there was possibly an increase in carapace width relative to other dimensions which allowed crabs to go from about 1.4 to 2.0 mm CW in one molt. This increase could be the result of a change from a length-dominated shape typical of zoeae to a width-dominated shape typical of

adults. Alternatively, mortality could have been high for this size class. Similar size-frequency patterns and large samples in July and August exclude the possibility that the size class was inadequately sampled.

Most pinnotherids in bivalves have a hardened carapace only during the invasive stage and when they leave the host to find a mate. A soft carapace may be an adaptation to reduce irritation and possible death to the host (Patton, 1967). *Dissodactylus mellitae*, on the other hand, has a hard, flat carapace in all stages, which certainly must protect it from the rough, moving spines of its host and the sandy substrate in which it dwells. Telford (1978) did not mention soft stages in *D. crinitichelis* or *D. primitivus* either, so a hard carapace may be a general characteristic of a pinnotherid genus which lives on the outside of its host.

Male-female pairs of *Dissodactylus mellitae* were found throughout the year (Bell, 1981), and the sex ratio was not significantly different from 1:1. Patton (1967) also found that most symbiotic decapods which live in groups exhibit a 1:1 sex ratio. Telford (1978) reports that female *D. primitivus* and *D. crinitichelis* inhabiting Caribbean echinoids outnumbered males (67:38 and 51:39, respectively); however, these collections were small, and more extensive long-term collections would be necessary to confirm the trend.

Female *Dissodactylus mellitae* grow slightly larger than males, and Telford (1978) also found that female *D. primitivus* grew larger than males. Larger size could allow females to carry more eggs (see below). Sexual dimorphism appears to be greater in bivalve-inhabiting pinnotherids than in *D. mellitae*. Females are more abundant and grow considerably larger than males (Christensen and McDermott, 1958; Pearce, 1966a; Silas and Alagarwami, 1967; Jones, 1977b). Male *Pinnotheres ostreum* die after mating while females live 1 or 2 more years (Christensen and McDermott, 1958). Small size and shortened life of males may allow more efficient use of host resources. The fact that adults of several bivalve-inhabiting pinnotherids occur singly except for occasional male-female mating pairs (Christensen and McDermott, 1958; Silas and Alagarwami, 1967; Jones, 1977a) also suggests that host resources are limited. Since adult *D. mellitae* appear in male-female pairs throughout the year and males grow as old and almost as large as females, resources may not be as limited on sand dollars.

Clutch size is proportional to carapace width in *Dissodactylus mellitae* (Fig. 4). Positive linear or curvilinear relationships between egg number and female size have been demonstrated for many other decapods (e.g. Jensen, 1958; Warner, 1967; Turoboyski, 1973; Telford, 1978), and Nelson (1980) has suggested that this correlation is closer in crustaceans than in other

animals because of the rigidity of the exoskeleton. Unlike other brachyurans and even other pinnotherids (Jones, 1977a, Fig. 7; Silas and Alagarwami, 1967, Fig. 1; own obs.), the clutch of *D. mellitae* is completely covered by the abdomen. Although abdominal coverage may protect eggs from being injured by sand dollar spines, it must severely limit clutch size as well, and *D. mellitae* may have smaller eggs and modified abdominal morphology to increase clutch size. Egg diameter (279 μm) is at the small end of the range for all crabs (Warner, 1977), and mean clutch size (206) is smaller even than other members of the genus (*D. crinitichelis*: 259; *D. primitivus*: 274; Telford, 1978). *D. primitivus* is twice the size of *D. mellitae*, and has eggs twice as large (515 μm ; Telford, 1978).

Assuming the population we studied was stable, the mean egg number produced by female *Dissodactylus mellitae* seems unusually low for a benthic invertebrate with pelagic larvae. Other pinnotherids have at least an order of magnitude more eggs per clutch than *Dissodactylus* spp. (e.g. *Pinnotheres ostreum*: 8 to 9.5×10^3 ; *P. pisum*: 5.8×10^3 ; Christensen and McDermott, 1958; *Pinnixa* spp.: 7 to 8×10^3 ; Pearce, 1966b). However, the number of clutches produced could affect total egg number. Some bivalve-inhabiting pinnotherids may live up to 2 or 3 y and produce 2 or more clutches per lifetime (Christensen and McDermott, 1958; Pearce, 1966a). The number of clutches per lifetime is unknown for *D. mellitae*, but with the short life span (12 to 15 mo) documented in this study, a female would have only 1 reproductive season of 10 to 12 wk (mid-April to July or mid-July to September). Pohle and Telford (1981) found that *D. crinitichelis* incubated clutches for 14 to 15 days, and oviposited another within 24 h of the release of the previous one. If this incubation period was applied to *D. mellitae*, a female could produce 5 to 6 clutches in a single season for a lifetime egg production of about 1000 to 1500 eggs, with a maximum of perhaps 2200 (maximum clutch size observed [373] times 6 clutches). Releases of partial clutches over a period of days would reduce the number of clutches which could be produced over a lifetime; however, partial releases have not been observed in other pinnotherids and only in the laboratory in *D. mellitae*, so they may not occur in the field.

The larval biology of *Dissodactylus mellitae* is poorly known. Data on ovigerous females and juvenile recruitment in Fig. 1 indicate that the length of larval life is less than 6 wk, but the number of zoeal and megalopal stages is unknown. *D. crinitichelis* had 3 zoeal stages and a megalopa before metamorphosing to a first crab stage in 18 d (Pohle and Telford, 1981). The megalopa of *D. crinitichelis* must feed on the host before metamorphosing to first crab, so it is the invasive stage of this species. The first stage crab appears

to be the invasive stage of several other pinnotherids, however, and has been found in the plankton as well as inside the host (Christensen and McDermott, 1958). First stage crabs capable of swimming were the smallest *D. mellitae* found on sand dollars, so they are probably the invasive stage, although the megalopae might settle and quickly metamorphose to a swimming first stage crab. One confounding factor in the search for the invasive stage of pinnotherids is that the megalops instar and the first true crab may be quite similar in size and appearance, even to the abdomen being folded under the cephalothorax (Hart, pers. comm.; cf. Pearce, 1966b). The problem can be solved by larval rearing and experimentation, as was done by Pohle and Telford (1981).

The length of time which larvae are in the plankton may have a profound effect upon survival, and consequently, life history patterns. In free-living marine decapods, larval life may range from 2 wk (Warner, 1977) to 9 mo (Allen, 1966), but complete suppression of larval stages is rare (Warner, 1977). Planktonic survival may be quite low; for *Aratus pisoni*, a grapsid crab living in mangrove swamps, Warner (1967) calculated 0.014 % survival from hatching through settlement, a period of 1 mo. A female *A. pisoni* carries 3 to 10×10^3 eggs and may produce up to 2.75×10^4 eggs in 7 clutches. Applied to the mean egg number of *D. mellitae* (206 ± 62.1), this percentage would yield 0.03 recruiting offspring per clutch, far below the number needed for replacement even if *D. mellitae* had 5 or 6 clutches in a lifetime. Other pinnotherids, however, could maintain populations under the constraints of this low survival. *Pinnotheres ostreum* has an egg number similar to *A. pisoni* and larval life of less than 1 mo (Sandoz and Hopkins, 1947; Christensen and McDermott, 1958); *P. pisum* (Christensen and McDermott, 1958), *Pinnixa faba* and *Pinnixa littoralis* (Pearce, 1966b) all have more than 5×10^3 eggs.

Because of such potentially high larval mortality, many decapods, including *Dissodactylus mellitae*, may have adaptations to increase larval survival. Abbreviated development reduces time spent in the plankton. *Pinnotheres moseri*, an obligate ascidian symbiont, has a larval life of only 24–36 h (Goodbody, 1960). *P. moseri* hatches as an advanced zoea resembling the 4th zoeal stage of *P. pisum* (Atkins, 1955), molts to a megalops, and settles. However, advanced zoeal stages were not released by *D. mellitae*, whose first zoeal stages are most similar to those of *D. crinitichelis*, with a larval life to megalopa of 12 d (Pohle and Telford, 1981), and those of *Pinnotheres taylori*, with a larval life to first crab of 28 d (Hart, 1935). Behavior of larvae with respect to depth and currents could also affect survival. Zoeae of several pinnotherids seek the bottom within 1 to 5 d after hatching (Lebour, 1928;

Welsh, 1932; Christensen and McDermott, 1958), which could reduce predation and aid in host detection.

Host-specific factors, such as chemical cues, may improve survival of settling symbionts and enhance infestation rates. Chemical detection of the host has been demonstrated for many pinnotherids (Johnson, 1952; Davenport et al., 1960; Sastry and Menzel, 1962; Gray et al., 1968; Derby and Atema, 1980). Bivalves, tubicolous polychaetes and ascidians may be frequent hosts for symbionts because they produce a continuous exhalant current which could contain body scents (Gotto, 1962). Echinoids also give off chemicals which can be detected by their symbionts. Johnson (1952) found that *Dissodactylus mellitae* was more attracted to water from its host *Mellita quinquesperforata* than any other pinnotherid-host pair tested.

Host habitat may also affect their invasibility. Gotto (1962) found that symbiotic copepods living on echinoderms had fewer eggs than those on other hosts, and postulated that because most echinoderms were large, abundant, moved slowly about the sediment surface and lived in sheltered subtidal waters, they could be invaded more easily. In addition, copepods with burrowing echinoderm hosts had more eggs than those on more accessible surface-dwelling echinoderms. Such differences in host habitat could affect egg numbers in pinnotherids also. Three species of *Dissodactylus* on echinoids have fewer than 300 eggs per clutch (Telford, 1978; this study), while *Pinnotheres* spp. inhabiting intertidal bivalves have 2 to 10×10^3 eggs (Christensen and McDermott, 1958; Pearce, 1966b; Silas and Alagarwami, 1967). Studies of several pinnotherids (Houghton, 1963; Gray et al., 1968; Beach, 1969; Kruczynski, 1973, 1974) indicated that infestations varied spatially, with higher numbers of crabs in sheltered or subtidal areas even when crab and host abundance were not correlated. *Mellita quinquesperforata* living in North Inlet may be easy to invade because it lives in subtidal, relatively low-current areas, and moves about the sediment surface, possibly even picking up crabs which are in the sand (Bell, 1981).

Finally, post-larval mortality of symbiotic animals may be considerably lower than in free-living species. Post-larval survival is often tied to food availability, and once a symbiont has found a host, food may no longer be a problem (Orton, 1920; Stauber, 1945). *Dissodactylus mellitae* appears to feed from oral grooves of sand dollars (Telford, 1982; own obs.) and may never lack food. Newly-settled young of free-living benthic animals are subject to much predation (Thorson, 1957), but symbiotic organisms may receive protection from predators (Ross, 1971; Bloom, 1975). Because *D. mellitae* lives on the underside of sand dollars and is

cryptically colored, post-metamorphic mortality may be considerably reduced.

Although the reproductive effort of *Dissodactylus mellitae* (about 2×10^3 eggs or less) appears to be similar to that of its congeners, it is considerably lower than other pinnotherids and brachyurans in general. Current knowledge of the larval biology of *Dissodactylus* is incomplete, but members of the genus do not appear to have any exceptional mortality-reducing adaptations which would counteract their relatively low offspring production. Because all members of the genus are associated with echinoids, benefits associated with these hosts, such as abundance, accessibility, residence in relatively benign habitats and adequate food could enhance survival considerably. Studies comparing the suitability of molluscan, polychaete and echinoderm hosts would improve our understanding of symbiosis and could explain the dichotomy between *Dissodactylus* and other members of the Pinnotheridae.

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