

Population biology of *Trapezia* spp. and other coral-associated decapods

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ABSTRACT: We describe the population structure of 3 coexisting species of *Trapezia* and 4 other common decapod species associated with the reef coral *Pocillopora* in the Eastern Pacific Ocean. Most species carry eggs throughout the year, and egg number is highly correlated with body size. *Trapezia* postlarvae (= postmegalopa) recruit in April and June only and reach adult size by the following January. Sex ratios vary among species and may be affected by the frequency of movement among coral heads. Decapod abundance is often higher on the shallow reef flat, where *Pocillopora* cover is more continuous and predatory fishes are less common. In contrast to many 'community' studies, area (coral head size) is not an important predictor variable, except for a modest effect on abundance. Instead, season and reef location emerge as the most important correlates with population structure of decapod species associated with *Pocillopora*.

INTRODUCTION

A rich fauna of decapod crustaceans inhabits the living branches of *Pocillopora* spp., a Pacific reef coral (Abele, 1976b; Abele and Patton, 1976; Castro, 1976). The community has been well studied, particularly in the Eastern Pacific Ocean (Abele, 1976a, 1976b; Abele and Patton, 1976; Castro, 1976, 1978, 1982; Glynn 1976, 1980, 1983a; Gotelli and Abele, 1983). Abele (1976a, 1979) compared species numbers and species-area curves for coral heads from the Bay of Panama and the Gulf of Chiriqui. Glynn (1976) reported on the distribution of 2 common species (*Trapezia ferruginea* Latreille, *Alpheus lottini* Guerin) on 119 heads collected from Uva Island, a patch reef in the Gulf of Chiriqui. Gotelli and Abele (1983) examined patterns of association and co-occurrence of species in this same collection. Community patterns have also been reported for collections from Australia (Patton, 1974; Austin et al., 1980; Black and Prince, 1983), Hawaii (Preston, 1973; Coles, 1980) and the Red Sea (associates of *Stylophora*; Edwards and Emberton, 1980). Abele (1984) summarizes community structure and colonization experiments in Australia and the Central Pacific.

In spite of these community studies, we still know little of the population biology of many coral-associated decapods (Castro, 1976). The purpose of this work is to document patterns in the population structure, body size, egg number, and fecundity of seven common species associated with *Pocillopora* in the Eastern Pacific. We return to Glynn's (1976) Uva Island corals, which were collected carefully on 4 sampling dates (Jan, Apr, Jun, Aug) and 2 reef locations (reef flat and reef flank; see Glynn [1976] for terminology). These data allow us to document spatial and temporal variation in several population measures.

We have concentrated on the patterns manifest by 3 closely related, syntopic xanthid crabs: *Trapezia ferruginea* Latreille, *Trapezia corallina* Gerstaecker, and *Trapezia formosa* (Smith). A fourth Eastern Pacific species, *Trapezia digitalis*, was collected only once at Uva and is not considered here. *Trapezia* spp. are brightly colored obligate associates of live pocilloporid corals; they feed on coral mucus (Knudsen, 1967; Patton, 1974; but see Crane, 1937). Individuals migrate between coral heads at night and establish male-female pairs (Castro, 1978), which may exclude other individuals from a coral head (Preston, 1973). *Trapezia* actively defend their host coral from attacks by the crown-of-thorns seastar, *Acanthaster* (Weber and Woodhead, 1970), as well as increasing coral vitality by promoting cleansing activities and branch elonga-

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tion (Glynn, 1983a). Although Eastern Pacific *Trapezia* are very similar in morphology and appearance, our comparative analysis reveals their population biology is quite distinct.

In addition to the common species of *Trapezia*, we present some brief notes on the biology and population structure of 4 other *Pocillopora* associates: a snapping shrimp (*Alpheus lottini* Guerin), 2 palaemonid shrimp (*Fennera chacei* Holthuis and *Harpiliopsis depressa* [Stimpson]), and a spider crab (*Teleophrys cristulipes* Stimpson). Taken together, these 7 species are typical co-occurring residents of a single coral head.

In a previous analysis (Gotelli and Abele, 1983), we detected subtle correlations of abundance among *Trapezia*: a positive correlation between *Trapezia ferruginea* and *Trapezia corallina* and a negative correlation between *Trapezia corallina* and *Trapezia formosa*. But our main finding was that indices of correlation and association among species were distributed randomly. In other words, the abundances of these 7 species appear to fluctuate independently of one another, at least in a statistical sense. This finding provides a rationale for our analysis, in which we consider the population structure of coral-associated decapods on a species-by-species basis.

MATERIALS AND METHODS

P. W. Glynn collected coral heads and their associated fauna during January (n = 56), April (n = 29), June (n = 24), and August (n = 10) 1973 from a patch reef at Uva Island, Gulf of Chiriqui, Panama. These sampling dates include the dry season (Jan, Apr) and the wet season (Jun, Aug). A total of 119 live coral heads were selected at random from the shallow reef flat (n = 52) and the deeper reef flank (n = 57). Intact coral heads were bagged and then broken off at the base. Bags were sealed and taken to the surface, where the length, width, and depth of each coral head was measured and epibionts were removed. These measurements were used to calculate coral head volume, which is correlated with surface area (Barry, 1965). Animals associated with the dead coral base were not included. All coral heads sampled were in the genus *Pocillopora*, including *P. damicornis*, *P. robusta*, *P. capitata*, and *P. lacera*. Most coral associates do not appear to differentiate among congeneric coral species (Garth, 1964; Patton, 1966; Castro, 1976).

All specimens of *Trapezia* from a single coral head were kept together. Unfortunately, the January samples were combined before it was realized that the *Trapezia* belonged to 3 species, not just 1. Consequently, some of our statistical analyses for *Trapezia* are incomplete and do not include the January data. A

series of measurements were taken on each individual, although carapace length (CL) was used as a primary measure of body size because it has no differential growth associated with the onset of sexual maturity (Finney and Abele, 1982).

A total of 1,388 individuals of *Trapezia* spp. were examined and divided into 3 age classes: postlarvae (= postmegalopa individuals that could not be sexed; less than 2.5 mm CL), juvenile males and females (= individuals less than 6.5 mm CL for *T. ferruginea* and *T. formosa*; 4.5 mm CL for *T. corallina*), and adult males and females (6.5 mm CL or larger; 4.5 mm CL for *T. corallina*). We used 6.5 mm CL (4.5 mm CL for *T. corallina*) as the size dividing mature from immature individuals of *T. ferruginea* and *T. formosa* based on morphometric studies of this species complex (Finney and Abele, 1982). However, any ovigerous female, regardless of size, was considered to be sexually mature. Ovigerous females of *T. ferruginea* ranged in size from 5.0 to 11.0 mm CL, those of *T. formosa* from 6.3 to 13.0 mm CL, and those of *T. corallina* from 3.5 to 10.1 mm CL.

We determined the number of eggs carried by females of different body sizes by first wet-weighing preserved egg samples of 250 to 2,500 eggs in increments of 250 eggs. The relation between egg weight and egg number was then determined by linear regression. The correlation coefficient of this relation is greater than .99. From the January samples, a group of 70 females (30 *Trapezia ferruginea*, 20 *T. corallina*, 20 *T. formosa*) were measured, and the entire egg mass of each individual was removed and wet-weighed. We estimated egg number from the regression on egg weight and regressed the resulting egg numbers on body dimensions.

To examine seasonal and locational variation in abundance, an analysis of covariance was used. Most species abundances are positively correlated with coral-head size, and the ANCOVA removes the confounding effects of area. All analyses were performed on log₁₀-transformed data. (To incorporate 0's, densities were increased by one before logarithms were taken.) Except for *Harpiliopsis depressa*, the log-log model provided the best linear fit.

Other population data were analysed as a multi-way contingency table. Each individual collected was classified by season (Jan, Apr, Jun, or Aug), location (reef flat or reef flank), and a dichotomous population variable (e.g. adult or juvenile). Significant interactions between population variables and season or location suggest that population structure varies temporally or spatially.

The ANCOVA's were computed using the regression technique (Huitema, 1980) on SPSS version 9.0, and the contingency tables were analysed using BMDP3F,

the Multi-way Contingency Tables program. All computations were performed on the Cyber 760, at the Florida State University Computing Center.

RESULTS

***Trapezia* spp. complex**

Egg number, recruitment, and body size

Egg diameters of the 3 species were similar (0.3 ± 0.5 mm). Individuals of *Trapezia ferruginea* carried from 6 to 7,606 eggs, *T. corallina* from 9 to 2,092 eggs, and *T. formosa* from 568 to 4,145 eggs. It is possible that the individuals carrying few eggs had just started to place them on the pleopods and that more would have been deposited later. In addition, females may have released larvae and not retained the egg capsules, so we may have underestimated egg number in some cases. There is a significant positive correlation between log egg number and log body size for *T. ferruginea* and *T. corallina* but not for *T. formosa* (Fig. 1).

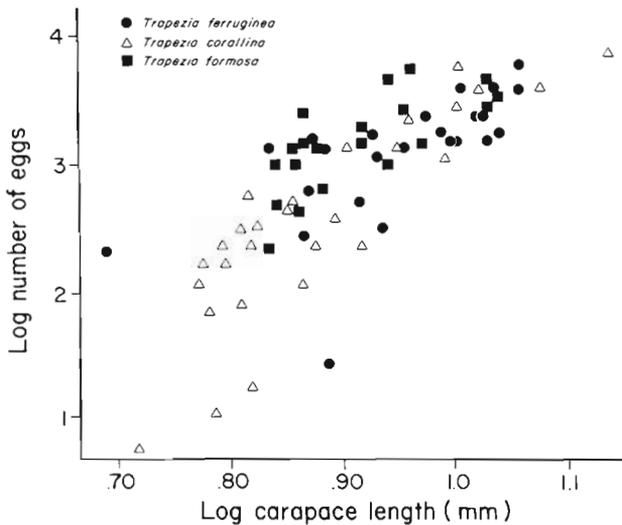


Fig. 1. Egg number as a function of carapace length for 3 species of *Trapezia*. All regression equations are on log-log scale. *Trapezia ferruginea*: $y = -3.47 + 6.26x$ ($r^2 = .69$; $p < .01$); *Trapezia corallina*: $y = -5.36 + 8.40x$ ($r^2 = .66$; $p < .01$); *Trapezia formosa*: $y = 1.87 + 1.29x$ ($r^2 = .09$; $p > .05$)

Thus, females that differ slightly in body size differ dramatically in egg number. For example, a 9 mm female of *T. ferruginea* would carry 399 eggs, whereas a 10 mm female would carry almost twice that number, 655.

The proportion of females carrying eggs varied significantly among species (Fig. 2 A). The fecundities of *Trapezia formosa* (90%) and *T. ferruginea* (81%) were constant throughout the year and were similar for reef flat and flank samples. For *T. corallina*, however, the

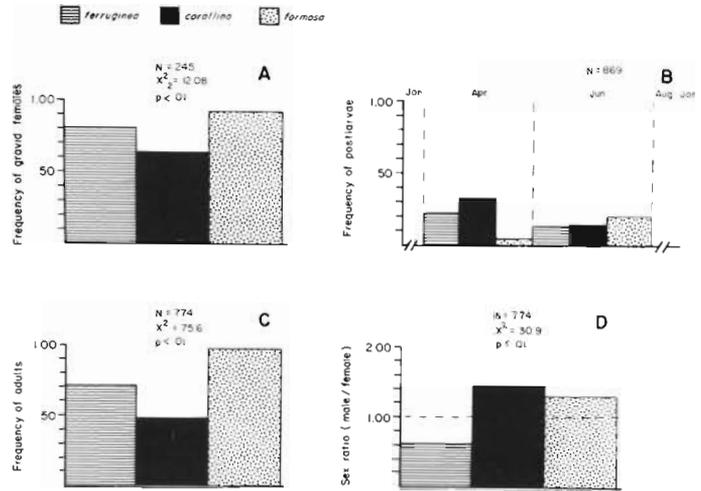


Fig. 2 (A). Frequency of occurrence of adult *Trapezia* females carrying eggs. (B) Frequency of occurrence of *Trapezia* postlarvae at 4 sampling dates. (C) Frequency of occurrence of adult *Trapezia*. (D) Total sex ratios (male/female) of *Trapezia*

occurrence of gravid females varied both seasonally and by reef location. Seasonally, fecundity was highest in January (96%), lowest in June (20%). Of the females collected on the reef flat, 45% were carrying eggs, compared to 80% for reef flank females.

For all 3 species of *Trapezia*, at least some females carried eggs at all sampling dates. Because eggs were carried throughout the year, one might expect continuous recruitment of postlarvae onto coral heads. But this was not the case. No postlarvae were collected during January or August. Recruitment of postlarvae varied among species, but was heaviest in April (except for *T. formosa*; Fig. 2 B). Flank and flat frequencies appear similar. Even within a season, postlarvae recruitment varied tremendously on a head-to-head basis.

The proportion of adults in the population also varies among species, from 48% for *Trapezia corallina* to 98% for *Trapezia formosa* (Fig. 2 C). These percentages do not vary significantly by season or reef location. The size-frequency distributions for each species over the 4 sampling periods are shown in Fig. 3 A-C. In all cases, the largest (mean sizes) crabs were collected during January and the smallest (except for female *T. ferruginea*) during August. Apparently, postlarvae of *T. corallina* that settle during April and June reach juvenile size by August and adult size by January. Our evidence is that the occurrence of juveniles increases

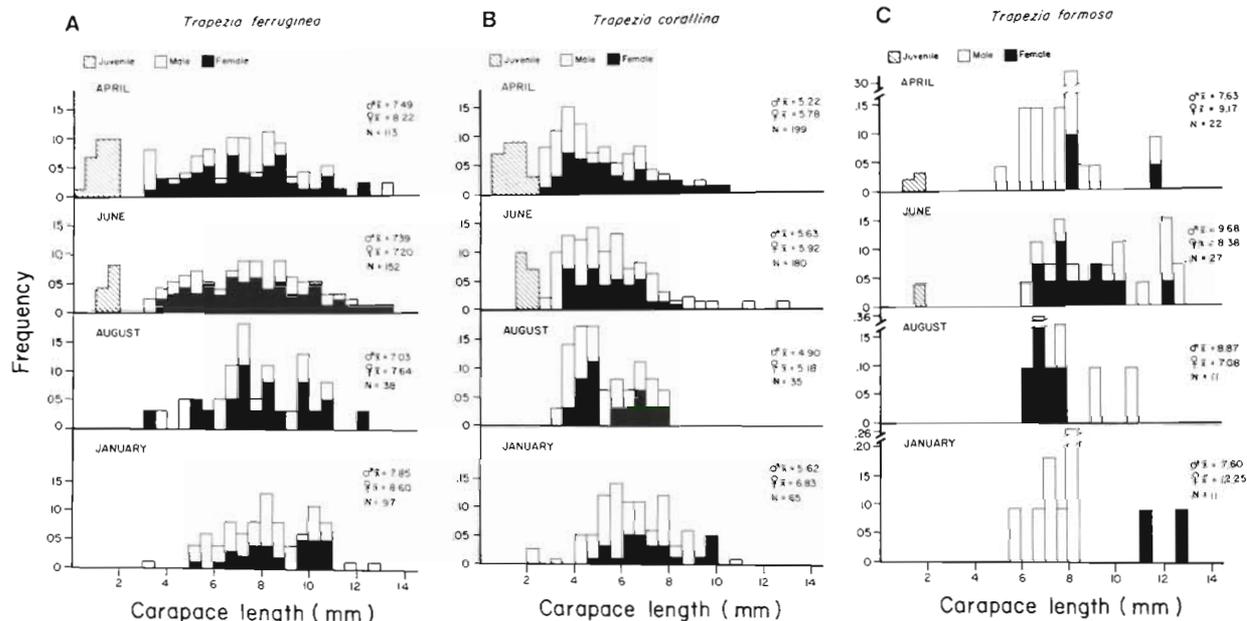


Fig. 3. Size-frequency distributions of *Trapezia* on 4 sampling dates in 1973. Average sizes are given by sex for each sample. Dark bars: females; clear bars: males; open bars: postlarvae. January sample is drawn last to illustrate seasonal patterns in body size

during August (50%), but decreases in January (36%), as individuals presumably grow to adult size. These seasonal changes in the percentage of juveniles are not statistically significant, but they are consistent with the hypothesis that *T. corallina* postlarvae that settle in April or June reach juvenile size in August and adult size in January. The mean sizes of *T. ferruginea* follow a similar pattern, but the percentage of juveniles is lowest in August (26%) and highest in January (38%). Only 1 juvenile of *T. formosa* was collected, so we cannot make any statements about the population structure of this species.

Density and distribution

Trapezia ferruginea and *T. corallina* were present on nearly every coral head, whereas *T. formosa* was present on only 55% of the coral heads. Frequency of occurrence is not affected by coral head size or season, but is affected by reef location. *Trapezia formosa* was present on 71% of the reef-flat heads, compared to only 37% of the reef-flank heads.

The abundance of *Trapezia formosa* is uncorrelated with coral head size (Table 1), but is significantly higher on the reef flat ($\bar{x} = 1.08$ individuals/head) than on the reef flank ($\bar{x} = 0.35$; ANCOVA $F_{1,55} = 7.29$, $p < 0.05$). However, this result is obtained because the frequency of occurrence is greater on the reef flat. If the analysis is restricted to those samples in which *T. for-*

Table 1. Regression models of $\log_{10}(\text{abundance} + 1)$ vs. $\log_{10}(\text{area})$ for 7 common coral associates

Species	N	Inter-cept	Slope	r ²	Significance of regression
<i>Trapezia ferruginea</i>	58	-.64	.41	.31	$p < .01$
<i>Trapezia corallina</i>	58	-.43	.37	.20	$p < .01$
<i>Trapezia formosa</i>	58	.01	.06	.00	$p = .49$
<i>Alpheus lottini</i>	119	-.34	.21	.10	$p < .01$
<i>Fennera chacei</i>	119	-.88	.44	.06	$p < .01$
<i>Harpiliopsis depressa</i>	119	-.34	.28	.07	$p < .01$
<i>Teleophrys cristulipes</i>	119	-1.52	.64	.21	$p < .01$

mosa is actually present, flank and flat densities are similar.

The abundance of *Trapezia ferruginea* is well correlated with coral head size (Table 1). As with *T. formosa*, the abundance of *T. ferruginea* is higher on the reef flat ($\bar{x} = 4.99$ indiv. head⁻¹) than on the reef flank ($\bar{x} = 3.52$; ANCOVA $F_{1,55} = 11.18$, $p < 0.01$). In this case, however, the result is not caused by differences in the frequency of occurrence at the two sites; *T. ferruginea* was absent from only one coral head in the entire collection. Seasonal differences in abundance are not significant. For *T. corallina*, abundance is also a function of coral-head size (Table 1), but in this case there were no significant effects of season or reef location on abundance.

Sex ratios

Sex ratio, both total and adult, does not vary by season or reef location, although differences among species are clear (Fig. 2 D). Of the *Trapezia ferruginea* collected 61% were females, compared to only 40% of *T. corallina* and 42% of *T. formosa*. The sex ratio for *T. formosa* does not differ significantly from unity, whereas the ratios for *T. ferruginea* and *T. corallina* are definitely skewed. Thus, the sex ratio of *T. ferruginea* is skewed toward females, that of *T. corallina* toward males, and that of *T. formosa* is unskewed (although this may be an artifact of small sample size). Night samples might reveal other patterns because of crustacean movements.

Notes on other *Pocillopora* associates

Alpheus lottini Guerin

This large (total length approx. 20 to 27 mm), conspicuous snapping shrimp is a common associate of pocilloporid corals throughout the Pacific. Adults associate as male-female pairs; usually, only a single pair occupies a coral head. The body sizes of coexisting males and females are positively correlated (Patton, 1974). Starved individuals will feed on coral mucus (Patton, 1974), although Coutiere (1899) found eggs in the stomach of one specimen. Stomach contents of Australian specimens were mostly debris and coral mucus (Patton, 1974). Like the *Trapezia* species, *Alpheus lottini* actively defends its coral host from attacks by corallivore *Acanthaster* (Glynn, 1976, 1980). The shrimp snaps aggressively at *Acanthaster* and will even pinch the seastar's ambulacral spines.

Alpheus lottini was present on 80% of the coral heads. Abundance is weakly correlated with coral head size (Table 1). Two coral heads contained 7 juvenile individuals, although most heads supported a single adult male-female pair. *A. lottini* was absent from only 5 coral heads, all of which were collected from the reef flank. These absences affect the estimates of average abundance per coral head. If all samples are used, reef flat heads have a slightly higher adjusted mean density (\bar{x} flat = 2.51 indiv. head⁻¹, \bar{x} flank = 1.87; ANCOVA $F_{1,116} = 10.56$, $p < 0.01$). If the empty heads are excluded, mean densities do not differ. Seasonal differences in density were not significant. There were no significant effects of coral-head size, location, or season on the adult sex ratio, adult-juvenile ratio, or gravid-non-gravid female ratio. The adult sex ratio was 1.0, 87% of the individuals collected were adults, and 91% of the females were carrying eggs. Eggs are small (diameter about 0.55 mm) and numerous, and

egg number is highly correlated with body size (Fig. 4).

Fennera chacei Holthuis

This small (total length approx. 4 to 6 mm) pontiniid shrimp has been collected only from *Pocillopora* (Abele, 1976a), although one report is from *Porites* (Holthuis, 1951). *Fennera chacei* ranges from the Eastern Pacific through the Indo-West Pacific, although it is rare in Australia (Patton, 1966). This shrimp is collected at the base of coral heads, often in large numbers (Abele, 1976a). Feeding habits are unknown.

Fennera chacei was present on 72% of the heads. Density (indiv. coral head⁻¹) can be quite high – as many as 49 individuals (all adults) were collected from a single head. However, coral head size explains only 6% of the variation in abundance (Table 1). Seasonal differences in abundance are highly significant (ANCOVA $F_{3,114} = 5.31$, $p < 0.01$). Density is highest in the wet season (Jun $\bar{x} = 5.3$ indiv. head⁻¹; Aug $\bar{x} = 7.5$) and lowest in the dry season (Jan $\bar{x} = 1.7$; April $\bar{x} = 2.5$). The difference is probably significant because most empty heads were collected in the dry season. If the analysis is repeated using only samples with *Fennera chacei* present, seasonal differences in density are not significant. Of the individuals collected 99% were adults. Only 6 juveniles were obtained (from 5 coral heads), all from the April samples. Of the adult females 93% were carrying eggs. The eggs are relatively large (0.4 to 0.5 mm) compared to body size, and egg number is highly correlated with body size (Fig. 4). The adult sex ratio is .91, skewed slightly toward females.

Harpiliopsis depressa (Stimpson)

This medium-sized (total length 16 to 25 mm) species of pontiniid shrimp is widespread throughout the Indo-West Pacific, extending to the Galapagos and Eastern Pacific (Bruce, 1981). *Harpiliopsis depressa* apparently has a long larval life (Bruce, 1970), and postponed settlement from the pelagic phase may be responsible for its widespread distribution (Bruce, 1970, 1976). Patton (1966) suggests that Australian specimens of *H. depressa* prefer *Stylophora* and *Seriatopora* corals, whereas the congeneric *H. beaupressi* prefers *Pocillopora*. In the Eastern Pacific, however, *H. depressa* is commonly collected from *Pocillopora* (Abele, 1976a). Feeding habits of *H. depressa* are undescribed. Unlike *H. beaupressi*, *H. depressa* has well-developed exopodites on the maxillipeds and may feed on plankton (Bruce, 1976). *Harpiliopsis depressa* is very similar to the congeneric *H. spinigera*,

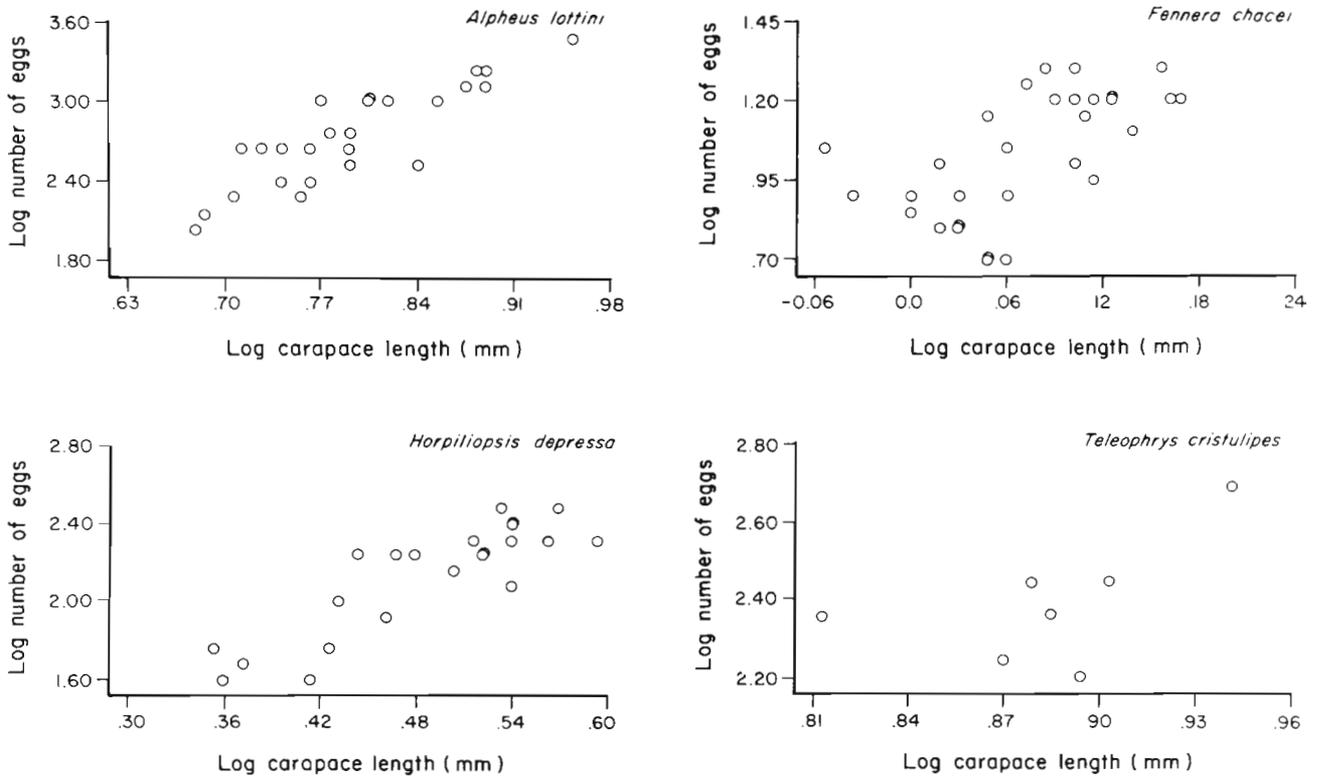


Fig. 4. Egg number as a function of carapace length for 4 decapod species associated with *Pocillopora*. *Alpheus lottini*: $y = -0.09 + 4.59x$ ($r^2 = .73$; $p < .01$); *Fennera chacei*: $y = .88 + 2.10x$ ($r^2 = .37$; $p < .01$); *Harpiliopsis depressa*: $y = .41 + 3.53x$ ($r^2 = .77$; $p < .01$); *Teleophrys cristulipes*: $y = .45 + 2.20x$ ($r^2 = .29$; $p > .05$)

and the 2 species can be reliably separated only on the basis of color (Bruce, 1976). In Australia, all 3 species of *Harpiliopsis* may be collected from the same coral head (Bruce, 1976). *Harpiliopsis beaupressi* does not occur in the Eastern Pacific, and *H. spinigera* is uncommon.

Harpiliopsis depressa was present on 92% of the coral heads. Frequency of occurrence is unaffected by coral head size, season, or reef location. Coral head size explains 7% of the variation in abundance (Table 1). The analysis of covariance revealed significant heterogeneity of regression slopes by season ($F_{3,101} = 3.04$, $p < 0.05$). Slopes are equivalent if empty coral heads are excluded from the analysis ($F_{3,101} = 2.56$, $p > 0.05$). The linear fit of the log-log regression model is not especially good, unless the empty heads are excluded. Thus, the poor fit of the model, rather than true seasonal variation, probably causes the heterogeneity of the regression slopes. Reef-flat and reef-flank densities do not differ significantly.

Of the individuals collected 86% were adults. This proportion was constant over all seasons and locations. The adult sex ratio was 0.40, skewed toward females. Sex ratios differ significantly by season and location. Seasonally, the sex ratio is 0.29 in April, 0.76 in June, and 0.39 in August. The sex ratio for reef-flank samples

is 0.31, compared to 0.54 for reef-flat samples. Overall, 20% of the adult females were carrying eggs.

Teleophrys cristulipes Stimpson

This spider crab (CL 5.5 to 6.9 mm) is usually collected in *Pocillopora*, but is also common in the rocky intertidal (Garth, 1958). Garth reports that specimens not found on *Pocillopora* are large, smooth-legged, and with a lumpy carapace. Individuals from coral heads are smaller, with cristate legs, and with spinous lateral margins. *Teleophrys cristulipes* is restricted to the Eastern Pacific (Rathbun, 1925) and ranges from the Gulf of California to Ecuador (Garth, 1958). Within this range, clinal variation in morphology is evident: in northern individuals the anterior branchial region of the carapace is enlarged, the rostrum is deeply cleft, and the propodus lacks ornamentation. In southern individuals the anterior branchial region is reduced, the rostrum has 2 shallow lobes, and 1 lateral tubercle or spine may be present on the propodus (Garth, 1939). *T. cristulipes* is very abundant in the Galapagos, and Galapagos specimens are larger than other Eastern Pacific specimens (Garth, 1939). In the Perlas Islands, Panama, abundance of *T. cristulipes* is negatively cor-

related with coral head size (Abele and Patton, 1976). Feeding habits are undescribed. In rocky intertidal pools, individuals have been observed (by SLG) ingesting the green alga *Caulerpa*.

Teleophrys cristulipes was present on 82% of the coral heads. Coral-head size accounts for 21% of the variation in abundance (Table 1). Seasonal differences in density are highly significant (ANCOVA $F_{3,114} = 29.19$, $p < 0.01$). Adjusted mean densities are similar in January ($\bar{x} = 3.00$ indiv. head⁻¹), April ($\bar{x} = 3.13$), and June ($\bar{x} = 3.89$), but are depressed in August ($\bar{x} = 0.33$). This difference occurs because 7 out of the 10 August samples had no individuals. If empty heads are excluded, seasonal differences are not significant (ANCOVA $F_{3,93} = 1.23$, $p > 0.05$).

In a presence-absence analysis, the presence by season interaction is highly significant ($\chi^2 = 19.77$, $p = 0.0002$). In August, *Teleophrys cristulipes* is present on only 20% of the heads, compared to 57% in January, 83% in April, and 100% in June. Coral head size also has a significant effect on occurrence. Of the small heads 27% were empty, compared to only 7% of the larger heads.

All of the population parameters appear constant by season and reef location. Of the individuals collected 21% were adults. The adult sex ratio is 1.25, skewed toward males. Of the adult females 50% were carrying eggs.

DISCUSSION

Except for *Trapezia formosa* and *Teleophrys cristulipes*, regressions of egg number on carapace length are significant for all species. This result is not surprising considering the morphological changes associated with egg production. Enlargement of the carapace in all 3 directions (= volumetric increase) allows an individual to increase egg production; egg number is related to female body size with a very high exponent. We are puzzled by the lack of significance for *T. formosa*; this result is atypical for morphometric studies of decapods. Perhaps it is related to the small size range of gravid females in our samples.

From the male's point of view, reproductive output may be increased by mating with a larger female or with several females. However, extreme differences in the body size of paired males and females are not expected because of behavioral interactions. Accordingly, paired male and female *Trapezia* are of similar body size, although females are slightly larger (Preston, 1973; Castro, 1978).

For the sponge crab *Cryptodromia*, McClay (1982) suggests that small males may be less susceptible to predation while searching for mates. However, his arguments apply to cryptic species, such as sponge or

spider crabs. *Trapezia* are brightly colored and conspicuous to predators; any individual that leaves the coral head by day is susceptible to predation, regardless of its size. Castro (1978) found that migration of *T. ferruginea* is suppressed in the presence of fish predators. But more males tended to migrate than females in his experiments (females 40%, males 87.6%, $p = .035$; data from Table 4 in Castro, 1978). Interestingly, the sex ratio for *T. ferruginea* in this study is significantly skewed toward females. If male *T. ferruginea* tend to migrate more often, they may suffer increased mortality, skewing the sex ratio.

The number of putative heterosexual pairs in this study is highly variable, from 1 to 4 pairs per coral head for both *Trapezia ferruginea* and *T. corallina* and single pairs for *T. formosa*. While coral head size is correlated with the number of pairs, it accounts for less than 30% of the variation in numbers (Table 1). The occurrence of multiple pairs is in contrast to results from the adjacent Bay of Panama (Abele and Patton, 1976; Castro, 1978), Australia (Patton, 1974), Hawaii (Preston, 1973), and the Maldives (Garth, 1964), where 1, or at most 2, pairs of *Trapezia* are found per coral head.

If, as Castro's (1978) data suggest, individuals migrate often, then perhaps the occurrence of a male and female together does not represent a monogamous pair. It is difficult to conceive of precise pairing in light of the heterogeneous assemblages of male and females found on coral heads at Uva Island.

Patterns of body size and population structure suggest that recruitment of *Trapezia* onto coral heads occurs in April or June; juvenile crabs grow to sexual maturity by January. Like other tropical brachyurans, female *Trapezia* carry eggs throughout the year. Yet, the distribution of postlarvae on coral heads is strikingly discontinuous (Fig. 2 C). We are puzzled by the complete absence of postlarvae in January and August. An extreme low tide killed many *Pocillopora* heads on the reef flat just prior to the January sampling (Glynn, 1976); postlarvae may also have been killed at this time. However, postlarvae were also missing from the deeper reef-flank corals, as well as from the August collections. Although adult *Trapezia* associate exclusively with live coral heads, nothing is known of the ecology of the dispersive larval and postlarval stages. Perhaps postlarvae recruit seasonally from other habitats; samples from nearby coral rubble might be revealing.

The abundance of *Trapezia ferruginea* and *T. corallina* is significantly correlated with coral-head size. Whereas seasonal effects on abundance are negligible, reef location appears quite important. The abundance of *T. ferruginea* and the frequency of occurrence of *T. formosa* are both higher on the reef flat. Total abun-

Table 2. Significant correlations among population and environmental variables. + indicates a significant correlation between 2 variables ($p < .05$). 'Conditional density' statistics were calculated only for samples in which individuals were present; all other statistics were calculated for all samples

Species	Populations measure	Area	Season	Location
<i>Trapezia ferruginea</i>	Density	+		+
	Conditional density	+		+
	Presence/absence			
	Adult/juvenile			
	Adult male/adult female			
	Male/female			
	Gravid/non-gravid female		+	+
<i>Trapezia corallina</i>	Density	+		
	Conditional density	+		
	Gravid/non-gravid female		+	+
<i>Trapezia formosa</i>	Density			+
	Presence/absence			+
<i>Alpheus lottini</i>	Density	+		
	Conditional density	+		+
<i>Fennera chacei</i>	Density	+	+	
	Conditional density	+		
	Adult/juvenile		+	
<i>Harpiliopsis depressa</i>	Density	+	+	
	Conditional density	+		
	Male/female		+	+
	Gravid/non-gravid female		+	+
<i>Teleophrys cristulipes</i>	Density	+	+	
	Conditional density	+		
	Presence/absence	+	+	

dances and species richness of all decapods are also higher on the reef flat (Edwards and Emberton, 1980; Gotelli and Abele, 1983). *Pocillopora* cover is more continuous and predatory fish are less common on the shallow reef flat (Glynn et al., 1972). Both factors could contribute to the greater abundance of decapods in this location.

In spite of their apparent morphological similarity, coexisting species of *Trapezia* are quite distinct in their population structure. This statement applies not only to *Trapezia* but also to other associates of *Pocillopora*. Table 2 summarizes the significant patterns for each species.

One notable result is the relative importance of coral head size to population structure. At the 'community' level, the area effect is extremely important. It dominates patterns of species richness and abundance (Abele, 1976b; Abele and Patton, 1976) and even affects measures of interspecific association (Gotelli and Abele, 1983). At the 'population' level, its effect is much weaker. Area correlates significantly with abundance for 6 of the 7 common species, but the correlation coefficients are all rather small (Table 1). Coral head size does influence the frequency of occurrence of *Teleophrys cristulipes*, but is not significantly

associated with any other population measures. Frequency of occurrence has an important effect on the measurement of abundance. In 6 cases (*Trapezia ferruginea*, *Trapezia formosa*, *Alpheus lottini*, *Fennera chacei*, *Harpiliopsis depressa*, *Teleophrys cristulipes*) we detected, with an analysis of covariance, seasonal or locational variation in the abundance of a species. But only for *T. ferruginea* did the average number of individuals per coral head actually differ. In the other cases, frequency of occurrence also varied by location or season. When the species actually occurred, abundances were similar; in other words, the conditional density of the species did not change.

Both season and reef location emerge as important factors influencing population structure. As we noted above, *Pocillopora* cover and predation intensity vary between reef flat and reef flank. Seasonal differences in water quality are also evident at Uva Island. Although seasonal upwelling does not occur in the Gulf of Chiriqui, this region experiences distinct wet and dry seasons (Dana, 1975; Glynn, 1977). During the wet season (May through Nov), sea surface temperatures and salinity are lower. In addition, freshwater runoff increases turbidity and reduces light penetration. Pesticide input may be high from this runoff

(Glynn, 1983b). Dana (1975) estimates that light penetration at 10 m may be 3 times greater during the dry season.

While the crustaceans depend on *Pocillopora* heads for a habitat and coral mucus for a food source (Patton, 1974), their presence is also essential for the health of the host coral. If symbionts are removed, *Pocillopora* mucus production drops, the polypal layer disintegrates, and massive tissue exfoliation occurs (Glynn, 1983a). Thus, interactions with the coral host are likely to influence crustacean population structure.

The patterns described in this study may no longer hold. Early in 1983 (Feb–Mar), extensive bleaching and massive death of *Pocillopora* and other corals occurred in the Gulf of Chiriqui. Bleached coral heads contained 9 or 10 crustacean symbionts, compared to 22 on healthy corals. Dead corals contained on average less than a single individual per colony (Glynn, 1983b). Although the cause of this bleaching and death is unknown, abnormally high water temperatures associated with a strong El Niño current (Philander, 1983; Glynn, 1984) have been implicated. Coral death and its effects on crustacean populations in the Gulf of Chiriqui are currently being monitored (Glynn and Gilchrist, in prep.).

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