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## Evidence of habitat structure-generated bottleneck in the recruitment process of the SW Atlantic crab *Cyrtograpsus angulatus*

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**Abstract** Shelters generated by the introduced reef-building polychaete *Ficopomatus enigmaticus* (Serpulidae) significantly enhance settlement of the crab *Cyrtograpsus angulatus* (Grapsidae) in a SW Atlantic coastal lagoon (Mar Chiquita, 37°32'S; 57°26'W; Argentina). However, their ultimate role in recruitment does not appear to be very important, suggesting a habitat-generated bottleneck that occurs between settlement and recruitment. Laboratory and field experiments show that newly settled crabs actively select refuges similar in size. Inside the reefs, decreases in crab density of each newly settled cohort mirror the ratio of decreases in the number of reef refuges of similar sizes, suggesting that habitat fractal structure determines the mortality rate after settlement. Field experiments using artificial shelters show that as crabs increase in size, they move outside reefs. Field tethering of juvenile- and adult-sized crabs without access to refuges showed that juvenile crabs suffer a much higher risk of mortality than adults. Our results show that the availability of small refuges provided by polychaete reefs enhances crab settlement, but, then, due to a decrease in the number of refuges as size increases, produces a demographic bottleneck during recruitment. Thus, independent of settlement intensity, enhanced survivorship in the smallest size classes due to refuge is not transmitted to larger size

classes. This is likely one reason why stock-recruitment relationships may not hold in species that use shelters during both recently settled and juvenile life stages. These results provide a good example of why habitat enhancement programs need to incorporate a comprehensive evaluation of the species' ontogenic ecology to avoid class size-specific bottlenecks.

### Introduction

Settlement and recruitment are two processes that affect population dynamics (Roughgarden et al. 1988). Active habitat selection by larvae and juveniles is a common strategy to increase settlement and recruitment success by decreasing mortality (Caddy 1986; Wahle and Steneck 1991; Iribarne et al. 1994; Eggleston and Armstrong 1995; Eggleston et al. 1997). In many cases, this selection is for highly structured habitats given that these habitats decrease predator foraging efficiency, favor survival, and eventually modify species abundance and distribution (Roberts and Ormond 1987; Hacker and Steneck 1990; Gee and Warwick 1994). However, although refuge availability ensures successful settlement, it is not necessarily directly related to successful recruitment. This lack of relationship is interesting given that it affects how we define the concept of recruitment. Understanding recruitment as the addition of individuals to local populations following settlement from pelagic larva (Caley et al. 1996) is not useful in these cases. Indeed, for most benthic invertebrates, early juvenile mortality is so high (i.e. Gosselin and Qian 1997) that survival after early mortality is a more biologically meaningful definition of recruitment (Hunt and Scheibling 1997). The key difference between early and late survival after settlement is often the availability of shelters while these young individuals are growing.

However, shelter-dwellers need refuges of approximately their body sizes in order to be maximally pro-

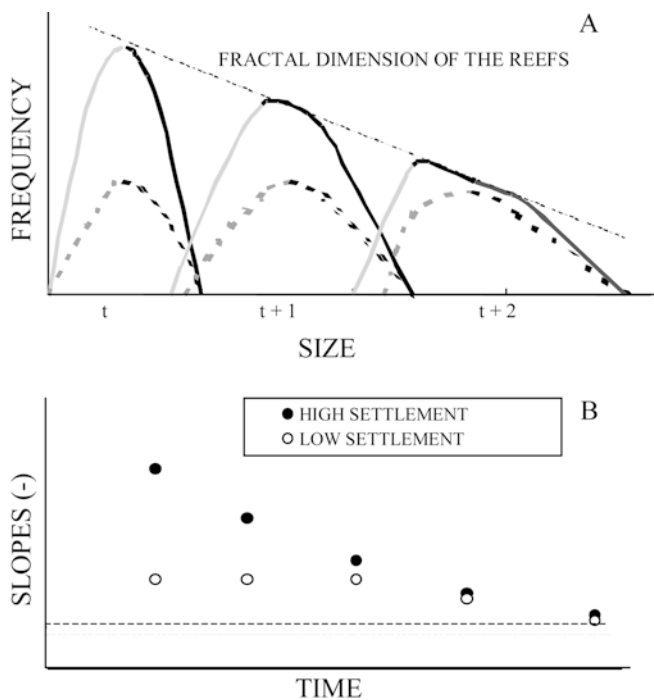
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tected against predators (Eggleston et al. 1990; Hacker and Steneck 1990). Thus, mortality could be a function of refuge availability, possibly leading to a population bottleneck during recruitment processes (Caddy 1986; Wahle and Steneck 1991). For example, during a massive settlement event, habitats become saturated, and organisms displaced from their refuges suffer high predation mortality (“musical chairs” hypothesis of recruitment; Caddy 1986). For this reason, recruitment success is not only modified by refuge availability, but also by the size structure of those refuges. Most often shelter-dwelling organisms will face a decline, at a variable rate, in the numbers of suitable shelters as they grow (Fig. 1) (Cobb and Caddy 1989). This change generates a set of self-similar shelters as size increases, which is essentially a fractal structure (see Mandelbrot 1977). The characteristics of these structures (i.e. the rate at which the availability of self-similar shelters change with size) have obvious relevance for species that rely on shelters for survival. Knowing the characteristics of a given habitat may help to predict potential “bottle-necks” during the recruitment process that could affect the adult population (Cobb and Caddy 1989). More-



**Fig. 1A, B** *Cyrtograpsus angulatus*. Hypothetical changes produced by the availability of refuges to crabs during the recruitment process. **A** Two different magnitudes of settlement: high settlement and low settlement throughout time ( $t$ ). With high settlement (cohort with solid line), the habitat is saturated and the slopes of each cohort will follow the slope of the decrease in refuge availability (panel A). If settlement is low (cohort with dashed line), there will be no differences in density during the early stages. However, once refuge availability becomes a limiting factor, both situations will match. The bold parts of the cohort line was used to calculate the slopes of each cohort throughout time. **B** The negative of those slopes were plotted against time and compared to the fractal dimension of the habitat (dashed line)

over, such knowledge could help in the implementation of habitat mitigation programs. Structurally complex artificial habitats have been used to enhance stocks of commercial fishes and shellfishes (see Dumbauld et al. 1993), but the importance of changes in habitat requirements with size and age have not received much attention. However, without knowing these factors, the result could be just the displacement of the “bottleneck” to larger sizes (Beck 1995).

The relationship between the introduced reef-building polychaete *Ficopomatus enigmaticus* (Polychaeta: Serpulidae) and the grapsid crab *Cyrtograpsus angulatus* in a SW Atlantic coastal lagoon (Mar Chiquita, 37°32'S; 57°26'W; Argentina) provided a good opportunity for studying habitat requirements as crabs increase in size. Individual polychaetes live in calcareous tubes, forming large (up to 7 m diameter, 0.5 m high), reef-like, circular structures (Obenat and Pezzani 1994; Schwindt et al. 2001), and spaces between these tubes provide refuge for numerous organisms, including crabs (Schwindt and Iribarne 2000). Megalopae of *C. angulatus* use these reefs as settlement sites, where they stay during early juvenile stages (Spivak et al. 1994). This crab species lives in intertidal areas from Puerto Deseado (48°S, Argentina) to Rio de Janeiro (27°S, Brazil; Boschi 1964). In estuaries, juveniles take shelter under rocks or other types of structures, but rocky substrates do not offer hiding places to larger crabs (Spivak and Politis 1989). Adult crabs remain superficially buried in muddy habitats, where they obtain some protection (Spivak and Politis 1989; Spivak 1997; Schwindt and Iribarne 2000). During settlement, megalopae actively selected reefs (Luppi et al. 2002), and there was no survival without refuge (Botto and Iribarne 1999; Luppi et al. 2002). Densities of juvenile crabs inhabiting inner reefs reached 12,667 individuals  $m^{-3}$  (Luppi and Bas 2002). Nevertheless, densities of small adults reached 167 crabs  $m^{-2}$  under the reefs, and in nearby open areas densities of larger crabs were  $<0.5$  crabs  $m^{-2}$  (Schwindt and Iribarne 2000). Therefore, although reefs significantly enhance settlement of *C. angulatus* (Spivak et al. 1994; Luppi et al. 2002), their ultimate role in recruitment does not appear to be very important. Thus, this system is appropriate for exploring the relationship between habitat structure and mortality of early stages of species that need refuges, such as *C. angulatus*.

Taking into account the information described above, the particular objectives here were to: (1) evaluate if crabs select refuges according to their size, (2) evaluate the habitat structure provided by the polychaete reef, (3) evaluate the size-frequency distribution of *C. angulatus* inhabiting the reefs, and, with these results, (4) analyze how habitat structure modifies the recruitment process.

## Materials and methods

This study was carried out in Mar Chiquita coastal lagoon during the summers of 2000 and 2001 (always from December to March).

The lagoon (46 km<sup>2</sup> area and a maximal depth of 1.2 m) receives sediment and water from creeks and artificial channels and seawater with semidiurnal tides. *Ficopomatus enigmaticus* reefs cover ~86% of the lagoon (Schwindt et al. 2001). Near the mouth of the lagoon, reefs are present in creeks, using the structures of bridges and consolidated Pleistocene continental sediments on the creek bottoms as settlement sites (Obenat and Pezzani 1994; Spivak et al. 1994).

To evaluate whether *Cyrtograpsus angulatus* exhibits refuge selection, and, if so, to determine the scaling relationship between refuge and crab sizes, a set of plastic pipes of different diameter sizes (2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 14, 16 mm; all 4.5 cm height) was used. Each set of pipes consisted of one pipe of each size attached to each other, to avoid extra-refuges between pipes, and was attached to a plastic base. Individuals of *C. angulatus* were collected from the reefs of *F. enigmaticus* and were placed alone in plastic containers (5 l, 22 cm diameter and 15 cm height,  $n=57$ ). Each vessel contained mud sieved through a 0.5-mm-mesh to eliminate hard particles, and water salinity was around 23 PSU. Then, each pipe set was placed at the center of the container, and the number of crabs that selected pipes or mud was registered after 12 h. The null hypothesis of no difference between both events was analyzed with a  $\chi^2$  test (Zar 1999).

If crabs selected the artificial refuges, measures were taken to determine the relationship between the sizes of the refuge and crab that inhabited it. Thus, measures of carapace width (CW), carapace length (CL) and pipe diameter (PD) that were selected by each crab were recorded at the end of the experiment. The null hypothesis of no relationship between variables (CW vs. PD and CL vs. PD) was tested with a correlation analysis (Zar 1999). There were no differences in the results using CW or CL, so CW was used in further analyses as the measure of crab size.

The same artificial shelters (20 sets) were placed in an area with *F. enigmaticus* reefs, to analyze if refuge selection occurred in the field. Crabs found inside the pipes were collected daily, and their CW and the PD of the pipes they were using were measured. In both cases, the null hypothesis of no relationship between crab size and pipe diameter was tested with a correlation analysis using a particular procedure. In this case selection of refuge cannot be completely random given that each individual can select only pipe diameters equal to, or larger than, their size. Thus, random selection with this constraint will never produce a correlation coefficient of 0. To avoid this problem a computer simulation procedure was used to recalculate  $r$  under random selection, but with this constraint. This simulation randomly generated pairs (CW with PD) using data from the experiment with the restriction that  $CW \geq PD$ . Each simulation generated the same number of pairs considered in the experiments (40 pairs for laboratory and 159 for field conditions). The procedure was repeated 100 times, and a correlation analysis was conducted for each simulation. Then, the correlation coefficient ( $r$ ) of the experiment was compared to the frequency distribution of  $r$  obtained with the simulation procedure (Iribarne et al 1996). Using this distribution, the mean of this event was calculated, and the null hypothesis of no differences between correlation coefficients was analyzed with a  $t$ -test after a Fisher transformation ( $Z$ -values) of the data obtained with the simulation (Zar 1999).

If individuals show a scaling relationship between body size and refuge diameter, habitat requirement will change with individual size and age. Thus, an analysis of refuge availability and the size spectrum of refuges is necessary to compare these factors with the size and number of individuals inhabiting reefs. This allows us to analyze if refuge availability is a limiting factor, and how this affects crab size distribution. To analyze refuge availability, six samples of *F. enigmaticus* reefs were embedded in paraffin and cut parallel to the vertical axis of the reef. Refuge availability was analyzed as a function of the distances between tubes. These distances were measured across transects parallel to the base. With these data, the fractal dimension ( $D$ ) was calculated, determined as the negative of the slope from the linear regression of the logarithm of the size spectrum of refuges ( $N$ ) against the logarithm of their frequency (Morse et al. 1985; Snover and Commito 1998).  $D$  can be viewed as the rate at which refuges are lost in relation to size.

To analyze how refuge availability affected the number and size of crabs inside reefs, size-frequency distributions of individual cohorts were followed through time. With this purpose, ten samples of reefs were taken weekly (cores of 10.5 cm in diameter, 12 cm in depth) during the settlement and growing seasons (from December to March in 2001 and 2002) of *C. angulatus*. In each sample, CW of all individuals was measured. Given that our interest was focused on determining how refuge loss affects crabs of different sizes within a cohort, the slope obtained from the mode to the right-hand tail of the cohort (following Williamson and Lawton 1991) was calculated. These slopes were compared with the decrease in refuge availability (fractal dimension of reefs) throughout time. In order to calculate the decrease in density, a linear regression between crab density in each cohort and average size of the cohort was performed. The null hypothesis of no difference with a slope equal to zero was evaluated with a  $t$ -test (Zar 1999).

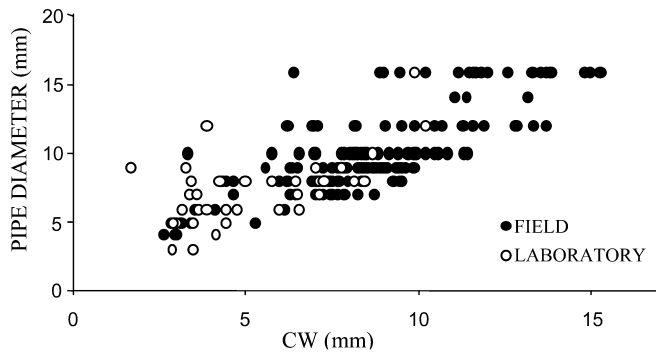
Changes in the density inside reefs as crab size increased may have been due to the combined effect of habitat limitation and migration. To analyze if migration occurred, pipe sets similar to the one described before were placed among reefs. This allowed us to infer whether migration occurred and at which sizes the crabs left the reefs. This information may serve as an indication of which shelter sizes are limiting (see Beck 1995). Pipe sets were deployed for 10 days, collecting crabs inside the pipes every day, at three different times during the growing season: in January, February and March. These data were compared with the size-frequency distribution inside the reefs. The null hypothesis of no differences between distributions was evaluated with a Kolmogorov-Smirnov test (Conover 1980).

The fate of crabs that left the reefs was the next question. To answer this, tethering experiments were performed to compare the relative risk of mortality in different habitats. We are aware of the limitations of this technique, but, in this case, it was used only to explore the spatial patterns of mortality due to predation (see Minello 1993; Beck 1995; Kneib and Scheele 2000). A total of 39 crabs were tethered with a 30-cm-long nylon monofilament line (0.5 mm width) tied around the cephalothorax, between the first and second leg, and attached to the substratum with stakes. Crabs were distributed in three different habitats (reefs, sediment and sediment with large blocks as refuges) and were of two size classes [juveniles between 9 and 12 mm CW (corresponding to sizes that no longer fit inside reefs) and adults between 29 and 33 mm CW]. Crabs were tethered between one low tide and the next (6 h), and the presence of autotomies was used to estimate the risk of predation (Spivak and Politis 1989). The null hypothesis of no difference in the proportion of crabs without autotomies between habitats and between size classes was analyzed with a Tukey multiple comparison test, among proportions after an angular transformation to fit the assumptions (Zar 1999).

## Results

Under laboratory conditions, 70% of the crabs ( $\chi^2=9.28$ ,  $P<0.005$ ) selected an artificial refuge, showing a correlation between crab (*Cyrtograpsus angulatus*) size and refuge diameter ( $r^2=0.39$ ,  $SE=0.01$ ,  $n=40$ ,  $P<0.001$ ; Fig. 2). The computer simulation of random pairs, using data from the experiment showed a correlation factor ( $r^2=0.05$ ,  $SE=0.02$ ,  $n=40$ ) significantly lower than the value obtained with the experiment ( $Z=2.14$ ,  $P<0.05$ ).

In the case of artificial refuges placed at the creek, the correlation between crab size and shelter size ( $r^2=0.54$ ,  $SE=0.002$ ,  $n=159$ ,  $P<0.001$ ) and the computer simulation average using these data ( $r^2=0.12$ ,  $SE=0.004$ ,  $n=159$ ,  $P<0.001$ ) were significant. However, the value



**Fig. 2** *Cyrtograpsus angulatus*. Correlations between carapace width (*CW*) of the crabs and the pipe diameter selected under laboratory and field conditions

obtained in the field (Fig. 2) was higher than the result of the computer simulation ( $Z = 3.33$ ,  $P < 0.001$ ).

Analyzing the shelter structure of reefs, each fractal dimension was obtained from a simple linear regression between the logarithm of the refuge sizes and the logarithm of their frequencies. The mean of these fractal dimensions ( $D = 1.68$ ,  $SD = 0.21$ ) was compared with the slopes of each cohort through time (Fig. 3). There was a significant decrease in crab density inside reefs when followed across time ( $b = -1,523$ ,  $SD = 253$ ,  $df = 21$ ,  $P < 0.0001$ ; Fig. 4).

The comparisons of size-frequency distributions between habitats showed differences at the three times sampled (A:  $D_{\max} = -0.62$ ,  $n_1 = 345$ ,  $n_2 = 99$ ; B:  $D_{\max} = -0.82$ ,  $n_1 = 282$ ,  $n_2 = 98$ ; C:  $D_{\max} = -0.64$ ,  $n_1 = 176$ ,  $n_2 = 98$ ). Only a small proportion of crabs was found inside the pipes placed between reefs, and their sizes (*CW*) were always larger than those of the crabs present inside the reefs (Fig. 5). Tethering experiments showed that adult crabs (29–33 mm *CW*) were not affected by habitat (reefs: 80% of crabs without autotomies; sediment with blocks: 66%; sediment: 83%; Tukey test

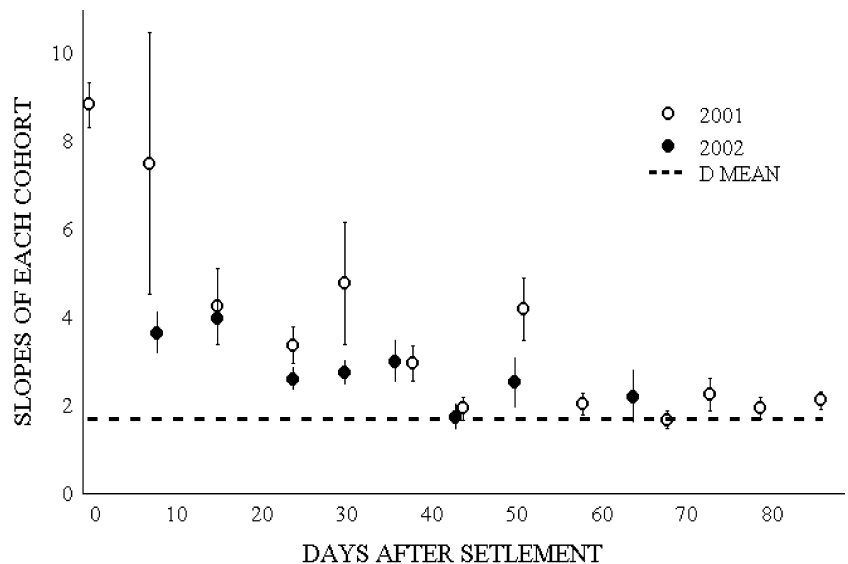
for proportions,  $P > 0.05$ ). Nevertheless, in the case of juveniles that are leaving reefs (9–12 mm *CW*), the proportion of crabs without autotomies tethered in sediment without refuges (16%) was lower compared with the other types of habitats with refuges (sediment with boulders: 80% of crabs without autotomies; polychaete reefs: 83%;  $P < 0.05$ ).

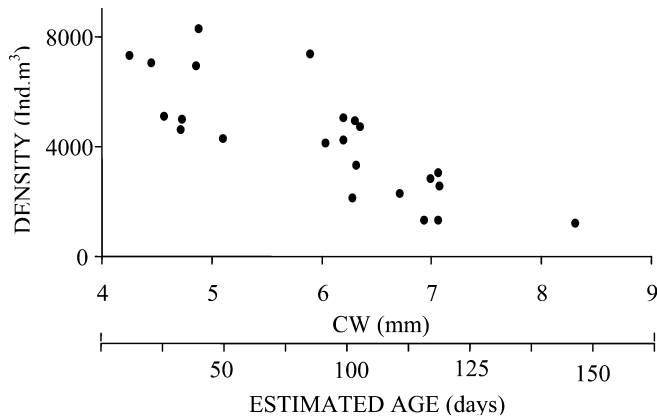
## Discussion

Our results show that the availability of small refuges provided by polychaete (*Ficopomatus enigmaticus*) reefs enhance crab (*Cyrtograpsus angulatus*) settlement, but, then, due to a decrease in the number of refuges as size increases, such reefs produce a crab-demographic bottleneck during the recruitment process.

It is known that the fractal dimension (i.e. the rate at which refuges are lost in relation to size) of vegetation influences the size distribution of plant-inhabiting arthropods (Morse et al. 1985). For example, plants with a higher fractal dimension have more space available for smaller animals than for larger ones (Shorrocks et al. 1991; Gunnarson 1992; Jeffries 1993), which is reflected in the size structure of the species that inhabit them. In this case, the fractal properties of the habitat used by crabs during early juvenile stages not only determine the size distribution of crabs inside reefs, but, most interestingly, determine their mortality rate and eventually regulate population size. The comparison between the slopes of each cohort and the fractal dimension of the reefs shows that as individuals grow they have to adjust to the number of available refuges, as we hypothesized. Depending on the mortality outside reefs, this could lead, independent of the settlement magnitude, to a similar number of individuals reaching the adult stage. Thus, if settlement is high, the habitat is saturated at smaller sizes, when

**Fig. 3** *Cyrtograpsus angulatus*. Magnitude of the slopes of each cohort compared to the fractal dimension of the reefs (dashed line) throughout time. Each point is the mean of the negative of the slope ( $\pm$  standard error)



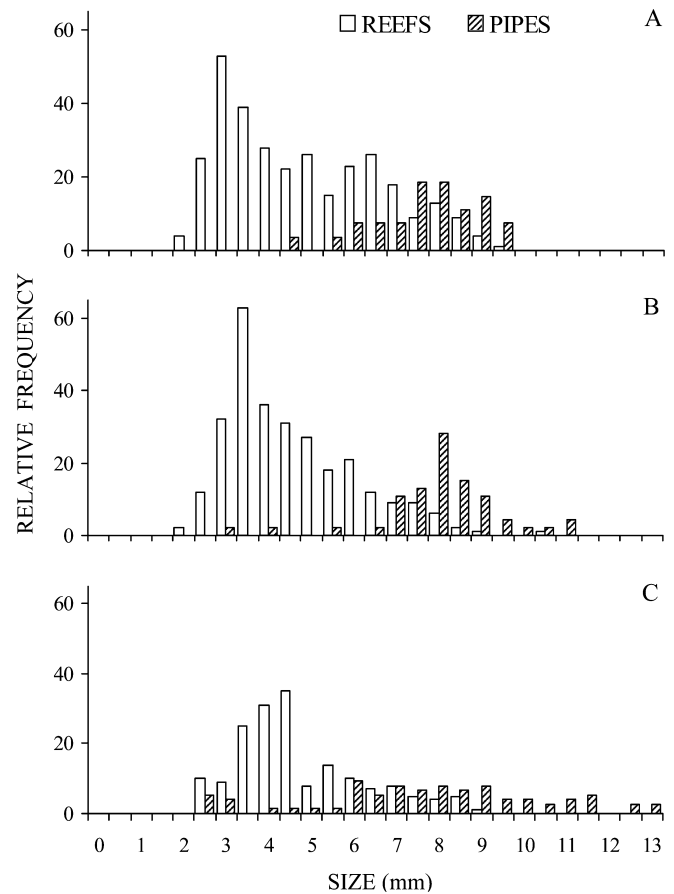


**Fig. 4** *Cyrtograpsus angulatus*. Linear regressions between the density of crabs present in each cohort and crab mean size (carapace width, *CW*) of each cohort. The lower scale for the *x*-axis represents the estimated age of the cohort at that size

crabs are more vulnerable to predation and cannibalism. With low abundances of recruits, the habitat is saturated at larger sizes. As a result, the magnitude of settlement intensity is not transmitted to that of the larger size classes.

The presence of crabs inside pipes provides further evidence supporting the demographic bottleneck hypothesis, as well as the results of tethering experiments. Comparison between the size-frequency distribution inside reefs and inside pipes showed that habitat was saturated. The number of refuges decreased until sizes of 8–10 mm; nevertheless, the sizes inside pipes were lower than this value. As size frequencies of crabs inside reefs decreased, those sizes became more frequent inside pipes. This pattern suggests that once habitat became saturated crabs left reefs looking for other refuges. Nevertheless, frequencies of crabs in pipes were smaller than expected from the decrease found inside the reefs, suggesting that a large part of this decrease was due to predation once the crabs left reefs. Our tethering experiments showed that the relative predation rate on juveniles without refuge was significantly higher than on those with refuge inside reefs. Therefore, crabs increased their mortality risk by leaving reefs before they became adults, at which time they became less vulnerable to predators.

Understanding the general patterns in the relationships between adult populations and recruitment is a major challenge (e.g. Bertness 1999). How recruitment is defined and how it is measured are critical for testing and understanding processes affecting marine communities (Caley et al. 1996). We started this work by presenting different definitions of recruitment. However, it is clear that, in our case, we must look beyond early life stages. A biologically meaningful definition of recruitment should include organisms that survive periods of high mortality before reaching adulthood, in this case, organisms that leave the reefs as juveniles. Generally, particular emphasis is placed on early juvenile stages



**Fig. 5A–C** *Cyrtograpsus angulatus*. Size-frequency distribution of crabs present in the pipes and inside the reefs in different months during the growing season: **A** 21–31 January; **B** 16–24 February; **C** 1–11 March (all 2002)

(Beck 1995), although, here, vulnerability is higher during the period after the crabs leave their refuges but before they become adults. Therefore, if we census the population in early juvenile stages, recruitment success will be very high (see also Luppi and Bas 2002), but it will not correlate with the number of adults. This is a good example of why habitat enhancement programs need to incorporate a comprehensive evaluation of species ecology to avoid misdirected and expensive programs with poor results (Beck 1995). This is likely one reason why stock-recruitment relationships may not hold in species that use shelters during both recently settled and juvenile life stages.

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