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DEPTH LIMITATION OF A TROPICAL INTERTIDAL XANTHID CRAB, *CATALEPTODIUS FLORIDANUS,* AND A SHALLOW-WATER MAJID, *PITHO ACULEATA:* RESULTS OF A CAGING EXPERIMENT

Norman A. Engstrom

ABSTRACT

Cataleptodius floridanus is an abundant (>100 individuals/m^2), small, xanthid crab inhabiting intertidal coral rubble on Glover's Reef, Belize, Central America, but it is uncommon in slightly deeper suitable habitats. To test the role of bonefish in limiting the depth distribution of the crab, a wire mesh cage extending from the shore line into deeper water was constructed to exclude bonefish from their normal foraging in the study area. The cage of 12 × 12 mm mesh allowed passage of *C. floridanus* and other small decapods. After 17 days *C. floridanus* in "deep" and "medium" depth quadrats inside the cage were more abundant and significantly larger than those in "deep" and "medium" depth quadrats outside the cage. Abundance and size distributions did not differ significantly between crabs collected from shallow quadrats inside and outside the cage. Heavy diurnal predation by bonefish in Belize restricts this species to very shallow water. *Pitho aculeata* abundance also increased inside the cage.

Brachyuran xanthid crabs are important members of many shallow marine communities in both temperate (McDermott, 1960; Sinclair, 1977) and tropical (Havens, 1974) regions. *Cataleptodius floridanus* is a common small herbivorous xanthid that occurs throughout the Caribbean (Voss, 1976). On Glover's Reef in Belize, Central America, *C. floridanus* is abundant amongst intertidal coral rubble (>100 crabs/m^2) but the species is uncommon in only slightly deeper water where coral rubble and vegetation occur (Fig. 1). In the Florida Keys this species' depth distribution is different (Hazlett *et al.*, 1977). There *C. floridanus* is somewhat more abundant in shallow water 6–30 m from the high tide line than it is intertidally, and reproductive output is also significantly greater in the deeper water than intertidally (Hazlett, 1975; Hazlett *et al.*, 1977). Hazlett related this distribution pattern to the presumably more favorable physiological conditions in shallow subtidal water compared to more extreme intertidal conditions. The tidal regime at Glover's Reef is very similar to that at Carrie Bow Cay only 32.5 km distant. The tides at Carrie Bow Cay, Belize, are comparable to those at Key West, Florida, in timing and pattern but the range at Key West is normally about 25 cm greater (Kjerfve *et al.*, 1982). Tides both in the Florida Keys and on the outer reefs of Belize are strongly influenced by meteorological conditions. The nearshore habitats in the Florida Keys and the Glover's Reef study site are physically similar.

Why is *Cataleptodius floridanus* in Belize extremely abundant intertidally but rare in slightly deeper water where conditions are presumably more favorable? Physical factors, interspecific competition, and/or predation could influence its distribution patterns. A small herbivorous majid spider crab, *Pitho aculeata,* is moderately common subtidally adjacent to the *C. floridanus* population on Glover's Reef and it is possible that interspecific competition restricts each species to different microhabitats. Predation and herbivory are often important forces influencing community structure (e.g., Connell, 1961; Paine, 1980; Sammarco, 1982), and recently the importance of fish predation on seasonal and spatial patterns of abundance of the dominant amphipods in subtropical sea grass beds has been firmly established (Young and Young, 1978; Stoner, 1979; Nelson *et al.*, 1982).

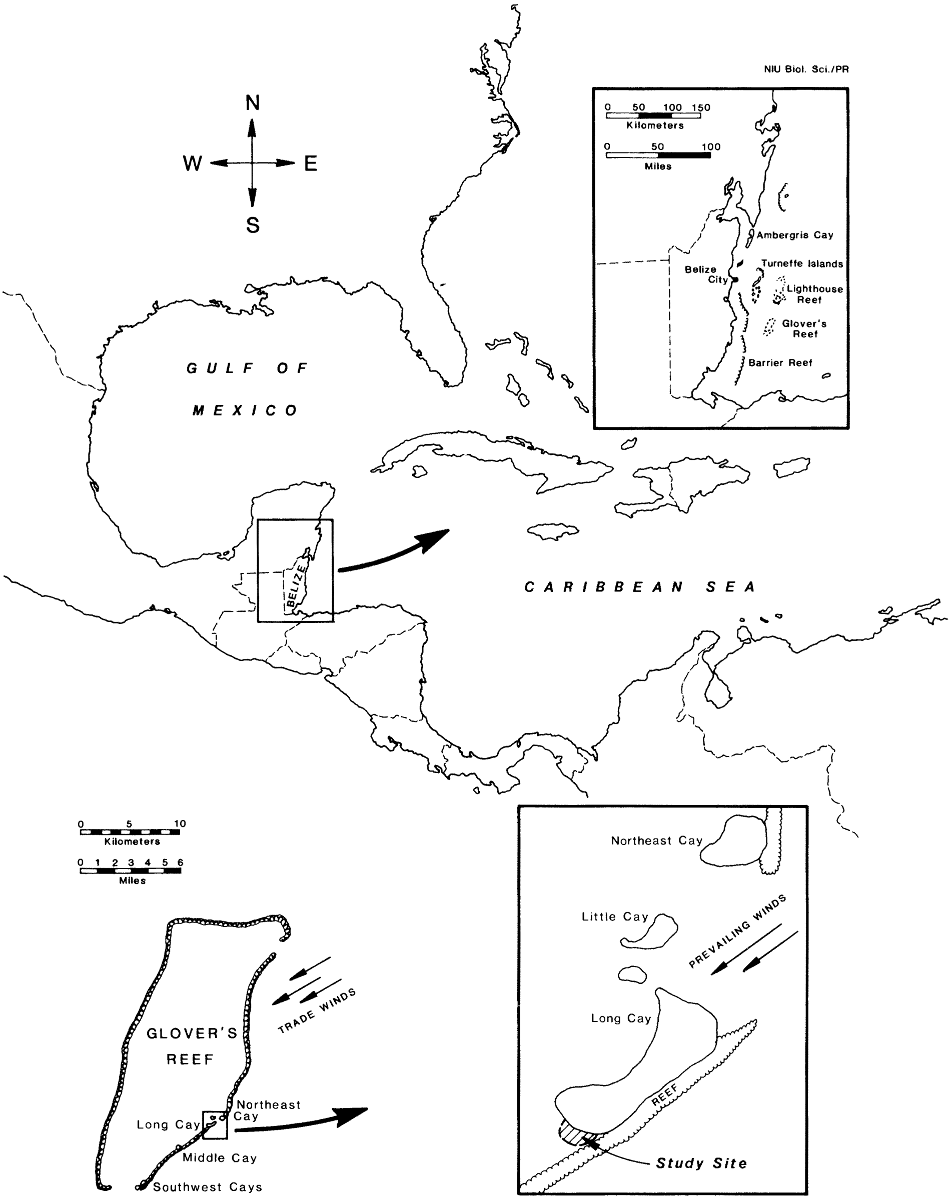

Fig. 1. Long Cay on Glover's Reef lies approximately 53 km from the coast of Belize on the west end of the Caribbean Sea. The study site is protected from prevailing wind-driven waves by the reef crest and by Long Cay.

Bonefish (*Albula vulpes*) are abundant on Glover's Reef, Belize, and schools forage through shallow sea grass beds and coral rubble habitats, sometimes even in water that is less than 10 cm deep. To test the possibility that *C. floridanus* is restricted to extremely shallow water by bonefish predation I constructed a wire mesh fence that excluded bonefish from a section of potential *C. floridanus* habitat extending from shore into deeper water.

METHODS

This study was done on Long Cay, Glover's Reef, Belize, Central America, from 28 June–20 July 1982. The site was on the southwest end of Long Cay where a dense population of *Cataleptodius floridanus* occurs intertidally (Fig. 1). On 30 June a 13 × 4.4 m cage (Fig. 2) of 12 × 12 mm galvanized steel wire mesh and standing 61 cm high was installed. The cage extended from the shoreline into water approximately 50 cm deep at high tide, so that at high tide the sides of the cage extended about 10 cm above the water level. The cage had no bottom or top and care was taken to minimize damaging or disturbing the natural features of the habitat during installation. At the bottom the cage was pushed against the substrate and firmly held in place with wooden stakes. Almost all *C. floridanus* were small enough to pass through the 12 × 12 mm mesh, as were small potential predators such as juvenile *Octopus briareum* and *Bathygobius* sp. Two sampling methods were used, quadrat collections and pushnet sweeps. The quadrat arrangement is shown in Fig. 2. Since optimal habitat for *C. floridanus* at Long Cay extends less than 30 m along the shore, outside (control) quadrats were placed within a few meters of the cage in order to assure that comparable microhabitats were sampled for control and experimental groups. The local tides are strongly influenced by wind, but their normal range is about 20 cm. The "shallow" quadrats were barely covered on most low tides and were completely exposed on spring low tides. The "medium" depth quadrats were located where the depth is generally about 10 cm at low tide, but may be completely exposed in exceptional spring tides during periods of offshore winds. The "deep" quadrats were located where the depth is about 30 cm on low tides and were never exposed. Each 0.91 × 0.91 m quadrat was sampled on a relatively wind-free day at low tide by carefully removing every piece of coral rubble. Working from the periphery of the quadrat toward the center, all crabs seen were captured and placed in a plastic bucket. Because *C. floridanus* specimens sometimes bury themselves when fleeing, buried coral rubble fragments also were removed from the sandy substratum and the sand was gently probed to a depth of approximately 5 cm. After removal of the coral rubble, the surface of the quadrat was searched for another 10 min to capture any emerging *C. floridanus* specimens. Crab carapace widths were measured to the nearest 0.1 mm with a vernier caliper, and wet weights were obtained to the nearest 0.01 g with an Ohaus portable beam balance. Because past experience showed that this procedure was too time-consuming to complete with all 12 quadrats in one day, the shallow quadrat outside the cage was sampled on 1 July and the remaining 11 quadrats were sampled at the end of the experiment on 17 July. Sampling of the shallow quadrat outside the cage was done early in the study to minimize the effect of any possible short-term reductions in numbers of *C. floridanus* that the removal might cause in the nearby quadrat inside the cage. At 2230, 17 July, a set of five pushnet sweeps was made outside the cage on the east and a similar set of five sweeps to the west of the cage, so that each set could be compared to a set of five sweeps made inside the cage as shown in Fig. 2. The principal purpose of making pushnet collections was to assess the abundance of *Pitho aculeata.* The mouth of the pushnet was 55 cm wide and each sweep was 6.4 m long, so 3.5 m^2 was sampled in each sweep. The mesh size was approximately 5 mm. Crabs collected with the pushnet were likewise weighed and measured. The feeding habits of bonefish schools were observed and the stomach contents of three specimens caught on hook and line were examined.

RESULTS

Cataleptodius floridanus was more abundant and larger inside the cage subtidally than outside the cage subtidally ("medium" and "deep" quadrats) (Fig. 3). Since *C. floridanus* matures in the Glover's Reef Long Cay population at approximately 12 mm carapace width, this size was chosen for use in comparing size distributions of *C. floridanus* samples using the χ^2 test or, when the sample sizes were too small, the Fisher exact test. For each statistical comparison a 2 × 2 contingency table was constructed with the columns headed as: number of crabs less than 12 mm carapace width and number of crabs equal to or greater than 12 mm carapace width. For each contingency table the rows are depths and sample location inside or outside the cage.

Outside the cage the medium depth sample differed from the shallow sample in size distribution ($\chi^2 = 5.84$, $P < 0.05$) and this can be attributed to a paucity of larger sized crabs in the subtidal sample (Fig. 3). The sizes of *C. floridanus* in

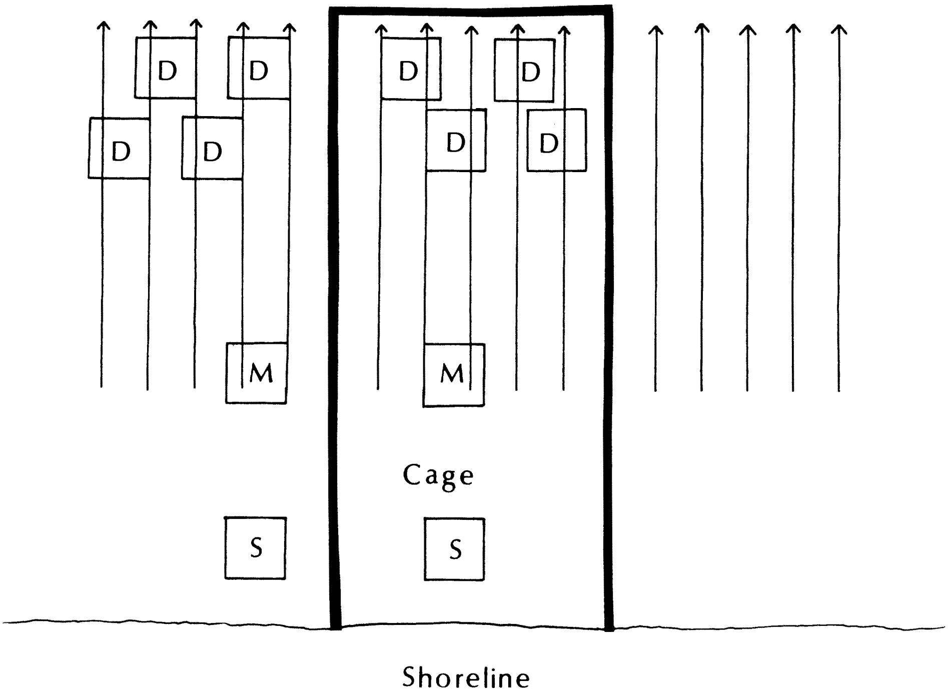

Fig. 2. Diagram of cage, quadrats, and pushnet sweeps. The cage was 13 m long and 4.4 m wide. "Shallow" (S), "medium" (M), and "deep" (D) quadrats measured 0.91 m × 0.91 m each. Pushnet sweeps were 55 cm wide by 6.4 m long (3.5 m^2). East is to the left, west is on the right.

the medium depth sample did not differ from those in the deep sample ($P = 0.72$, Fisher exact test) outside the cage.

An analogous set of size comparisons inside the cage shows that the medium sample did not differ from the shallow sample ($\chi^2 = 0.03$, $P > 0.05$). The medium and deep collections did not differ significantly from each other either ($\chi^2 = 0.02$, $P > 0.10$).

In comparisons of samples from outside the cage with those inside the cage, the shallow samples did not differ significantly in size frequency ($\chi^2 = 0.68$, $P > 0.10$). The medium depth samples differed markedly ($P < 0.02$, Fisher exact test) because few adults were outside the cage and crabs greater than 12 mm carapace width were common inside the cage. The deep samples did not differ from each other at the 5% level ($P = 0.09$, Fisher exact test) but the sample sizes were very small. Pooling all the subtidal samples and comparing medium and deep *C. floridanus* outside the cage to medium and deep *C. floridanus* inside the cage shows a very significant difference ($\chi^2 = 6.96$, $P < 0.01$) that reflects the relative abundance of large crabs inside the cage and their scarcity outside. There was an increase in subtidal abundance of *C. floridanus* inside the cage versus outside the cage, but the shallow collections inside and outside were similar (Table 1). The overall result was that caging allowed more large *C. floridanus* to live subtidally but had no apparent effect on either size or numbers of intertidal *C. floridanus*.

Very few crabs were collected in the pushnet collections. The majid spider crab *Pitho aculeata* was more abundant (13 specimens) than *Cataleptodius floridanus*

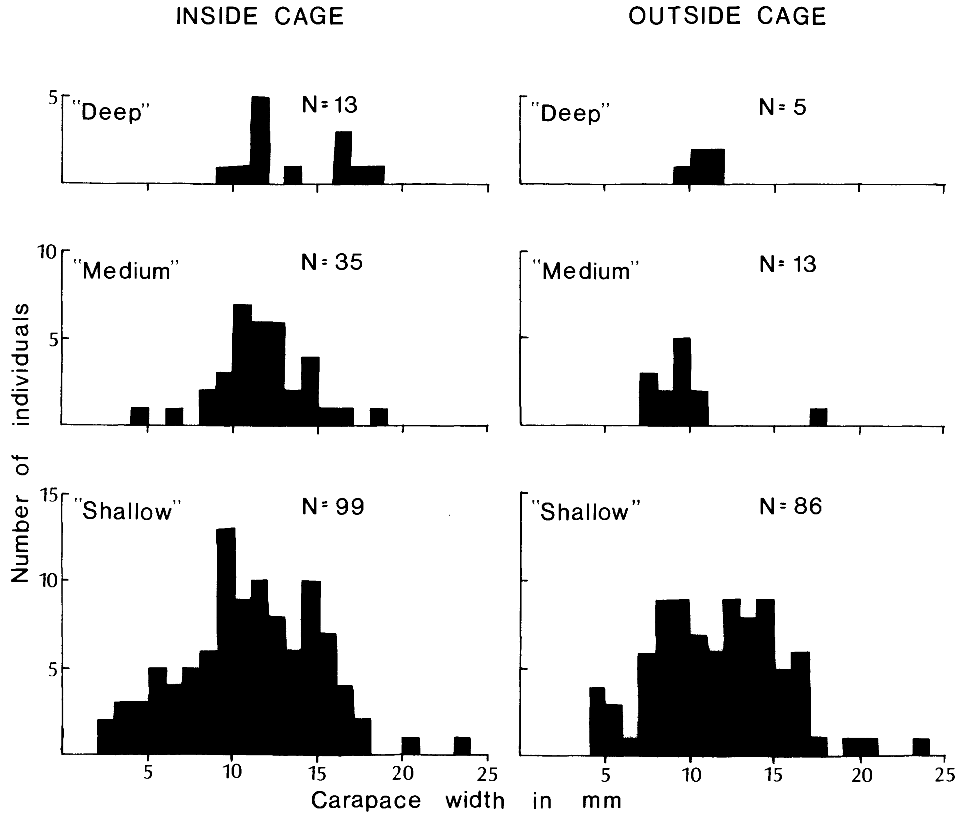

Fig. 3. Size frequencies of *Cataleptodius floridanus* collected in "shallow," "medium," and "deep" depth quadrats inside and outside the bonefish exclusion cage. The "shallow" samples were similar to each other. "Deep" and "medium" depth samples from outside the cage lacked substantial numbers of mature (12 mm carapace width) *C. floridanus,* whereas "medium" and "deep" samples inside the cage contained several adults.

(1 specimen) in the 15 pushnet sweeps. This nocturnal (Heck, 1977) herbivore was never seen or collected in the "shallow" area, but does occur in the slightly deeper areas accessible to bonefish. Though these numbers are very low, interesting and significant patterns are present. At least one specimen of *P. aculeata* was collected in every sweep inside the cage (5/5) whereas specimens were present only in 3 of the 10 pushnet sweeps outside the cage, 2/5 on the east and 1/5 on

Table 1. Abundance of *Cataleptodius floridanus* collected from quadrats. Deep collections are from four quadrats inside the cage and four outside. Medium and shallow data are from one quadrat each inside and outside.

	Inside		Outside	
Depth	Number	Abundance	Number	Abundance
Deep	13	(3.9/m^2)	5	(1.5/m^2)
Medium	35	(42.3/m^2)	13	(15.7/m^2)
Shallow	99	(120/m^2)	86	(104/m^2)

Table 2. *Pitho aculeata* specimens collected in pushnet samples inside and outside the cage as indicated by the arrows in Fig. 2.

Location	Carapace width (in mm)	Wet weight (in g)	Sex
Inside cage (5 samples—17.5 m²)	11.4	1.96	berried ♀
	9.7	0.71	♀
	8.2	0.58	immature
	8.3	0.43	immature
	8.3	0.47	immature
	8.0	0.42	immature
	7.5	0.33	immature
	6.8	0.24	immature
	5.7	0.13	immature
Outside cage (10 samples—35 m²)	5.1	0.10	immature
	3.6	0.02	immature
	3.3	0.02	immature
	3.0	0.02	immature

the west. Thus, *P. aculeata* was caught consistently inside the cage but not outside and this difference is significant ($P = 0.019$, Fisher exact test). In addition, all of the *P. aculeata* individuals captured by pushnet inside the cage (Table 2) were larger than the largest specimen outside the cage ($P < 0.05$, Wald-Wolfowitz runs test). Large individuals of *P. aculeata* were occasionally seen outside the cage during this study but they were not abundant.

Bonefish are known to consume benthic crustaceans in addition to mollusks (Bohlke and Chaplin, 1968; Warmke and Erdman, 1963). Schools of bonefish foraged through the study area regularly, though no systematic attempt was made to quantify their density. Fifty-one bonefish appear in a 35 mm photo that framed a portion of one school foraging in the study area. The fish in the photo are about 40–50 cm in length. Larger individuals forage in smaller schools. The main flats over which the bonefish forage are approximately 50 × 150 m. The stomach contents of three bonefish caught on hook and line were examined. One contained the remains of three specimens of *Pitho* sp. plus unidentifiable material; one contained the carapace of one *Cataleptodius* and one *Pitho,* and the remains of several pagurid hermit crabs (including their gastropod shells); the third was empty.

DISCUSSION

Prevention of bonefish from foraging in shallow subtidal flats allowed the xanthid crab *Cataleptodius floridanus* to extend its local range. Individuals of *C. floridanus* are territorial (personal observations) and individuals are not wide ranging (Hazlett *et al.,* 1977), but within just three weeks substantial numbers of them occupied the subtidal habitat adjacent to an intertidal population. Most of these crabs probably moved down from the intertidal population, and were replaced in the shallow water by small scale movements of crabs along the shoreline. Crabs of all sizes moved into deeper water as shown by the comparable size frequencies at the three depths inside the cage (Fig. 3). By foraging as close to shore as water depth will allow them to, the bonefish would normally harvest almost all of the emigrants. This results in very low populations of small inconspicuous *C. floridanus* in deeper water at this site (Fig. 3). The intertidal population of *C. floridanus* was not significantly affected by caging out bonefish because the bonefish cannot forage in that portion of the intertidal zone. Therefore, the intertidal coral rubble habitat serves as a refuge for *C. floridanus*. Predation also limits the populations of *Pitho aculeata*. This species is mainly nocturnal and is cryptically colored, factors which would reduce predation. Nevertheless, *P. aculeata* specimens are found and eaten by bonefish and only low population densities are maintained at the study site where most specimens are small, as in *C. floridanus*. The rapid increase in abundance of *C. floridanus* subtidally inside the cage indicates that physical factors such as temperature, substrate, or food availability are not excluding this species from the subtidal habitats. Both crab species increased in abundance inside the cage; therefore, interspecific competition between them is apparently not an important factor in preventing their mutual occupation of subtidal habitats, at least at the population densities reached during this experiment.

Predation by the bonefish *Albula vulpes* is important in controlling the abundance and depth distribution of the xanthid crab *Cataleptodius floridanus,* and also suppresses populations of the majid crab *Pitho aculeata* at Glover's Reef. Conversely, these crabs are important food sources for this game fish. Glover's Reef, 53 km offshore from Belize, is isolated and accessible only by private boat, so gamefish species such as bonefish are not heavily exploited there. This short-term caging experiment, in which bonefish were eliminated briefly from a small portion of Glover's Reef, is analogous to longer term reduction of bonefish by sport fishermen and tourists in the heavily trafficked Florida Keys. In the present study the crabs were undoubtedly in the early stages of colonizing the caged subtidal habitat. In the Florida Keys Hazlett *et al.* (1977) studied crab populations that had been ecologically released from naturally higher levels of fish predation. It should follow that an equilibrium condition with higher subtidal densities of *C. floridanus* will have been reached in the Florida Keys. Large predatory fish were not regularly seen in the study areas of Hazlett *et al.*, and the *C. floridanus* they collected were generally much larger than those in my study area, a result also consistent with reduced predation pressure in the Keys (Hazlett, personal communication). Therefore, the contrasting depth distributions and abundance patterns of *C. floridanus* on Glover's Reef and in the Florida Keys provide comparisons which complement rather than conflict with each other. These comparisons support the hypothesis that bonefish are important in regulating local abundance and distribution patterns of *Cataleptodius floridanus* in the Caribbean Sea and adjacent waters. This study also suggests that bonefish predation is an important selective agent that places a premium on the competitive ability of *C. floridanus* individuals to defend and maintain territories in the refugium portion of their habitat. The comparison of the population distribution of *C. floridanus* on a remote atoll in Belize with populations in the Florida Keys reveals the importance of undisturbed habitats for studies in which ecological experiments have not already been performed.

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