PREDATION AND SURGE STRESS AS FACTORS IN THE DISTRIBUTION OF TWO COMATULID CRINOID SPECIES

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Abstract: Two comatulid crinoid species of the genus *Davidaster* (formerly genus *Nemaster*) are abundant in the Caribbean at Discovery Bay, Jamaica: *D. rubiginosa* and *D. discoidea*. We tested the hypotheses that their populations are limited to depths below 10 m due to high predation pressure or due to high surge stress, and that the two species are differentially affected by surge stress. We found no evidence of predation. *D. rubiginosa* appears to be more resistant to surge than *D. discoidea*. Its arms were more likely to be extended, rather than curled, in high surge. Also, it occurred high on coral promontories, while *D. discoidea* was found low on these promontories. Finally *D. rubiginosa* was relatively more abundant than *D.discoidea* at shallow depths, and less abundant than *D. discoidea* at deeper depths. D. *rubiginosa* also seems to prefer areas of higher water movement, and may be limited at deeper depths where water movement may be low.

Key words: Davidaster discoidea, Davidaster rubiginosa, *living fossils, resistance to surge*

INTRODUCTION

500 million years ago, tropical reefs looked very different. Up until the Mesozoic period 250 million years ago, sessile sea lilies (Echinodermata: Crinoidea) were abundant at all depths, forming thick depositional layers in the fossil record (Macurda and Meyer 1983). It is hypothesized that their sudden disappearance from waters above 100 m is linked to the radiation of predatory teleost fish in the Mesozoic period. Now, only members of Comatulidae, a more derived, non-stalked, mobile order, remain in shallow waters (Meyer and Macurda 1977).

Two comatulid crinoid species of the genus *Davidaster* (formerly genus *Nemaster*) are abundant in the Caribbean at Discovery Bay, Jamaica: the smaller, more slender and delicate, gray-colored *D. discoidea,* and the often orange-colored, more robust *D. rubiginosa* (Hendler et al. 1995). During the day, these crinoids hide their disc-shaped calyx in crevices in coral promontories along the reef and extend their arms, catching passing plankton in the water current (Macurda 1973). These species, however, are only abundant at depths below about 10 m. Like their stalked sea lily ancestors, these crinoids may be limited to these depths because of predation pressure.

Another hypothesis is that intolerance to high surge stress limits them to calmer, deeper waters. Macurda (1973) found both species to be rheophobic (current-avoiding); however, Andrea (1979) found *D. rubiginosa* to be slightly rheophilic (current-seeking) and so surge may affect these two species differently. If the more robust *D. rubiginosa* is able to tolerate higher wave stress, then we expect it to extend its arms during times of high surge while *D. discoidea* would have a more protective posture, curling its arms. Additionally, we expect *D. rubiginosa* to be more abundant than *D. discoidea* at shallower depths. Lastly, we predicted that at shallower depths, *D. discoidea* would be found lower on promontories than *D. rubiginosa* to avoid surge stress, but that at deeper depths, where there is less surge stress, there would be no difference in relative height on promontories between the two species.

METHODS

We sampled the crinoid population in

Discovery Bay, Jamaica on 3 - 8 March 2004, at Mooring 1, Dancing Lady and Dairy Bull reefs. *D. rubiginosa* and *D. discoidea* were identified using *Reef Creature Identification* (Humann 1992).

Tests of predation hypothesis

We collected two *D. rubiginosa* and one *D. discoidea* from Mooring 1 on 3 March 2004 and tethered them for 24 hours at approximately 1 m on the west back reef and noted any evidence of predation. We also released these same crinoids amidst a "feeding frenzy" started by crushing up a *Tripneustes ventricosus* and attracting predatory fish to the area. Any predation on the crinoids was noted. On 8 March 2004 we collected two *D. rubiginosa* and brought them down to about 10 m at Dancing Lady reef. We created another "feeding frenzy" and observed any predation.

Tests of surge stress hypothesis

We surveyed the crinoid population at depths ranging from about 8 to 20 m. At all depths we followed a compass bearing and recorded every observed crinoid from both species along that transect for approximately 30 minutes. We measured the relative height (low, mid level, or high) at which the crinoids occurred on the promontories and whether their arms were fully extended or curled (defined as having arms either curled up or completely hidden in a crevice).

Surge was bidirectional; we measured the level of surge by timing how long it took a piece of synthetic sponge to move 15 cm in one direction. Water surge was then grouped into 3 categories for analysis; low (3 - 4.9 cm/sec), medium (5 - 8 cm/sec), and high (> 8 cm/sec). Depths were also categorized for analysis: shallow (< 13 m), medium (between 13 and 16 m) and deep (> 16 m).

RESULTS

Tests of predation hypothesis

After 24 h there was no visible sign of predation on the tethered crinoids. When crinoids were presented to fish (two sergeant majors, one squirrelfish and three threespot damselfish) along with *T. ventricosus* at 1 m depth, fish fed on urchin parts, but not on crinoid parts. When the same test was done at 10 m, one initial phase yellowhead wrasse, three juvenile bluehead wrasse, and one juvenile spanish hogfish were present; all ate pieces of urchin. The yellowhead wrasse took one bite of a *D. discoidea* arm, but spat it out. No other feeding on the crinoids was observed.

Tests of surge stress hypothesis

As surge varied between days due to weather, we were able to measure a range of levels (3 - 15 cm/s). Surge, independent of depth, did not affect arm extension in *D. rubiginosa*, although there was a trend for arms to be more curled at high surge ($G = 4.72$, $df = 2$, $P = 0.094$; Table 1). Surge did affect arm extension in *D. discoidea*. Arms were generally extended at low surge and curled at higher surge ($G = 30.64$, $df = 2$, $P < 0.0001$; Table 1). No crinoids were observed shallower than about 9 m in the areas we sampled. *D. rubiginosa* was relatively more abundant at shallower depths than *D. discoidea*, while *D. discoidea* was relatively more abundant at deeper depths ($G = 16.77$, $df = 2$, $P < 0.0001$; Table 2). *D. rubiginosa* was found relatively higher on promontories than *D. discoidea* ($G = 26.59$, $df = 2$, $P < 0.0001$; Table 3). However, there was no significant relationship between relative height on promontories and depth for either *D. rubiginosa* or *D. discoidea* ($G = 5.53$, $df = 4$, $P = 0.24$ and $G = 6.11$, $df = 4$, $P = 0.19$, respectively; Table 4).

Table 1. Number of crinoids observed with arms extended or curled at low, mid and high wave surge for *D. rubiginosa* and *D. discoidea*.

	D. rubiginosa		*D. discoidea*	
Surge	# extended	# curled	# extended	# curled
Low (3 - 4.9 cm/s)	9	1	37	1
Mid (5 - 8 cm/s)	10	9	5	8
High (> 8 cm/s)	3	1	0	3
Total	22	11	42	12

Table 2. Number of *D. rubiginosa* and *D. discoidea* observed at shallow, mid and deep depths.

Depth	*D. rubiginosa*	*D. discoidea*
Shallow (< 13 m)	15	7
Mid (13 - 16 m)	27	34
Deep (> 16 m)	6	30
Total	48	71

Table 3. Total number of *D. rubiginosa* and *D. discoidea* observed low, mid and high on coral promontories at all depths.

Relative height on promontory	*D. rubiginosa*	*D. discoidea*
Low	6	32
Mid	13	21
High	21	6
Total	40	59

DISCUSSION

The results of our predation tests do not support the hypothesis that these comatulid crinoids are absent from shallower depths due to predation pressure. At Discovery Bay, there may be no or few natural predators of these crinoids. This could be due to chemical defenses, which have been found in Great Barrier Reef crinoids (Macurda and Meyer 1983), or to the morphology of the organisms, which are mostly hard skeleton and have little nutritive value (Meyer and Macurda 1977). However, our results do not rule out predation entirely. It is possible that diurnal crinoid predators were not present, as Discovery Bay is overfished and

Table 4. Number of *D. rubiginosa* and *D. discoidea* observed at low, mid and high on coral promontories at shallow, mid and deep depths.

	D. rubiginosa			*D. discoidea*		
	Relative height on promontory			Relative height on promontory		
Depth	Low	Mid	High	Low	Mid	High
Shallow (< 13 m)	3	7	5	6	1	0
Mid (13 - 16 m)	3	4	12	13	6	3
Deep (> 16 m)	0	2	4	13	14	3
Total	6	13	21	32	21	6

lacks many fish species which normally occur on coral reefs, or that predators are nocturnal and thus excluded from our study. Crabs, for example, have been observed as predators (Macurda and Meyer 1983), and may be primarily nocturnal.

High surge clearly affects *D. discoidea* more than *D. rubiginosa*. This can be seen by the arm extension of *D. rubiginosa* and curling of *D. discoidea* during high surge. *D. rubiginosa* (more rheophilic) was found to be relatively more common at shallower depths than *D. discoidea* (more rheophobic). Surge stress is greater at shallow depths (Andrea 1979), and so our results support the hypothesis that the two species are affected by surge stress differently. The fact that *D. rubiginosa* is not found at depths less than 9 m and that it is found in crevices would suggest that there is some upper threshold surge level above which it cannot tolerate. *D. discoidea* may have a similar upper surge threshold which is less than that of *D. rubiginosa*.

The finding that *D. rubiginosa* was found relatively higher on promontories across all depths than *D. discoidea* also corresponds to the rheophilic and rheophobic nature of the two species. *D. rubiginosa* tends to be higher on the promontories at greater depths but was found at all heights at shallow depths. *D. discoidea* tends to be lower on the promontories at shallower depths but was found at all heights at deep depths. As surge decreases with depth, *D. rubiginosa* may have to be relatively higher on promontories to meet its water movement demands. Conversely, in shallow water *D. discoidea* may have to be relatively lower on promontories to escape heavy surge.

These results support the hypothesis that these two species of crinoids are unable to tolerate the high surge found at shallow depths and are limited to deeper, calmer areas. Future studies could compare relative abundances of these two species between sites with different levels of surge stress (i.e., a protected cove vs. the fore reef). Determining if these comatulid crinoids are chemically defended, and if such chemicals are unpalatable to fish or other predators, could more conclusively rule out predation as a factor in crinoid distribution.

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