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Responses of Two Coral Reef Toadfishes (Batrachoididae) to the Demise of Their Primary Prey, the Sea Urchin *Diadema antillarum*

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In 1983–84 the sea urchin *Diadema antillarum*, which was abundant on coral reefs throughout the Caribbean, suffered a mass mortality. Its densities decreased by about 95% throughout most of its range. In Panama, prior to that mortality event, two reef toadfishes, *Amphichthys cryptocentrus* and *Sanopus barbatus* fed almost exclusively on *Diadema*. Two and a half years after that event the abundance of at least one toadfish appears to be at the pre-event level and both species are actively breeding. After the event these "specialist" fishes changed their diets in different ways. The diet of *A. cryptocentrus* has become generalized and now includes a broad range of mobile benthic invertebrates (crabs, hermit crabs, gastropods, octopods, echinoids). The diet of *S. barbatus* now consists primarily of fishes, but also includes a few mobile benthic invertebrates. The ability of *Diadema* predators to maintain their populations at high levels may reduce the potential for *Diadema* populations to recover.

UNTIL recently the sea urchin *Diadema antillarum* was an abundant and ecologically influential organism on Caribbean coral reefs (see references cited in Lessios et al., 1984a, 1984b). Many reef fishes included this urchin in their diets and it constituted the major item eaten by several species at sites in the eastern Caribbean (Randall, 1967). In Jan.–May 1983 populations of *Diadema* on the Caribbean coast of Panama suffered a rapid mass mortality, which subsequently affected the species throughout most of its geographic range (Lessios, et al., 1984a, 1984b; Hughes et al., 1985). In San Blas the mortality reduced *Diadema* populations by

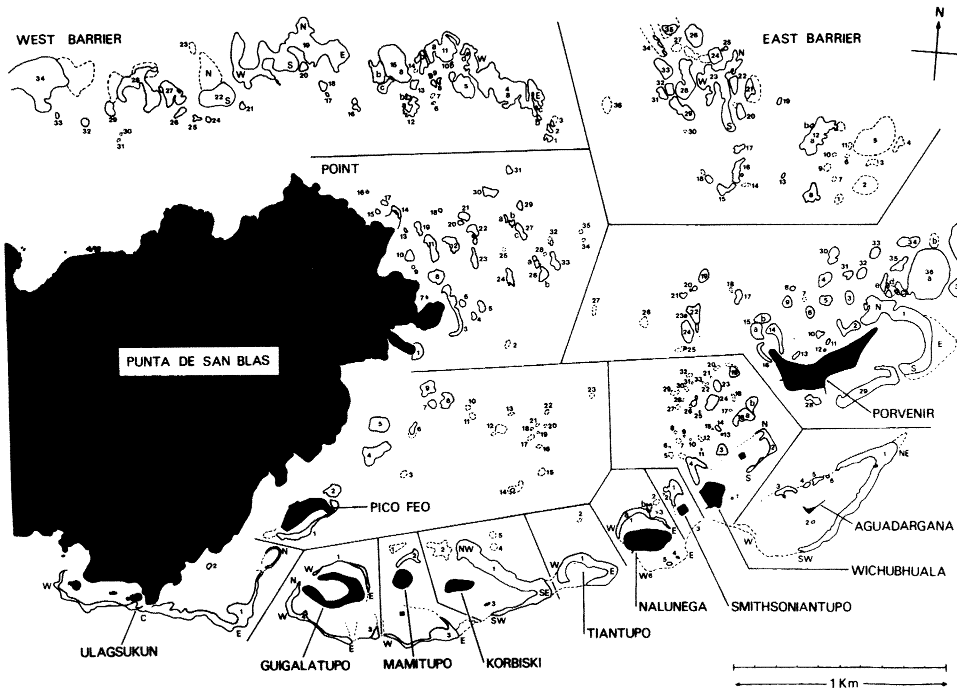

Fig. 1. Patch reefs of San Blas Point. Solid lines define emergent reefs, dashed lines define submerged reefs. Substrate between reefs consists of sand, mainly covered with macroalgae and seagrasses.

95% (Lessios et al., 1984a) and those populations did not recover in the subsequent 3 yr (H. A. Lessios, pers. comm.).

Prior to the mortality event two species of San Blas toadfishes (Batrachoididae), *Amphichthys cryptocentrus* and *Sanopus barbatus,* fed almost exclusively on *D. antillarum* (Hoffman and Robertson, 1983). Here I describe the responses of those fishes to the abrupt loss of their primary prey.

Methods

Study area.—Data were collected at the same site in the Archipielago de San Blas (Fig. 1) both before (Hoffman and Robertson, 1983) and after the *Diadema* mortality.

Gut content analyses.—The mortality affected San Blas populations of *D. antillarum* in April–May 1983 (Lessios et al., 1984a, 1984b). Information on the toadfishes' diets was collected during 1977 and 1981 (Hoffman and Robertson [1983]) and Sept. 1983–Jan. 1986. Specimens were collected from shallow reefs immediately to the east of Punta de San Blas (Fig. 1) in both cases. Hoffman and Robertson (1983) found that both species were most likely to have fresh material in their guts in the morning. Consequently the 1984–86 series of specimens were collected in the morning. Fishes were collected with Quinaldine anaesthetic and dissected within 1 h of capture. All identifiable material in the guts was recorded and measured.

Reproductive activity.—The degree of activity of the ovaries of females collected for gut analyses was recorded. Ripe ovaries are readily recognizable since both species produce eggs about 5 mm in diameter. Hoffman and Robertson (1983) found males of *A. cryptocentrus* with aggregations of small juveniles (2–3 cm long) in their burrows and searches were made for such juveniles in the shelters of both species during the 1984–86 series of collections.

Population change in A. cryptocentrus.—*Amphichthys cryptocentrus* was by far the more abundant of the two toadfishes before the *Diadema* mortality (Hoffman and Robertson, 1983). During a 6 mo period in 1978 a series of censuses was made of the *A. cryptocentrus* population

TABLE 1. GUT CONTENTS OF *Amphichthys cryptocentrus* BEFORE AND AFTER *Diadema* MORTALITY.

Item	Before[a]		After		
	Proportion of fish with items	Proportion of items in total gut contents	Proportion of fish with items	Proportion of items in total gut contents	Size[b] of items (cm)
Echinoids					
Diadema	.80	.85	.03	.01	8.0
Echinometra and *Eucidaris*	.00	0	.20	.06	4.0 (3.0–5.0)
Crabs	.06	.08	.66	.36	1.8 (1.0–6.0)
Gastropods	.06	.08	.40	.32	1.1 (0.5–4.5)
Hermit crabs	.00	0	.29	.15	1.6 (0.8–5.0)
Octopods	.00	0	.11	.05	20.0 (15.0–36.0)
Scallops	.00	0	.06	.02	2.1 (2.0–2.2)
Lobster	.00	0	.03	.01	3.0
Fishes	.00	0	.03	.01	4.0
Empty	.09	—	.09	—	
N	35	39	35	94	

[a] Data from Hoffman and Robertson (1983).
[b] $\bar{X}$ (range). Echinoids = test diameter, crabs = carapace width, gastropods and hermit crabs = shell length, octopods = arm tip to tip, lobster/shrimp = head to tail length, fish = total length, scallop = shell width.

in one 0.225 ha area immediately to the west of Smithsoniantupo (Fig.1). Since May 1983, when the *Diadema* mortality was in progress, this same area has been censused at approximately monthly intervals. No estimate was made of the population density of *S. barbartus* before or after the mortality event.

RESULTS

Gut analyses.—Amphichthys cryptocentrus.—Prior to the *Diadema* die-off that urchin represented almost the entire gut contents of *A. cryptocentrus* (Table 1). In terms of numerical abundance, the main items present in *A. cryptocentrus* after the mortality were crabs, gastropods, and hermit crabs. However, when prey size also is taken into account, a larger variety of prey contributed substantially to the biomass of the diet of that toadfish. Individuals of the three most abundant prey groups (gastropods, hermit crabs, and crabs) typically were considerably smaller than individuals of two less abundant prey groups (octopods and echinoids) (Table 1). Thus all five of these prey types are important components of the new diet of *A. cryptocentrus.*

TABLE 2. GUT CONTENTS OF *Sanopus barbatus* BEFORE AND AFTER THE *Diadema* MORTALITY.

Item	Before[a]		After		
	Proportion of fish with items	Proportion of items in total gut contents	Proportion of fish with items	Proportion of items in total gut contents	Size[b] of items (cm)
Diadema	.92	1.00	.00	.00	—
Fishes	.00	.00	.44	.48	12.0 (10.0–15.0)
Shrimps	.00	.00	.11	.10	3.5 (2.0–5.0)
Scallops	.00	.00	.06	.05	1.5
Hermit crabs	.00	.00	.11	.29	1.7 (1.2–2.5)
Crabs	.00	.00	.06	.05	2.0
Gastropods	.00	.00	.06	.05	1.0
Empty	.08	—	.28	—	
N	13	13	18	21	

[a] Data from Hoffman and Robertson (1983).
[b] See Table 1.

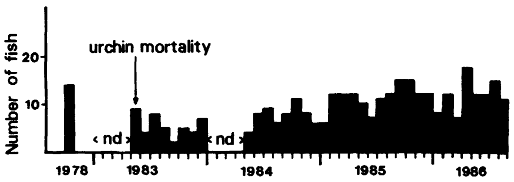

Fig. 2. Numbers of *Amphichthys cryptocentrus* counted in a 0.225 ha area during regular censuses. The 1978 data point is the mean (SD = 1.5) for 32 censuses over 8 mo (data for individual censuses are not available); the 1983–86 data are from censuses at monthly intervals. ND = no data.

Sanopus barbatus.—Before the *Diadema* mortality that urchin was the only item found in the guts of *S. barbatus* (Table 2). Fishes were not only the most abundant item present in the guts of *S. barbatus* after the mortality but were also considerably larger (10–15 cm long) than the other items found (two hermit crabs in 1.2 cm shells, a 2 cm scallop and two shrimps 2–5 cm long). The only recognizable fish was a goatfish (Mullidae).

Most toadfishes are cryptically colored and shaped fishes that normally lie motionless on the bottom (Collette and Russo, 1981; Collette, 1983) or in shelters or burrows. Among those that eat fishes no special adaptations for prey capture have been described and most species probably simply sit and wait for fish that have not noticed them to come within striking range. However, *S. barbatus* has distinctive behaviors that may constitute a prey-capture mechanism aimed specifically at fishes. A distinctive feature of *S. barbatus*, which has a cryptic, mottled coloration, is the presence of 1–3 eyelike spots on its tail (Collette, 1983). In San Blas I found individuals of this species in small caves or under coral overhangs at the coral-sand interface around the edges of reefs. When I encountered these fish in the early morning they often were lying exposed on a sandy bottom 0.5–1 m outside their shelters. In that situation the anterior 40% of the fish was very pale and blended in with the substrate while the posterior 60% was considerably darker than normal and the "eye" spots on the partly folded tail fin were quite prominent. The slender dark tail was curled laterally forwards and positioned near the head. On several occasions when I first noticed the fish I mistook the tail for the front half of a moray eel that was extended from a hole in the substrate. Reef fishes often are attracted by, and closely approach and follow moray eels that are moving about on a reef in daylight (pers. obs.). The resemblance of *S. barbatus* tail to a moray may be mimetic and serve to attract prey fishes to within striking distance of the toadfish's camouflaged head.

Reproductive activity.—Among 35 *A. cryptocentrus* collected I found four males with juveniles in their burrows and five females with ripe or nearly ripe eggs. I also found three male *S. barbatus* with recently hatched fry in their holes. In the area in which the *A. cryptocentrus* population was monitored I counted up to four large (10–15 cm total length) solitary juveniles during 1985, and frequently saw similar sized individuals at other localities. In addition, while collecting *S. barbatus* I encountered large juveniles of that species.

Abundances of toadfishes.—At the time of the *Diadema* mortality the *A. cryptocentrus* population was about one third lower than it had been 5 yr previously. For the remainder of 1983 it was about half the 1978 level, and by the end of 1985 it increased to the same as the 1978 level (Fig. 2). Some of the variation in numbers encountered during the post-mortality censuses probably is due to movements of *A. cryptocentrus* in and out of the monitored area (Hoffman and Robertson, 1983). When collecting *A. cryptocentrus* for gut analyses I encountered similar densities in other patches of the same habitat type in different parts of the study area.

Sanopus barbatus was relatively uncommon both before and 2.5 yr after the *Diadema* mortality, but was not noticeably rarer during the second data collection period.

Discussion

The two Panamanian toadfishes responded in different ways to the abrupt loss of the prey on which they had fed almost exclusively. *Amphichthys cryptocentrus* switched to a generalized diet that incorporated most major types of mobile benthic invertebrates. Its new diet resembles that of other Caribbean toadfishes (Collette, 1974, 1983; Collette and Russo, 1983). *Sanopus barbatus*, on the other hand, switched primarily to fishes. If I am correct in suggesting that *S. barbatus* is employing mimetic behaviors that function specifically for capturing fishes, then that toadfish's prior concentration on *Diadema* probably represented opportunistic use of a superabundant and readily accessible food source that was easier to exploit than were fishes.

The only published data of which I am aware that considers how consumers of *Diadema* responded to the mass mortality is that of Reinthal et al. (1984). These authors showed that, in Belize, the triggerfish *Balistes vetula* was successfully feeding on a variety of benthic invertebrates 1–2 mo after the mortality event. However, since those authors had no data on that species' diet at that site prior to the mortality event it is not clear whether *B. vetula*'s diet actually changed.

The available data indicate that if the near elimination of the two Panamanian toadfishes primary food source had any deleterious effect on them it was slight and temporary. First, both species have continued to breed and both have subadult recruits entering their populations. Second, although the size of the monitored population of *A. cryptocentrus* was lower at the time of the mortality than previously, that reduction is not likely to have reflected mortality due to starvation. Since adults of that species are fairly large (up to 25 cm standard length, and 950 grams), and are very sedentary, it seems unlikely that their metabolic requirements would be sufficiently high for them to die-off as abruptly as *Diadema* did. Consequently the *A. cryptocentrus* population probably was low before the *Diadema* mortality could have had any effect on it. Even if the *Diadema* mortality was responsible for part of the lowered level of *A. cryptocentrus* population shortly after the mortality, that toadfish population subsequently returned to the pre-mortality (1978) level. This occurred in the absence of any noticeable increase in the *Diadema* population in the study area since the 1983 mortality event (H. A. Lessios, pers. comm.; Aug. 1986).

One other reef fish that consumes *Diadema*, *B. vetula*, also appears not to have been adversely affected by the *Diadema* mortality in Panama. Although *B. vetula* has been uncommon on the shallow nearshore reefs of the study area for the past decade, in early 1985 there was a mass arrival of its pelagic juveniles onto those reefs. This influx of juveniles, which occurred on reefs along over 200 km of the Panama coast, was about 100 times greater than influxes noted during any of the preceding 6 yr (D. R. Robertson, unpubl. data).

The ability of some of *Diadema*'s predators, particularly ones that might be regarded as food specialists, to switch their diets and successfully withstand an abrupt, drastic, and persistent reduction in the population of their prey may have profound, long term effects on the ecology of Caribbean coral reefs. If such predators can exert sufficient pressure on the reduced *Diadema* populations, they may substantially retard population growth of that prey.

Diet switching by the San Blas toadfishes demonstrates that dietary specialization by coral reef fishes can represent opportunistic use of an abundant resource and that one must be cautious when interpreting narrow diets. Further, the results presented here show that one cannot readily predict the responses of consumers to major changes in the abundance of prey, i.e., whether they can change their diets and, if so, how they would do so. One might expect obligate dietary specialization to be unlikely when other members of a family or genus of fishes have different diets, especially generalized diets, and predict that diet switching by *A. cryptocentrus* and *S. barbatus* was likely because other Caribbean batrachoidids have generalized diets. However, such is not necessarily the case. Members of the family Chaetodontidae use a variety of planktonic and benthic foods, including hard corals (Anderson et al., 1981). Some exclusively corallivorous chaetodontids evidently are obligate diet specialists, since drastic reductions in the abundance of hard corals do lead to rapid reductions in the abundance of some (but not all) of those fishes (Williams, 1986). However, "specialist" corallivores do not necessarily respond in this manner. On eastern Pacific coral reefs in Panama the tetraodontid *Arothron meleagris* is an abundant fish that feeds almost exclusively on hard corals (Glynn et al., 1972). Although populations of these corals recently were reduced by 70–95% the density of *A. meleagris* has not declined and its feeding remains concentrated on corals (Glynn, 1985). It seems likely that *A. meleagris* could switch its diet, since elsewhere in the eastern Pacific it consumes foods other than corals (H. Guzman, pers. comm., 1986). One can only speculate at what point, in terms of the abundance of the prey, such switching might occur and whether such a switch would be deleterious to *A. meleagris*. Although *A. meleagris* is common on Panamanian reefs its impact on reef growth is slight (Glynn et al., 1972; Glynn, 1985) and it seems unlikely that the recovery of the prey population will be affected by either a failure of this consumer to rapidly change it's diet or to switch and maintain itself on other foods. Clearly, the nature of predator-prey relationships that involve coral reef fishes are not readily predictable.

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