

Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panamá indicate food limitation

D. R. Robertson *

Smithsonian Tropical Research Institute, Balbao, Panamá

Date of final manuscript acceptance: August 23, 1991. Communicated by J. M. Lawrence, Tampa

Abstract. In 1983/1984, *Diadema antillarum* suffered mass mortalities throughout its West Atlantic range. Its populations were reduced by 95% and subsequently have failed to recover. These die-offs led to sustained increases in the abundance of soft algae, including types eaten by herbivorous reef fishes. I monitored adult populations of three herbivorous surgeonfishes (*Acanthurus coeruleus*, *A. chirurgus* and *A. bahianus*) between 1978 and 1990, and the recruitment of their pelagic juveniles between 1979 and 1989, on six patch reefs in Panamá. Adult populations of *A. coeruleus* and *A. chirurgus*, which largely restrict their feeding to reef substrata, increased by averages of 250 and 160%, respectively, after the die-off of *D. antillarum* in 1983. No increases occurred in the adult populations of *A. bahianus*, which often feeds in off-reef habitats unaffected by *D. antillarum*. Average annual levels of juvenile recruitment of all three surgeonfishes did not differ before and after the die-off. These results support the hypothesis that adult populations of two herbivorous fishes that are strongly reliant on reef algae for food previously were limited by competition with *D. antillarum*.

Introduction

When intensive studies of the ecology of reef fishes began some 20 yr ago, populations of reef fishes were thought to be stable and controlled by intra- and interspecific competition (reviewed by Sale 1980). Data on the dynamics of reef-fish populations and the results of manipulative field studies led to this view being largely replaced by one which holds that populations tend not to be saturated, and that abundances tend to fluctuate and be controlled largely by variation in the recruitment of planktonic juveniles. More recently, attention has been directed to assessing how interactions, particularly intraspecific inter-

actions between benthic juveniles and adults, can dampen or compensate for effects of recruitment variation and influence or control population size (for reviews see Sale 1980, 1984, and Doherty and Williams 1988, 1989). Very few studies have experimentally examined whether the sizes of reef-fish populations may be limited by food supplies (e.g. Forrester 1990).

Prior to 1983, the echinoid *Diadema antillarum* was an abundant (densities up to 70 m⁻²) and conspicuous member of the macro-invertebrate fauna in shallow habitats on coral reefs throughout the Caribbean (Lessios 1988 a). Beginning early in 1983 on the coast of Panamá, mass mortalities of this sea urchin occurred at points throughout its geographic range (Lessios et al. 1984 a, b). Populations of *D. antillarum* in the present study area suffered a mass die-off in April–May of 1983, and, within several weeks, declined by about 95% from an initial average density of 3.5 m⁻² (Lessios et al. 1984 a). Those populations remained at <10% of the premortality level at the end of 1990 (Lessios 1988 b and personal communication).

Small-scale experiments performed prior to the die-off of *Diadema antillarum* indicated that this sea urchin might have substantial effects on the abundance and community structure of benthic algae on coral reefs, and that it was involved in food competition with herbivorous reef fishes (Ogden 1976, Wanders 1977, Williams 1981, Hay and Taylor 1985). The die-off of *D. antillarum* enabled researchers to examine in detail its previous impact on communities of benthic algae (Liddell and Ohlhorst 1986, Hughes et al. 1987, Carpenter 1988, Levitan 1988) and the feeding activity of herbivorous fishes (Carpenter 1988, 1990, Morrison 1988), and to assess whether populations of herbivorous fishes were numerically limited by food competition with this sea urchin (Carpenter 1990). A program of regular monitoring of adult populations and recruitment of three herbivorous surgeonfishes that I had begun on coral reefs in Panamá several years prior to the die-off enabled me to test the food-limitation hypothesis by determining whether their populations increased after the die-off.

* Mailing address: Unit 0948, APO AA, 34002-0948, USA

Materials and methods

Study area

The study area, off Punta de San Blas (9°34'N; 78°58'W) on the Caribbean coast of Panamá, has been described earlier (Robertson 1988), and is figured in Robertson (1987). Six discrete, isolated patch reefs (see Robertson 1988) were used in this study. They ranged from 0.15 to 0.67 ha in area.

Study organisms and their feeding ecology

The three species of Caribbean surgeonfishes, *Acanthurus coeruleus*, *A. chirurgus*, and *A. bahianus*, feed on benthic algae. Large individuals eat primarily small fleshy turf algae and filamentous algae, consuming at least 30 different genera, as well as spermatophytes. *A. chirurgus* and *A. bahianus* also ingest substantial quantities of sediment and detritus. Newly recruited juveniles feed mainly on small filamentous algae and detritus (Randall 1967, Clavijo 1974).

Juvenile *Acanthurus coeruleus* recruit onto hard reef substrata while those of the other two species are found primarily in habitats that contain only scattered coral and rock cover around the fringes of reefs, particularly in shallow back-reef areas and seagrass beds immediately adjacent to reefs. Newly recruited *A. coeruleus* are more solitary and sedentary than are recruits of the other two species, which often move around in small schools of up to a dozen or so individuals. Adults and large juveniles of all three species are mobile and frequently form schools when feeding on a reef. Such feeding schools may include all three species and contain up to ~100 individuals.

Casual observations indicated that, while *Acanthurus coeruleus* and *A. chirurgus* largely restrict their feeding to reef substrata, *A. bahianus* uses a broader range of feeding habitats and often feeds 10 to 15 m away from a reef in surrounding sand areas and seagrass beds. To confirm these observations, I made counts between 13.00 and 16.30 hrs, when these fishes feed actively, of the total number of adults of each species on 12 patch-reefs and the number of adults feeding on sand and seagrass areas surrounding each reef. The counts were made several years after the sea urchin die-off. I used these data to compare the proportions of the adult populations of each species that used off-reef feeding habitats.

Monitoring of adult populations and recruitment

While some studies of the population dynamics of reef fishes consider only total population size, others focus on the abundance of adults (see Forrester 1990 for review). From the standpoint of the ecology of a community, it may not matter at what stage each individual is in its life history, and total abundance may be the appropriate population parameter to consider. However, maturity marks the point at which an individual potentially becomes successful in an evolutionary sense. Since change in adult numbers provides an indication of change in the individual's chance of success, it is important to consider the dynamics of adult populations. Settlement of a juvenile fish from the oceanic environment onto a reef is another important transitional event in the individual's life history, since it marks the point at which benthic processes begin to act on the individual and the individual begins to contribute to the benthic population. In this study I restricted my attention to adults and juvenile recruits, i.e., fish that settled during the month preceding the census in which they were recorded.

The methods used to census adults and recruits are described in detail in an earlier study (Robertson 1988). Entire adult populations on each of the six study reefs were censused once a year, in September or October of 1978 and of 1981–1990, inclusive. Settlement of planktonic juveniles of all three species occurs year-round and recruits were censused monthly, just before full moon when there is

little settlement activity (own unpublished data). Censusing of recruits extended from November 1978 until November 1989, except during one 5 mo period in 1980, for which recruitment was estimated (see Robertson 1988).

Data analyses

Because some adults of all three surgeonfishes probably live for more than one year (Munro 1983), consecutive censuses of adults do not provide fully independent data points. To minimize this problem I used a Wilcoxon paired-sample test (T) that compared the mean number of adults present on each reef (derived from the annual censuses) before the die-off with the mean number present on the same reef after the die-off, with the six reefs providing six replicates. Since there was an expectation of a population increase following a release from competition I used a one-tailed test. I also compared the mean annual levels of recruitment on the study reefs before and after the die-off using the same test, in this case a two-tailed test since there was no expectation of any particular difference.

I compared the relative abundances of adults of the three species in seagrass and sand habitats using a Kruskal-Wallis ANOVA by ranks (in abundance), followed by nonparametric multiple comparisons of differences between each pair of species.

These analyses followed Sokal and Rohlf (1981) and Zar (1974).

Results

Usage of off-reef feeding habitats by the three surgeonfishes

On average, about half the population of adult *Acanthurus bahianus* on each patch-reef was found feeding in sand and seagrass areas around reefs during the part of the day when feeding activity is high. In contrast, feeding adults of *A. coeruleus* rarely ranged into off-reef habitats, while only ~15% (on average) of a local population of *A. chirurgus* did so (Table 1).

Changes in adult populations after the die-off of *Diadema antillarum*

The abundances of adults of all species combined were not consistently greater after the die-off (1983–1990) than before (1978–1982) [Fig. 1; Wilcoxon T ($n=6$), $P=0.1$]. However, while population sizes of *Acanthurus bahianus* showed no consistent pattern of change after the die-off [Fig. 2, Wilcoxon T ($n=6$), $P>0.25$], there were consistent increases in the mean population sizes of both *A. coeruleus* and *A. chirurgus* after that event [Fig. 2; two Wilcoxon T ($n=6$) tests, both $P<0.01$].

The mean numbers of *Acanthurus coeruleus* and *A. chirurgus* on all reefs combined increased by 2.5- and 1.6-fold, respectively, after the die-off (Fig. 1B). Levels of increase by both species varied considerably among the six reefs. While the numbers of both had increased markedly on some reefs within 6 mo of the die-off, on other reefs the populations did not increase noticeably until 3.5 yr after that event (Fig. 2). While the peak of total population size (on all reefs combined) of *A. chirurgus* had been reached within 6 mo of the die-off, the total

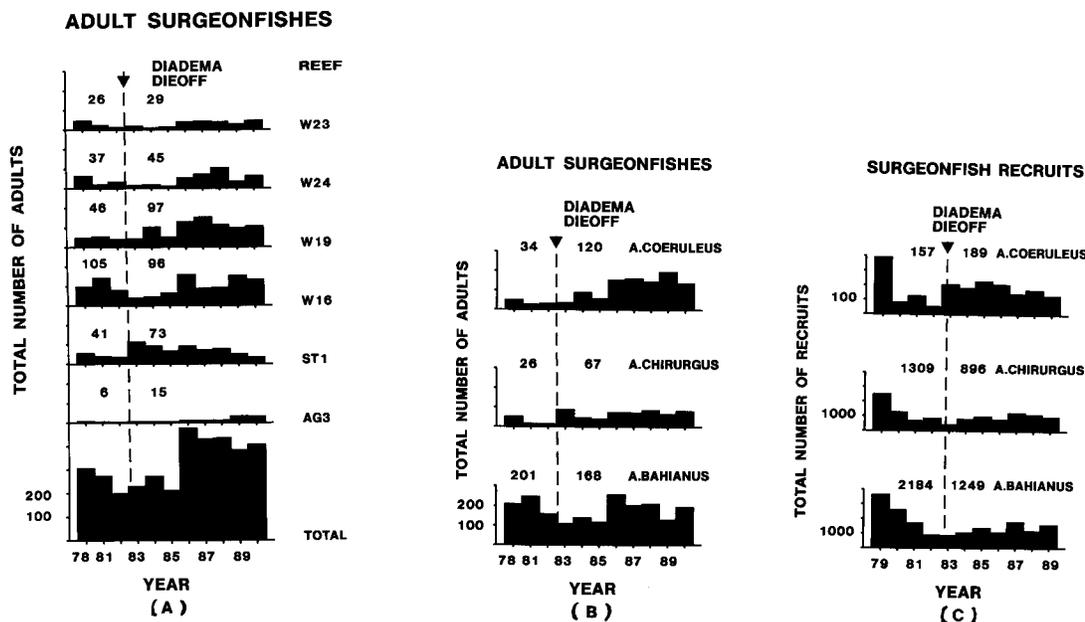


Fig. 1. *Acanthurus coeruleus*, *A. chirurgus* and *A. bahianus*. Change in adult populations and recruitment of three surgeonfishes. (A) Combined adult populations of all three species on each of the six patch reefs, and on all reefs combined; (B) total adult population of each species on all reefs combined; (C) total annual recruitment by each species on all reefs combined. Reefs are those described in an

earlier study (Robertson 1988). Values inside histograms are mean adult population per annual census (adults were not censused in 1979 and 1980) and mean annual recruitment level. Dashed line indicates timing of die-off of *Diadema antillarum* relative to census dates in 1983

	<i>A. coeruleus</i>	<i>A. chirurgus</i>	<i>A. bahianus</i>
Percent of adult population feeding in sand/seagrass			
per reef: median (range) ^a	0 (0-4)	8 (0-50)	49 (12-92)
total for all reefs	<1	14	47
Number of fish			
per reef: median (range)	20 (2-39)	11 (2-31)	28 (10-84)
total for all reefs	252	176	387

Table 1. *Acanthurus coeruleus*, *A. chirurgus* and *A. bahianus*. Abundances of adult surgeonfishes feeding in seagrass and sand surrounding 12 patch reefs

^a Kruskal-Wallis ANOVA by ranks: $\chi^2 = 18.8$, $P < 0.001$; nonparametric multiple comparisons: all three combinations differ at $P < 0.01$

population of *A. coeruleus* did not reach near its maximum level until several years later (Fig. 1 B).

Levels of recruitment before and after the *Diadema antillarum* die-off

There were no consistent differences in mean numbers of juveniles recruiting each year before (1979-1982) and after (1983-1989) the die off in any species (Fig. 2, Wilcoxon T ($n=6$), $P > 0.05$ in all three cases). Mean annual levels of recruitment by each species on all reefs combined did not differ before and after the die-off (Fig. 1, three T tests, using square-root-transformed data, each $P > 0.05$).

Discussion

Effects of *Diadema antillarum* on algal abundances

Small-scale experiments conducted prior to the die-off of *Diadema antillarum* at several Caribbean localities, in-

cluding the present study area, showed that grazing by that sea urchin reduced the abundance of small, fleshy turf algae that are eaten by herbivorous fishes, including surgeonfishes (Wanders 1977, Sammarco 1982, Foster 1985, 1987). At various Caribbean sites, the biomass of algae increased rapidly and markedly following the die-off, particularly in shallow habitats. The levels of those increases varied among localities. Filamentous algae, fleshy turf algae and macroalgae, including genera eaten by surgeonfishes, increased in abundance at the expense of crustose coralline algae (Liddell and Ohlhorst 1986, Hughes et al. 1987, Carpenter 1985, 1988, 1990, Levitan 1988). Increases in the biomass of soft algae were maintained, although not necessarily at maximum levels, for at least several years after the die-off (Carpenter 1988, Lessios 1988 a). Increases in the abundances of fleshy turf algae and macroalgae, including genera consumed by surgeonfishes, occurred on several reefs (one of which was used in the present study) at Punta de San Blas between 1983 and 1987 (Lessios 1988 a, M. J. Shulman and D. R. Robertson unpublished data). These increases, which ranged up to 30-fold, were unevenly distributed between reefs.

Surgeonfish population responses

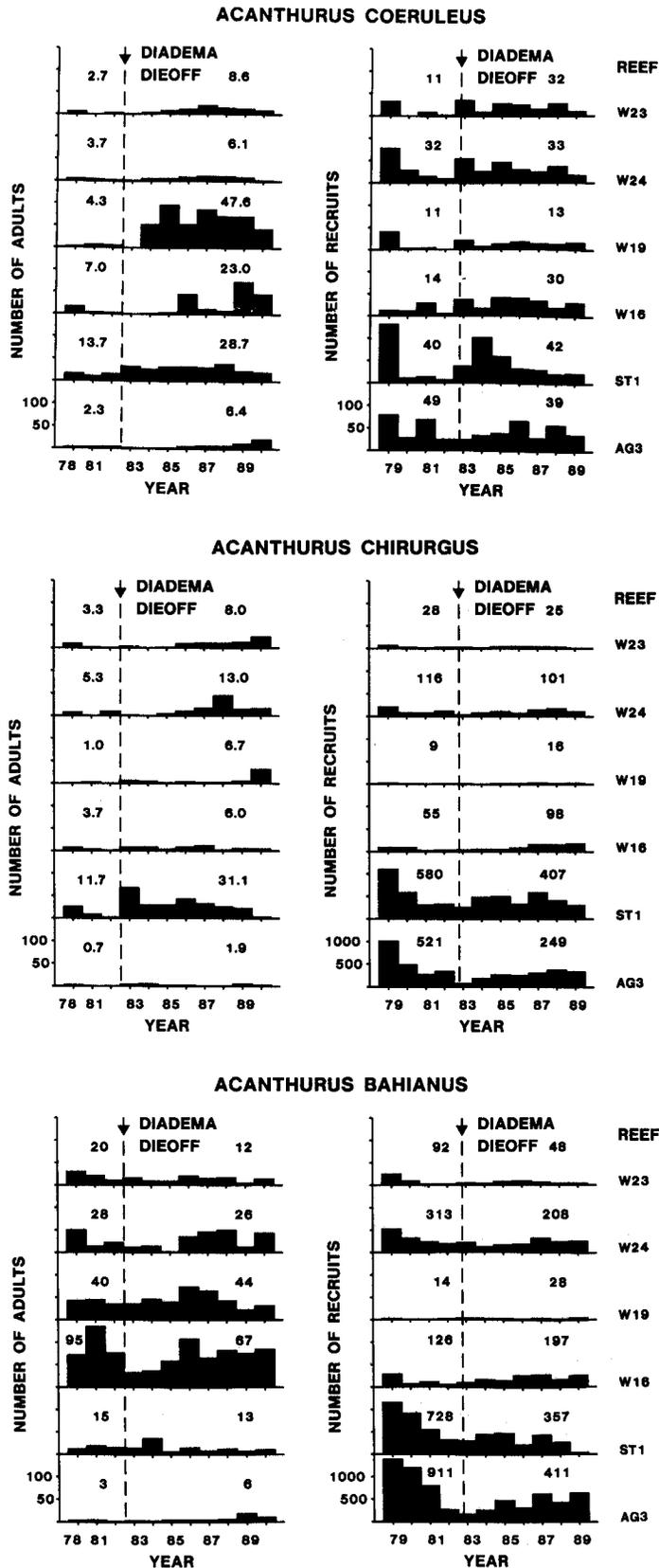


Fig. 2. *Acanthurus coeruleus*, *A. chirurgus* and *A. bahianus*. Abundances of adults and recruits of each species on each of six patch reefs before and after die-off of *Diadema antillarum*. For adults, data are numbers present during each annual census; for recruits, data are combined numbers from all monthly censuses in each year. Further details as in legend to Fig. 1

Following the die-off of *Diadema antillarum* in Panamá, adult populations of *Acanthurus coeruleus* and *A. chirurgus* increased, and did so without any concomittant increase in recruitment. These results support the hypothesis that those two species competed for food with *D. antillarum* (Hay and Taylor 1985) and that such competition limited their population sizes (Carpenter 1990). However, such population increases following the loss of a competitor do not preclude concomittant limitation of population size by both low recruitment and food availability either before or after that loss. The failure of adult populations of *A. bahianus* to increase in the absence of changes in levels of recruitment also is consistent with the competition hypothesis, since *A. bahianus* is much less reliant than its congeners on feeding habitats that previously were most affected by *D. antillarum*. While it is possible that these differences in habitat usage by the three surgeonfishes only developed after the die-off, analogous differences were documented at another site prior to the die-off: Lewis and Wainwright (1985) found that, in Belize, *A. bahianus* was concentrated in a reef habitat that contained low densities of *D. antillarum*, while the greatest densities of *A. coeruleus* and *A. chirurgus* occurred in reef habitats where *D. antillarum* was most abundant. Carpenter's (1990) data also indicate that (after the mortality of *D. antillarum*) the habitat distribution of *A. bahianus* differed from that of the other two species at St. Croix.

Increases in the adult populations of *Acanthurus coeruleus* and *A. chirurgus* in Panamá could have been due to a variety of factors, including increased survival and/or growth of juveniles, increased survivorship of adults, and changes in patterns of long-term relocations of fish between reefs. There was considerable variation among the six study reefs in the extent, timing and persistence of increases in the adult populations of *A. coeruleus* and *A. chirurgus*, and in patterns of change in abundance from year to year well after the die-off. Such variation may reflect variation in the quality of different reefs as habitats for the different species, variation in changes in algal communities (Lessios 1988 a), and relocation of fish between reefs (see Robertson 1988). Differences in the rates of increase of adult populations of *A. coeruleus* and *A. chirurgus* after the die-off may be due, in part, to differences in their relative rates of recruitment (i.e., the ratio of the annual level of recruitment to the size of the adult population), since relative recruitment rates were lower in the species that increased more slowly, *A. coeruleus* (Figs. 1 and 2). Whatever its precise cause, the delay in the general increase in populations of *A. coeruleus* indicates that the detection of population responses of long-lived organisms to "positive" changes in their environment may require long-term studies, particularly if the responses are not large.

Although levels of recruitment did not differ before and after the die-off in any species, I cannot exclude the possibility that *Diadema antillarum* affected the survivorship of newly settled surgeonfishes prior to the die-off. Since I censused recruits 1 to 2 wk after they had settled,

the lack of a change in recruitment after the die-off could, in part, reflect higher early survivorship of settlers. Mortality tends to be high in juvenile fishes during the first few days after settlement (Doherty and Sale 1986, Victor 1986, Sale and Ferrell 1988, Booth 1991), and newly recruited herbivorous reef fishes appear to starve in some situations (Tsuda and Bryan 1973).

The results of the present study complement and extend those obtained by Carpenter (1990) at St. Croix, in the northeastern Caribbean. Premortality densities and levels of mortality of *Diadema antillarum* were similar at St. Croix and Panamá (Lessios 1988a). Increases in the abundances of herbivorous fishes and their food algae occurred after the die-off at both sites, and the increases in the average abundances of surgeonfishes were similar at the two sites. However, unlike the situation in Panamá, it is unclear how increases in abundances of fishes at St. Croix were related to recruitment dynamics, since Carpenter did not monitor recruitment. Further, since Carpenter censused fish on transects in several different habitats within the same reef, we cannot distinguish between increases in abundance in a particular habitat due to redistributions of fish within that reef versus those due to increases in total population size on the entire reef. Because densities of *D. antillarum* used to vary considerably among different reef habitats (e.g. Lewis and Wainwright 1985, Morrison 1988), some spatial redistributions of fish in response to such a die-off might be expected (e.g. see Morrison 1988). The increases in abundances of adults of two species observed in Panamá, however, do reflect increases in the total sizes of their populations on entire reefs. While adult populations of the three species changed to differing degrees at Panamá, we do not know whether similar changes occurred at St. Croix, since Carpenter did not distinguish between juveniles and adults, and did not distinguish between the species in the premortality censuses.

We have no clear picture of how the increases in abundances of surgeonfishes in Panamá and St. Croix relate to responses of other members of the herbivorous fish community at either site. Carpenter (1990) recorded increases in the abundances of (unidentified) juvenile parrotfishes, and increases in the abundances of larger individuals of two out of five identified parrotfishes. However, data on the dynamics of the recruitment of those scarids are lacking. There are no data available on responses of the other major group of herbivorous reef fishes, the territorial damselfishes, to the die-off of *Diadema antillarum*. These fishes are abundant, are known to interact with that sea urchin (e.g. Williams 1981), and to aggressively exclude surgeonfishes and parrotfishes from their territories (e.g. Thresher 1976, Robertson 1984, Foster 1985).

Evidence for food limitation of reef fish populations

Existing data that bear on the question of whether the sizes of populations of reef fishes are food-limited concern population responses to both natural and manipulated changes in food supplies (Table 2). Two manipulative studies indicate that segments of populations of two

West Pacific plantivores are food-limited at one site (Table 2). Although food availability limits the growth of juveniles of a third species at that same site (Jones 1986), its effect on population size has not been investigated.

Three major natural events in recent years have produced substantial changes on large spatial scales in the abundances of two major classes of benthic foods (corals and algae) used by a variety of reef fishes. The results of studies of these events have been mixed and, in many cases, their relevance to the question of food limitation is difficult to interpret with confidence:

(1) Mass mortality of corals in the Eastern tropical Pacific during the 1982–83 El Niño event appeared to have no effect on populations of one corallivorous pufferfish (Guzman and Robertson 1989). One territorial, herbivorous damselfish showed no apparent response to a large increase in the availability of apparently suitable habitat and substrata for algal growth following that mortality (Wellington and Victor 1985). However, while these results are consistent with a lack of food limitation, there is no information on the dynamics of those populations either before or after the event and on how those dynamics related to recruitment dynamics.

(2) Mass coral mortality due to predation by a starfish produced substantial declines in populations of obligate corallivores at three Central and West Pacific sites. However, there were few increases in populations of herbivores and, in fact, one study found that populations of many herbivores declined (Williams 1986). Conclusions about the causes of a general lack of increase in herbivore abundances are limited by the absence of data on changes in the abundance of food algae, by various aspects of the designs of those studies and, in one case, by confounding effects of structural degradation of habitats. Only one study related population responses to patterns of recruitment. Bouchon-Navaro et al. (1985) noted low recruitment of juvenile corallivores as well as declines in their overall population densities after the coral die-off. However, it is unclear whether such low recruitment reflected a decline in actual settlement or the effects of resource changes on the juveniles.

(3) One small-scale study did not detect an effect of mass mortality of *Diadema antillarum* on a population of one of its specialized predators, which switched to other prey after the urchin die-off (Table 2). The die-off of *D. antillarum* produced increases in the abundances of food algae for herbivorous reef fishes, and increases in the populations of some fishes that were likely to have competed with this sea urchin. Since those increases were not related to temporal fluctuations in recruitment at at least one site, population sizes do seem to have been food-limited. Interpretation of the results of both herbivore studies is hindered by the lack of proper controls.

These studies provide varying amounts of information about the extent and mechanisms of food limitation of populations of reef fishes. While the response of a population to a severe reduction in a food source can show whether the species concerned was an obligate specialist-consumer of that food, we need to know the size of the population change in relation to the size of the food decrease in order to assess whether population size was

Table 2. Effects of change in food abundance of reef fishes, as reported in the literature. +: increase, -: decrease; (+), (-): increase, decrease in habitat availability also. "Effect" column shows, in parentheses, no. of species affected/total number of species. In "Source" column, conclusions about effects of food change on population may be limited, due to (a) lack of concurrent controls; (b) lack of "before/after" comparison; (c) no data on "before"

and "after" population fluctuations; (d) no data on relation of population change to recruitment fluctuations; (e) short-term and/or small-scale study; (f) result could reflect redistributions of fish and/or population change; (g) change in food abundance not measured; (h) method of measurement insensitive to non-extreme population change; (i) effect probably also due to change in habitat structure

Locality and resource	Event	Food change	Type of consumer	Effect	Source	
Caribbean Sea						
Algae	} <i>Diadema</i> sp. removed	+	surgeon- and parrotfishes	increased <i>local</i> density (?)	Hay and Taylor (1985) (e, f)	
Algae		+	surgeon- and parrotfishes	incr. local density (3/3 and 2/5)	Carpenter (1990) (a, c, d, e, f)	
Algae		} <i>Diadema</i> sp. die-off	+	surgeonfishes	incr. adult populations (2/3)	Present study (a)
<i>Diadema</i> sp.			-	toadfish	no apparent change (1/1)	Robertson (1987) (a, c, d, e)
East Pacific						
Coral	} El Niño coral kill	-	pufferfish	no apparent effect (1/1)	Guzman and Robertson (1989) (a, c, d)	
Algae		+ (+)	damsel fish	no change in total density (1/1)	Wellington and Victor (1985) (a, c, d, g)	
Tahiti						
Coral	}	- (-)	butterflyfishes	decreased total abundance (10/10)	Bouchon-Navaro et al. (1985) (a, c)	
Australia		} <i>Acanthaster</i> sp. coral predation	- (-)	butterflyfishes	decreased total abundance (4/6)	Williams (1986) (c, d, h)
Coral			+ (+)	herbivores	few increases in total abundance (2/38)	Williams (1986) (g, h)
Algae		}	- (-)	corallivores	decreased <i>local</i> abundance (6/6)	} Sano et al. (1984) (b, c, d, e, f, g, i)
Okinawa	+ (+)		herbivores	few increases in <i>local</i> abundance (2/8)		
Australia						
Plankton	Competitors removed	+?	damsel fish	increased juvenile abundance (1/1)	Thresher (1983) (e, g)	
Plankton	Food added	+	damsel fish	incr. adult density (1/1)	Forrester (1990)	

food-limited. If recruitment remains unchanged, an increase in population size following an increase in the food supply does show that the pre-existing population was food-limited. A population increase in response to the loss of a species that shared the same food supply (e.g. *Diadema antillarum*) indicates the mechanism of that food limitation (i.e., competition). Only one experimental study has measured the effects of food limitation on juvenile growth and survivorship and, hence, on adult population size (Forrester 1990).

So few comprehensive data are available at present that we can say little more than that food limitation does appear to occur in a few species, and that the evidence that it does not affect the populations of others is equivocal in almost all cases. There is an obvious need for detailed, multiyear, experimental studies on a range of fishes that consume different types of food and may experience food limitation by a variety of different mechanisms. However, natural "experiments" such as that discussed here can complement small-scale manipulative studies. The significance of natural events may be difficult to interpret with rigor, since realistic, precise controls may be impracticable, and a substantial set of "before" data on population dynamics often will be unobtainable. However, such events have the advantage of involving much larger changes in resource availability on much larger spatial scales than can be achieved with manipulative experiments, and of potentially having community-wide impacts. Thus, they have a much broader scope than manipulative experiments can achieve.

Acknowledgements. This research was supported by funds from the Smithsonian Institution (Scholarly Studies Program) and by STRI's general research funds. The Government of the Republic of Panamá and the Kuna General Congress permitted research in San Blas. J. Brawn, J. Christy, H. Lessios, M. Shulman and two anonymous referees provided useful comments on the manuscript.

Literature cited

- Booth, D. J. (1991). The effects of sampling frequency on estimates of recruitment of the domino damselfish *Dascyllus albisella* Gill. *J. exp. mar. Biol. Ecol.* 145: 149–159
- Bouchon-Navaro, Y., Bouchon, C., Harmelin-Vivien, M. (1985). Impacts of coral degradation on a chaetodontid fish assemblage (Mooréa, French Polynesia). *Proc. 5th int. coral Reef Congr.* 5: 427–432 [Gabrie, C. et al. (eds.) Antenne Museum-EPHE, Moorea, French Polynesia]
- Carpenter, R. C. (1985). Sea urchin mass mortality effects on reef algal abundance, species composition and net metabolism and other coral reef herbivores. *Proc. 5th int. Coral Reef Congr.* 4: 53–60 [Gabrie, C. et al. (eds.) Antenne Museum-EPHE, Moorea, French Polynesia]
- Carpenter, R. C. (1988). Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. *Proc. natn. Acad. Sci. U.S.A.* 85: 511–514
- Carpenter, R. C. (1990). Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. *Mar. Biol.* 104: 79–86
- Clavijo, I. (1974). A contribution on feeding habits of three species of acanthurids (Pisces) from the West Indies. M. Sc. thesis. Florida Atlantic University, Boca Raton
- Doherty, P. J., Sale, P. F. (1986). Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* 4: 225–234
- Doherty, P. J., Williams, D. McB. (1988). The replenishment of coral reef fish populations. *Oceanogr. mar. Biol. A. Rev.* 26: 487–551
- Doherty, P. J., Williams, D. McB. (1989). Are local populations of coral reef fishes equilibrium assemblages? The empirical database. *Proc. 6th int. coral Reef Symp.* 1: 131–139 [Choat, J. H. et al. (eds.) Sixth International Coral Reef Symposium Executive Committee, Townsville]
- Forrester, G. E. (1990). Factors influencing the juvenile demography of a coral reef fish. *Ecology* 71: 1666–1681
- Foster, S. A. (1985). Size dependent territory defense by a damselfish. A determinant of resource use by group-foraging surgeonfishes. *Oecologia* 67: 499–505
- Foster, S. A. (1987). The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*: effects of habitat and surge. *J. exp. mar. Biol. Ecol.* 105: 1–20
- Guzman, H. M., Robertson, D. R. (1989). Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. *Mar. Ecol. Prog. Ser.* 55: 121–131
- Hay, M. E., Taylor, P. R. (1985). Competition between herbivorous fishes and urchins in Caribbean reefs. *Oecologia* 65: 591–598
- Hughes, T. P., Reed, D. C., Boyle, M. J. (1987). Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J. exp. mar. Biol. Ecol.* 113: 39–59
- Jones, G. P. (1986). Food availability affects growth in a coral reef fish. *Oecologia* 70: 136–139
- Lessios, H. A. (1988a). Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *A. Rev. Ecol. Syst.* 19: 371–393
- Lessios, H. A. (1988b). Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panamá. *Mar. Biol.* 99: 515–526
- Lessios, H. A., Cubit, J. D., Robertson, D. R., Shulman, M. J., Parker, M. R., Garrity, S. D., Levings, S. C. (1984a). Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs* 3: 173–182
- Lessios, H. A., Robertson, D. R., Cubit, J. D. (1984b). Spread of *Diadema* mass mortality through the Caribbean. *Science, N.Y.* 226: 335–337
- Levitan, D. R. (1988). Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at St. John, US Virgin Islands. *J. exp. mar. Biol. Ecol.* 119: 167–178
- Lewis, S. M., Wainwright P. (1985). Herbivore abundance and grazing intensity on a Caribbean coral reef. *J. exp. mar. Biol. Ecol.* 87: 215–228
- Liddell, W. D., Ohlhorst, S. L. (1986). Changes in benthic community composition following the mass mortality of *Diadema* in Jamaica. *J. exp. mar. Biol. Ecol.* 95: 271–278
- Morrison, D. (1988). Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* 69: 1367–1382
- Munro, J. L. (1983). Epilogue. In: Munro, J. L. (ed.) *Progress in coral reef fisheries research, 1973–1982*. Caribbean Coral Reef Fisheries Resources ICLARM, Manila, p. 249–265
- Ogden, J. C. (1976). Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquat. Bot.* 2: 103–116
- Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Stud. trop. Oceanogr.* 5: 665–847
- Robertson, D. R. (1984). Cohabitation of competing territorial damselfishes on a Caribbean coral reef. *Ecology* 65: 1121–1135
- Robertson, D. R. (1987). Responses of two coral reef toadfishes (Batrachoididae) to the demise of their primary prey, the sea urchin *Diadema antillarum*. *Copeia* 1987: 637–642
- Robertson, D. R. (1988). Abundances of surgeonfishes on patch-reefs in Caribbean Panamá: due to settlement, or post-settlement events? *Mar. Biol.* 97: 495–501
- Sale, P. F. (1980). The ecology of fishes on coral reefs. *Oceanogr. mar. Biol. A. Rev.* 18: 367–421
- Sale, P. F. (1984). The structure of communities of fish on coral reefs and the merit of a hypothesis-testing manipulative approach to

- ecology. In: Strong, D. R., Simberloff, D., Abele, L. G., Thistle, A. B. (eds.) *Ecological community: conceptual issues and the evidence*. Princeton University Press, Princeton, N. J., p. 478–490
- Sale, P. F., Ferrell, D. J. (1988). Early survivorship of juvenile coral reef fishes. *Coral Reefs* 7: 117–124
- Sammarco, P. W. (1982). Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *J. exp. mar. Biol. Ecol.* 65: 83–105
- Sano, M., Shimizu, M., Nose Y. (1984). Changes in the structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. *Pacif. Sci.* 38: 51–79
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry*. 2nd ed. The principles and practice of statistics in biological research. W. H. Freeman & Co., San Francisco
- Thresher, R. E. (1976). Field analysis of the territoriality of the threespot damselfish, *Eupomacentrus planifrons* (Pomacentridae). *Copeia* 1976: 266–276
- Thresher, R. E. (1983). Habitat effects on reproductive success in the coral reef fish, *Acanthochromis polyacanthus* (Pomacentridae). *Ecology* 64: 1184–1199
- Tsuda, R. T., Bryan, H. T. (1973). Food preference of juvenile *Siganus rostratus* and *S. spinus* in Guam. *Copeia* 1973: 604–606
- Victor, B. C. (1986). Larval settlement and juvenile mortality in a recruitment-limited coral reef-fish population. *Ecol. Monogr.* 56: 145–160
- Wanders, J. W. B. (1977). The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) III: The significance of grazing. *Aquat. Bot.* 3: 357–390
- Wellington, G. M., Victor, B. C. (1985). El Niño mass coral mortality: a test of resource limitation on a coral reef damselfish population. *Oecologia* 68: 15–19
- Williams, A. H. (1981). An analysis of competitive interactions in a patchy back reef environment. *Ecology* 62: 1107–1120
- Williams, D. McB. (1986). Temporal variation in the structure of reef slope fish communities (Central Great Barrier Reef): short-term effects of *Acanthaster planci* infestation. *Mar. Ecol. Prog. Ser.* 28: 157–164
- Zar, J. H. (1974). *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey