

El Niño mass coral mortality: a test of resource limitation in a coral reef damselfish population

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Summary. The mass mortality of reef corals in the eastern Pacific as a result of the 1982–1983 El Niño oceanographic anomaly permitted the first large scale test of resource limitation for a coral reef fish. Population densities of territorial herbivorous damselfish did not respond to the massive regional increase in space available for the cultivation of algal food following the El Niño event. The proportion of juveniles in the population was low and new recruits were uncommon, indicating that recruitment rates rather than resource supply probably control the abundance of this coral reef damselfish.

In 1982–1983 a massive and well-documented oceanographic anomaly, the El Niño Southern Oscillation (El Niño), occurred in the tropical Pacific ocean. For a period of fifteen months starting in June 1982 the normally westward flowing equatorial current slowed and then reversed itself (Firing et al. 1983; Halpern et al. 1983; Philander 1983). Among many other oceanographic and meteorological effects, sea surface temperatures in the eastern Pacific reached 30–32° C (2 to 4° C above normal highs), and remained elevated for several months. These unusually high temperatures resulted in the reduction of huge stocks of pelagic fishes, reproductive failure and high mortality among seabirds and marine mammals (Schreiber and Schreiber 1983; Barber and Chavez 1983), and the widespread death of large tracts of reef corals (Lessios et al. 1983; Glynn 1983, 1984). Large-scale natural disturbances, such as El Niño and the recent Hurricane Allen (Woodley et al. 1981), provide excellent opportunities for testing ecological hypotheses that require massive manipulations beyond the abilities of investigators.

There is at present a major disagreement over the conditions determining population sizes and the maintenance of diversity in coral reef fishes. The traditional view holds that coral reef fish communities exist at or near equilibrium, are relatively stable, and characterized by fine specializations due to present or past competition for limited supplies of food and space (Roughgarden 1974; Smith 1978; Anderson et al. 1981; Gladfelter and Johnson 1983; Ebersole 1985). An explicit assumption here is that populations exist

at, or near the carrying capacity of the environment sufficiently long for competition to be an evolutionary force. Other views hold that coexistence need not require differential competitive abilities or niche diversification even though populations may be limited by their resources. These explanations include chance recruitment, or the 'lottery hypothesis' (Sale 1977), density-dependent stock/recruitment relationships (Sale 1982; cf. Abrams 1984), and stochastic variation in rates of mortality and births (Chesson and Warner 1981). Several recent studies have indicated that rather than being limited by the supply of resources, reef fish populations may be controlled by the availability of larval recruits (Williams 1980; Victor 1983; Doherty 1983). Their findings challenge those explanations for species coexistence that require some form of resource limitation. These studies to date, however, have been limited to small-scale manipulations and thus potentially subject to random spatial variation not indicative of regional or global patterns.

The mass mortality of reef corals in the eastern Pacific associated with the 1982–1983 El Niño event resulted in a massive regional increase in available substrate and algal food for resident damselfish. This large-scale event provided a unique opportunity to test the hypothesis that these reef fish were resource limited. The purpose of this study therefore was to document how a massive increase in resources affected damselfish population on Contadora Reef (Pacific, Panamá). Using pre-El Niño (1979) census data for comparison, we predicted an increase in damselfish populations if space were previously limiting. Alternatively, little or no change might be expected if populations were controlled by factors unrelated to resource abundance, such as recruitment from the plankton or predation.

Materials and methods

Study site and species

The study site was located on a fringing reef on the southwestern corner of Isla Contadora (8°37'23" N; 79°02'31" W), Perlas Archipelago in the Gulf of Panamá. The reef forms a veneer approximately 0.6 m thick over a series of juxtaposed tuffaceous sandstone ridges and is approximately 3.2 ha in extent (Wellington 1982). The branching coral, *Pocillopora damicornis* forms a near-monotypic cover in shallow water (reef flat and slope zones) from -0.5 to -0.6 m (MLWS) while scattered colonies

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of massive corals, *Pavona gigantea* are predominant at the reef base (-7.0 to -10.0 m MLWS). Prior to El Niño, living *Pocillopora* colonies comprised 80–85% of the substrate covering the reef flat and slope (Wellington 1982).

The Acapulco damselfish, *Stegastes* (= *Eupomacentrus*) *acapulcoensis* (Fowler) is one of the most abundant residents on coral reefs in the tropical eastern Pacific, ranging from lower Baja California to Peru (Thomson et al. 1979). These fish are herbivorous and territorial, and cultivate mats, or gardens of algae, on rock and dead coral substrates. The algal mat, approximately 0.12 m² in area, is used for food and nesting sites, and is vigorously defended from conspecifics, other herbivores (e.g. parrotfish) and egg predators (e.g. wrasses and pufferfish). Damselfish also defend the surrounding area to a radius of 1 m from the algal mat. While the algal mats themselves are exclusive, adjacent conspecifics will share defended surrounding areas. The potential upper limit to population size is therefore determined by the size of the algal mat and not the area of the entire territory per se (Wellington 1982).

Sampling procedures

Densities of coral cover were estimated along linear transect lines placed parallel to depth contours on the reef flat and slope. Using a 30 m plastic fiber tape draped over the substrate, the proportion of living and dead coral was calculated from the linear distances covered by each substrate in contact with the tape. The transects surveyed in 1984 (post-El Niño) were compared with those taken in the same areas during 1979 (pre-El Niño) (Wellington 1982).

Since adult damselfish maintain discrete, nonoverlapping algal mats (one mat per fish), densities were estimated by counting the number of algal mats which occurred, either partially or entirely, within 0.5 m on either side of the transect line (Wellington 1982). The number of recently settled juveniles (≤ 20 mm standard length), easily spotted because of their bright blue coloration, were counted along these same transects.

Topographic complexity

To determine whether the mass coral mortality altered the availability of refuge sites, we compared pre-El Niño (1979) topographic complexity values with those of post-El Niño (1984) from the same areas on the reef. In 1984, we also measured and compared the topographic complexity and densities of damselfish in areas of both high and low live coral cover immediately adjacent to one another to determine if changes in the amount of substrate for algal mats or topographic complexity, or both had an effect on damselfish abundance.

Shelter sites were estimated by measuring the topographic complexity of the substratum. The index of topographic complexity used is defined by the formula: $1 - L_i/L_c$, where L_i equals the minimum distance between two points measured with a plastic tape and L_c the maximum distance measured with a chain transect (88 links/m). Values approaching zero indicate low topographic complexity, while those approaching unity indicate greater complexity.

Size and age distribution of damselfish

The standard lengths of all damselfish encountered along a transect line passing through the reef flat, slope and base

of Contadora Reef were visually estimated (to the nearest 5 mm) and recorded. Twenty damselfish of various sizes were collected and two of the three pairs of otoliths were removed from these individuals. The sagittae, the largest pair, were extracted from the floor of the braincase, while the mid-sized pair, the lapilli, were removed from the sides of the cranium. The otoliths were cleaned, dried, and placed in a drop of immersion oil on glass slides. Otoliths that were not clear (mainly those from larger fish) were ground by hand on a glass plate with Carborundum grit 600 in immersion oil.

The age of each individual was determined by counting the number of daily incremental marks on the otolith (Victor 1982). The upper limit of the length of the larval life for this species was estimated as the age of the smallest individuals encountered, which were about 10 mm standard length. Since *Stegastes* species in the Caribbean settle at about 8–10 mm (Victor, unpublished data), it is very likely that these individuals were newly recruited.

Results

Changes in coral cover and damselfish densities

Coral mortality during the 1982–1983 El Niño event was widespread and severe throughout the tropical eastern Pacific region (Glynn 1984). Bleaching (the expulsion of endosymbiotic zooxanthellae) of corals with subsequent tissue death and skeletal fouling was first observed on the Contadora reef (Gulf of Panamá) in June 1983. By July, only a small percentage of corals remained alive (Glynn 1984).

A previous study at this site indicated that living pocilloporid corals, which had dominated the reef flat and slope zones, provided an abundance of shelter sites but limited the establishment of extensive algal gardens (Wellington 1982). A high percentage of living corals left few areas available for algal mats, hence corals were often killed by damselfish in order to create hard surfaces to establish algal gardens. Observations revealed that densities of damselfish were higher in areas with access to nonbranching corals. Massive pavonid corals were easier to kill than branching pocilloporid species and less effort was probably required to maintain an algal mat since branching corals could rapidly recover from damselfish damage. However, these nonbranching corals only represented 1 to 2% of the live coral cover in shallow water (< 7 m depth). Therefore, areas available for algal gardens appeared to be potentially limiting, at least locally. We predicted that if resources were limiting, damselfish populations in the now mostly dead tracts of coral would have increased in response to this massive increase in available substrate and the supply of algal food.

Live coral cover in November 1979 was high ($79.8 \pm 13.4\%$ of the substrate, $n=8$), yet by November 1984 it was very low ($3.9 \pm 1.9\%$, $n=11$; significantly different, $P < 0.001$, Mann-Whitney U-test) (Fig. 1). Damselfish densities, however, had not changed significantly between the 1979 and 1984 censuses, despite the more than four-fold increase in available substrate now covered with a dense algal turf. In 1979 there were 0.35 damselfish per m² (S.E. = 0.04, $n=12$ transects) while in 1984 there were 0.42 damselfish per m² (S.E. = 0.03, $n=17$ transects; $P > 0.10$, Mann-Whitney U-test). At the reef base (10 m depth), where live coral cover had averaged 16% and damselfish densities

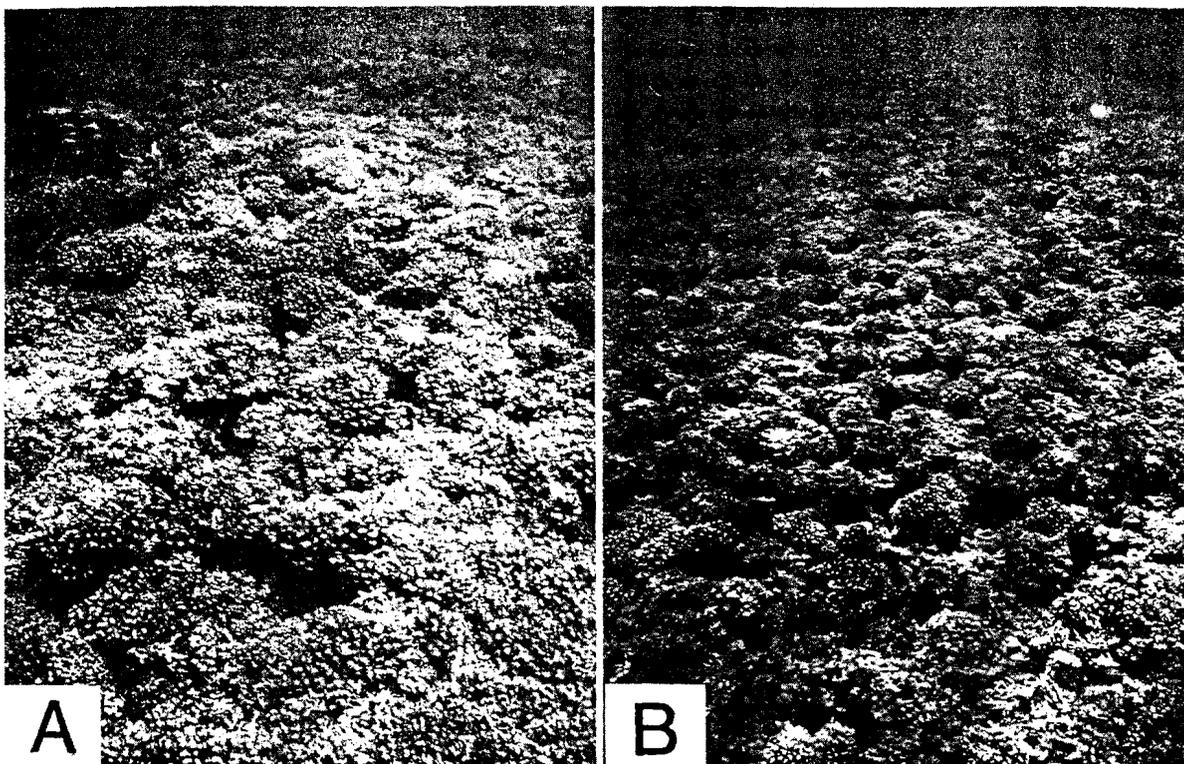


Fig. 1A, B. The reef slope at Contadora Reef, Panamá dominated by living pocilloporid corals in November 1979 A. During the 1982-83 El Niño event these corals suffered high mortality. By November 1984, the dead coral skeletons were covered with a dense mat of algae B. A few surviving colonies can be seen at the bottom of photograph B

were 0.13 per m^2 (S.E. = 0.03, $n=4$ transects), live coral cover was reduced to about 6%, but damselfish densities remained about the same (0.14 per m^2 , S.E. = 0.03, $n=4$ transects; $P > 0.25$, Mann-Whitney U-test).

A few areas of the Contadora reef still have patches of high coral cover despite the widespread devastation in the eastern Pacific. Presumably, some areas were not exposed to lethally high temperatures, and, since corals are capable of regeneration if some parts of the colony escape destruction (Glynn 1976; Highsmith 1982), these areas are rapidly returning to original levels of live coral cover. These live patches (up to 100 m^2 in extent) are often just a few meters away from dead tracts of coral, permitting a simultaneous comparison of damselfish densities in areas with different proportions of live coral cover. We found that damselfish densities within patches with approximately 80% live coral cover were virtually the same as in adjacent areas with <1% live coral cover (Table 1). These results also indicate that substrate on which to cultivate an algal garden is apparently not a limiting resource.

Topographic complexity

The seemingly incongruous finding that damselfish are not utilizing dead tracts of coral to any greater degree than they utilize mostly living tracts could be explained if these dead coral tracts now provide sufficiently less shelter to make up for the advantages of increased supplies of substrate available for food production. Measurements of the structure within live coral cover areas and adjacent tracts do not support this hypothesis; dead coral tracts had identical topographic complexity values to those measured in ar-

Table 1. Densities of damselfish (*Stegastes acapulcoensis*) and associated topographic complexity in areas of high live coral cover: 80.6% (S.E. = 1.75, $n=10$ transects), and low live coral cover: 0.9% (S.E. = 0.86, $n=10$ transects) on the reef slope at Contadora. Censuses were conducted in November 1984 and indicate no differences in either damselfish densities or topographic complexity in areas of high versus low live coral cover. Error limits represent standard error of the mean and sample sizes are based on 10 m^2 transects. Significance level based on Mann-Whitney U-test

| | Live coral cover | | Significance |
|--|-------------------------------|-------------------------------|--------------|
| | High | Low | |
| Damselfish densities (individuals/ m^2) | 0.32 ± 0.13 ($n=10$) | 0.33 ± 0.20 ($n=10$) | $p > 0.5$ |
| Topographic complexity ^a | 0.42 ± 0.02 ($n=7$) | 0.42 ± 0.01 ($n=7$) | $p > 0.75$ |

^a For definition see Methods section

reas with over 80% live coral cover (Table 1). Similar results were obtained for comparisons of topographic complexity measured on the same transects before and after El Niño (1979: 0.40, S.E. = 0.09; 1984: 0.41, S.E. = 0.05, $n=11$ and 16 transects respectively; $P > 0.25$, Mann-Whitney U-test). The only observable difference between dead and predominantly live areas of reef was the proportion of the substrate covered with algae. Since many areas of now-dead coral substrate are not occupied by any damselfish at all, it is likely that damselfish populations are low enough that even areas with high coral cover provide sufficient amounts of

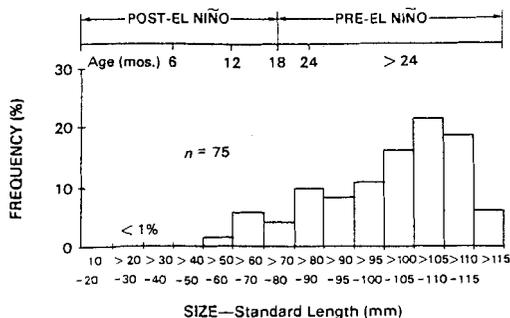


Fig. 2. Size-frequency distribution of *Stegastes acapulcoensis* at Contadora Reef in November 1984. This population is skewed towards larger size classes; less than 1% of the population was composed of fish smaller than 50 mm S.L. Ages were determined from counts of daily increments on otoliths. These estimates indicate that only 12% of the population recruited since the El Niño event ("post-El Niño") while 88% were present at or before coral mortality occurred ("pre-El Niño")

dead coral substrate to support typical densities of damselfish.

Size and age distribution of damselfish

Our analysis of the daily increments on the otoliths of damselfish on Contadora Reef indicated that this species has a short larval life. New recruits (about 10 mm SL) were only one month old. Juveniles reached 40 mm SL within their first six months on the reef and 60 mm SL by the end of a year. By the end of their second year on the reef, Acapulco damselfish had attained about 85 mm SL. Larger individuals were significantly older, however, the older otolith increments on these fish became extremely narrow and were often interrupted, such that accurate age determinations were impossible. This is a common problem for older and larger fishes and is presumably a result of greatly reduced growth rates.

If there were a numerical response to an increase in food resources, we would expect to find a large proportion of young (<16 mos) damselfish in the population. The size and age structure of the damselfish population on Contadora Reef in 1984 suggests a possible answer for why damselfish populations have not increased. The majority of the population were full-sized adults, well over two years old, while individuals under eighteen months of age (those less than 75 mm) accounted for only 12% of the population (Fig. 2). New juvenile recruits, less than about one month old, were extremely uncommon with fewer than one per 100 m² ($n=17$ transects), even though our censuses were conducted during what should have been the peak recruitment season (since the planktonic larval duration is one month and peak spawning occurs between September and November, D.R. Robertson, pers. comm.). It appears, then, that there was a short supply of planktonic larval recruits to this reef.

Discussion

These findings indicate that damselfish populations have not responded to the large-scale increases in suitable substrate made available by El Niño coral mortalities. The paucity of newly-settled juvenile recruits and the low

numbers of post-El Niño juveniles in the population support the hypothesis of a recruitment-limited population. We contend that sixteen months, since the coral mortality occurred, should have been sufficient time for a response since these damselfish have high fecundity (several thousand eggs per clutch) (Thresher 1984, p. 168), reproduce over an extended season (pers. obs.), and spend only a short time as larvae in the plankton.

While recruitment limitation is suggested here as the mechanism controlling population size we cannot dismiss alternative possibilities that a population increase may have been prevented by other factors such as high juvenile mortality. However, since new recruits were rare in the population it is most likely that the population is being limited during the planktonic stage. Regardless of the exact mechanism, the absence of a numerical response to such a large increase in resources is strong evidence that adult populations of Acapulco damselfish may exist well below the carrying capacity of the reef.

Recent studies in Australia have shown that experimentally reducing the densities of damselfish on patch reefs has no effect on the subsequent recruitment of juveniles, indicating that density-dependent factors may not limit the size of damselfish populations on this small experimental scale (Williams 1980; Doherty 1983). Furthermore, experimental reductions of habitat on Caribbean patch reefs have shown that neither areas for algal mats nor refuge sites are limiting adult populations of damselfish (Robertson et al. 1981). Our study widens the scope of these investigations to a large geographic scale; even regional increases in the supply of food and space, probably to the entire population of a species, do not apparently result in a population increase after 16 mos. It is important to note that damselfishes, because of their dependence on the substrate for food, their pronounced territoriality, and their extreme relative abundance, would be the most likely of reef fishes to have their population size limited by the supply of food and space. The finding that these fishes in particular are limited not by resources but probably by the supply of larval recruits suggests that resource-limitation may be more the rare exception than the rule for coral reef fish populations.

While these data show that populations of *S. acapulcoensis* are not likely to be limited by their resources, our findings should not be interpreted to mean that intra- or interspecific competition does not occur, or is unimportant. Some explanations for species coexistence and maintenance of diversity assume that reef fish populations exist at carrying capacity and are subject to competition for limited resources. Examples of space (Waldner and Robertson 1980; Robertson and Lassig 1980; Ebersole 1985) and food partitioning (Gladfelter and Johnson 1983) provide some evidence in support of this view. Is it possible, however, for competition to be an importance evolutionary force when populations are limited by recruitment, as indicated here, or by juvenile mortality? We think so. If resources vary in quality, competition, either within or between species, is possible even if populations are not at or near their carrying capacity. For example, the quality of resources available to damselfish may not be uniform over the entire reef; shallow water algal mats appear to be more productive per unit area than those in deeper water (pers. obs.). In theory, when resource quality varies in a predictable manner and it confers differential fitness, we see no reason why intraspe-

cific and interspecific competition could not occur within recruitment limited populations. This situation could eventually lead to resource partitioning and specialization in habitat or food.

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