

A NEW RECORD OF ANEMONE BARRENS IN THE GALÁPAGOS

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Continuous carpets of the anemone *Aiptasia* sp. were recorded on vast areas of shallow reef platforms along the eastern shore of Fernandina Island in December 2000 and March 2001. The *Aiptasia* sp. carpets have replaced diverse assemblages of algae, invertebrates, and fishes that once characterized these platforms. Virtually the only other mega-invertebrate that persists in these areas is the pencil urchin *Eucidaris thouarsii*. Patches of the alga *Padina* sp. are occasionally present, although somewhat covered with *Aiptasia* sp. anemones. Fishes are very low in abundance and diversity. Hence, we describe the anemone-dominated habitat as anemone barrens—the term barrens has been applied previously in many parts of the world to habitats of similarly reduced diversity created by high densities of grazing sea urchins. We define anemone 'barrens' as areas of considerably reduced diversity (of species, or biogenic structure, or both) caused by the unchecked spread of a single species or guild, or by an exotic agent of disturbance, or both. Like urchins in urchin barrens, a carpet of anemones might have a high biomass. Anemone barrens might also have moderate levels of primary production due to symbiotic zooxanthellae in *Aiptasia* anemones (Muller-Parker 1984). Extending the comparison, urchin barrens also have moderate levels of primary production due to algal turfs and microphytobenthos.

The upper depth limit of the anemone zone was about 1.5 m, and the greatest depth was 15 m where rock gave way to sand. At Punta Espinosa on the northeastern corner of Fernandina, two of the authors (SAS and TAO) noted that the anemones covered most of the inner part of the bay at depths from 2 to 10 m. While being towed from west to east toward Punta Espinosa and using a diver's benthic sled to maintain a depth of 5 to 7 m, we observed that the upper depth limit of the barrens deepened as exposure to oceanic swell increased, and that the anemone carpet stopped abruptly about 250 m from Punta Espinosa. Wellington's (1975) transect B, located about 300 m from Punta Espinosa, was now entirely carpeted with the anemones where previously a macro-algal community of *Ulva*, *Amphiroa*, and *Codium* had covered almost 100% of the reef platform to 10 m depth (Wellington 1975). Surviving specimens of the alga *Padina* within the barrens were smothered by anemones. The food supply of the large population of marine iguanas on the sheltered side of the peninsula now appears to be limited to a narrow zone of *Ulva lobata* shallower than 2 m.

When did the anemone barrens first appear? Wellington (1975) did not record them in his detailed study of the bottom communities at Punta Espinosa, and

he believes that, if present, they must have been rare (G.M. Wellington, pers. comm.). Jaime Peñaherrera recalls first seeing anemone patches there in 1995, although he had dived in the area two years previous to that. One of the authors (PCM) has surveyed Punta Mangle and Punta Espinosa annually for sea cucumbers since 1993. She noted in August 1997 that crustose and erect coralline algae had replaced the once dominant *Ulva* and foliose red algal turf soon after commencement of the El Niño. The once common brown algae, *Padina* and *Hydroclathrus*, however, still persisted in smaller patches. The formerly common ophiuroids were uncommon in 1997.

In June 1998, Fernando Rivera (pers. comm.) first observed patches of presumably the same anemone at Punta Mangle (at the southeast corner of Fernandina). By February 1999, the anemones were much more conspicuous along that coast and were also observed in Puerto Priscilla (also called Punta Gavilán) between Punta Mangle and Punta Espinosa.

In November 1999, PCM recorded that the anemone had spread throughout sheltered areas of Punta Mangle, Puerto Priscilla, and Punta Espinosa and covered much of the bottom from about 1.5 to 10 m depth. She also observed that the amount of loose sediment had also apparently increased at that time. Fernando Rivera (pers. comm.) noted that the anemone had covered some areas that had once contained the algal turfs of the territorial herbivorous damsel fishes *Stegastes leucurus beebei* and *S. arcifrons*.

On 2 June 1999, Dr. Cleveland Hickman (pers. comm.) found the anemone in great abundance at Punta Espinosa and collected specimens for identification (Fig.1). Dr.



Figure 1. *Aiptasia* sp. (photo taken by Dr. Cleveland Hickman of a specimen taken at Punta Espinosa 1999).

Daphne Fautin (University of Kansas) then provisionally placed the specimens in the genus *Aiptasia*.

These anemones have since been observed in other locations in the Galápagos Islands. In February 2001, Dr. Koichi Fujiwara (pers. comm.) observed anemones in abundance at Cabo Douglas at the northwest extremity of Fernandina. In January 2001, SAS recorded the same anemone under rocks at about 1 m depth in the lagoon at Playa Mansa (near Bahia Tortuga) and in Academy Bay, Santa Cruz Island. In March 2001, we observed the anemone in small patches on the western coast of Isabela at 5 to 10 m depth. Both sites are near mangroves, and this may be a preferred habitat throughout the archipelago. When we overturned rocks exposing the anemones, the damselfish, *Stegastes arcifrons*, quickly attacked them.

Anemones can reproduce sexually and asexually. The latter method, termed cloning, most commonly occurs by longitudinal fission, inverse budding or marginal budding, but pedal laceration is the method used by *Aiptasia* (Muller-Parker, pers. comm.) Cloning is common in some anemone species and results in extensive patches of clones on reef bottoms. Cloning is considered to be adaptive in the colonization of space because clones inherit high fitness from the adjacent parent (Shick 1991, Ayre and Grosberg 1995) and because budded clones can colonize space rapidly (G. Muller-Parker, pers. comm.). Pedal laceration in *Aiptasia* entails very low reproductive effort (Hunter 1984), and this process also ensures that symbiotic zooxanthellae are contained in the propagules (Muller-Parker and D'Elia 1997). The presence of zooxanthellae in the tissues of *Aiptasia* enhances the growth of asexually reproducing colonies when food is scarce (Clayton and Lasker 1985), and this would engender a particular advantage in bright environments such as the Galápagos reefs that are currently carpeted with *Aiptasia*. The ecological advantages provided by low reproductive effort and the contributions of reduced carbon from zooxanthellae are compatible and likely contribute to the recent success of *Aiptasia* on these shallow reefs (see Hunter 1984, Clayton and Lasker 1985, Muller-Parker and D'Elia 1997).

There are other examples around the world of clones spreading over small to large areas, usually in sheltered reef habitats. In Europe and on the west coast of North America, the anemone *Metridium senile* grows over large areas in the shallow subtidal (Purcell and Kitting 1982, Anthony and Svane 1995). *Metridium* responds to disturbance by increasing the rate of pedal lacerates and longitudinal fission. *Anthopleura elegantissima* proliferates at sheltered intertidal sites on the North American west coast (Ayre and Grosberg 1995). At Moorea, Society Islands, the anemone *Heteractis magnifica* covered very large areas of reef until cyclones broke up the anemone fields into small patches (D. Fautin, pers. comm.). Similarly, on a fringing coral reef at Eilat in the northern Red Sea, the corallimorpharian anemone *Rhodactis rhodostoma* covered up to 69% of the inner reef flat after a catastrophic low tide in 1970 partially caused by consecutive days of strong

wind from the north (Chadwick-Furman and Spiegel 2000). They suggested that this species has become an alternative dominant species replacing stony corals in that system.

One explanatory hypothesis for the recent spread of the *Aiptasia* anemone in the Galápagos is that the biological assemblages on the shallow reef flats of Fernandina were particularly vulnerable to the higher temperatures (and other conditions) associated with the 1990s El Niño events (El Niño is a cyclical warming of central and eastern Pacific surface waters centered along the equator). The ensuing mass mortality of the existing assemblage led to the availability of space for colonization by the opportunistic anemone species *Aiptasia* sp. In theory, colonial anemones can pre-empt space and exclude re-colonization of competitors by consuming any propagules that would otherwise recruit to the area. Similar interspecific adult-larval interactions are known to shape some infaunal communities dominated by polychaetes (Woodin 1974a, 1974b). Such a positive feedback might stabilize a resulting alternative community state, *i.e.*, the anemone barrens, over time if no predatory or physical limiting mechanisms intervene.

The two species of territorial damselfishes mentioned above, *Stegastes leucurus beebei* and *S. arcifrons*, are known predators of the *Aiptasia* anemone in the Galápagos (Grove and Lavenberg 1997, and SAS personal observations). The damselfishes do not stray far from small to medium boulder habitats or other crevice refuges, and are thus not common on the open areas of platform reefs such as those we observed to be covered with *Aiptasia*. In cases where damselfish turf areas were usurped by anemones as mentioned previously, El Niño conditions likely dispersed the damselfishes by decreasing preferred foods, thus providing opportunities for anemones to invade areas that were previously tended by damselfishes (F. Rivera, pers. comm.). If *Aiptasia* enjoys a size refuge from damselfish predation, then established anemone mats could persist even when damselfishes reinvade old territories.

The holothurian *Stichopus fuscus* is a suspected predator of *Aiptasia* in the Galápagos because Bermeo-Sarmiento (1995) found 'cnidarian polyps' in this benthic-feeder's gut. Holothurians like *Stichopus fuscus* are more likely to inhabit open habitats because of their chemical and other defenses, but a very intense sea cucumber fishery (Okey *et al.* 2002) has considerably reduced this species throughout the Galápagos concurrently with the appearance of the anemone barrens.

The nudibranch *Burghia major* preys on *Aiptasia pulchella* in Hawaii, as do the puffer fish *Arothron meleagris* and the butterfly fishes *Chaetodon auriga* and *Chaetodon unimaculatus* (Muller-Parker 1984). The puffer fish *A. meleagris* has been recorded in the Galápagos (Anon 2001), but it is uncommon (TAO personal observations); the butterfly fish *C. auriga* has been reported as rare in the Galápagos and only at the northern islands of Darwin and Wolf (Humann, 1993) and *C. unimaculatus* has not been recorded in the

Galápagos. However, two other *Chaetodon* species are somewhat common in some locations. Ates (1989) found that more than 50 fish species around the world prey on anemones, and 13 species include anemones as a large portion of their diets. He predicted anemone consumption would be revealed in many more fishes.

Hawksbill turtles, *Eretmochelys imbricata*, are known to eat anemones (Den Hartog 1980). Mayor *et al.* (1998) found that the anemone-like zoanthid *Zoanthus sociatus* made up the bulk of hawksbill diets at St. Croix, U.S. Virgin Islands, and Leon (2000) found that the anemone-like corallimorpharian made up a major proportion of hawksbill diets in the Dominican Republic. Loggerhead sea turtles, *Caretta caretta*, eat sessile benthic cnidarians including anemones (Plotkin *et al.* 1993), and other sea turtle species might eat anemones when available. Neither species of these sea turtles is conspicuous in Galápagos. Sea turtles in general probably consume benthic invertebrates in some proportion to the abundance or availability of the prey (see Carr and Stancyk 1975). Turtles such as the hawksbill were considerably more abundant in other areas in the past than they are today (NRC 1990, Bjorndal *et al.* 1993), and such turtles might have effectively controlled their prey populations and strongly shaped shallow reef ecosystems (Jackson 1997, Bjorndal *et al.* 2000, Jackson 2001). The relative absence of these predators in Galápagos might further enable the spread of prey such as anemones. Elsewhere, anemones are also consumed by bearded seals, *Erignathus barbatus*, (Finley and Evans 1983) and a number of bird species around the world (Ates 1991).

It appears that predators of *Aiptasia* in the vicinity of the Galápagos anemone barrens have not controlled the spread of this species on these platform reefs. More information is needed on the identities, histories, and abundances of the predators of *Aiptasia* in the Galápagos.

Several studies (Chadwick-Furman and Spiegel 2000, Anthony and Svane 1995, Shick 1991) lend support to the general hypothesis that catastrophic disturbances can lead to barrens dominated by anemones. The extreme low tide in the northern Red Sea was presumably a natural, albeit rare, event. In the Red Sea example, it is possible that the anemone-coral assemblages have adapted to that rare disturbance, albeit on a broad temporal scale. Similarly, did the Galápagos fauna on these shallow reef platforms ever adapt to the apparent deleterious effects of El Niño events that are as severe as those recently observed? Observed increases in the frequency and intensity of El Niño events corresponding with sudden shifts in community states would lend weight to the notion that exotic disturbances or natural disturbances with exotic (new) characteristics may have led to an alternative community state that can persist for several years.

It would not be surprising if the severe 1997-98 El Niño event was the proximate cause of the expansion of an anemone, probably already present in low abundance in the archipelago, but this would not rule out the possibil-

ity that a concurrent decline or loss of predators of *Aiptasia* was a key reason for the appearance of the anemone barrens. Distinguishing the relative roles of these two general explanations is the task of our continuing investigation of the anemone barrens phenomenon.

Notwithstanding the cause of the appearance of the barrens, their persistence raises many other urgent or interesting questions. What impact might these barrens have on the marine iguana population that is already stressed from reduced algal food during El Niño events? Are the barrens a stable alternative community state, or are they an ephemeral phenomenon that will give way to the previously diverse invertebrate, algal, and fish community? At present, we cannot answer these questions as too little is known of the biology or ecology of this anemone in the Galápagos.

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