

# A Maritime Accident Provides Evidence for Alternate Stable States in Benthic Communities on Coral Reefs

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**Abstract.** An *a posteriori* examination of the site of a ship wreck on the outer edge of the Great Barrier Reef revealed a unique, macroalgal-dominated benthic community. The persistence of community structure throughout a year of observation in an environment characterised by intensely grazed microalgae, and in the absence of a measurable wreck-derived influence, provides circumstantial evidence that it represents an alternate stable state. A mechanism for effecting state shifts in coral reef algal communities involves the size-dependent response by grazing organisms to algae in a perturbed environment.

## Introduction

Shallow marine hard bottom communities range from those with a high biomass dominated by large attached algae (e.g. kelp beds) to those having a low biomass of small encrusting and symbiotic algae, which occur in many coral reef habitats. A structural dichotomy exists between multi-layered benthic algal assemblages which include overstory and/or canopy-forming macroalgae, and uni-layered assemblages composed of turfing or crustose coralline algae (termed "microalgae" hereafter). Functionally, the bulk of the primary production in macroalgal-dominated communities enters detritus food webs (Mann 1982) while that in microalgal-dominated communities is consumed primarily by grazers (Chapman 1981; Hatcher 1982). Temperate hard-bottom communities are subject to dramatic shifts from macro to microalgal dominance (North 1971; Mann 1977), which can result in new and apparently stable communities with an altered species composition and reduced algal standing crop, productivity and commercial yield (Chapman 1981; Wharton and Mann 1981). Such changes in the fundamental structure of marine benthic communities have

usually been shown to be the direct result of destructive grazing by benthic echinoderms in numerical or behavioural response to reduced predation (Estes and Palmisano 1974; Lawrence 1975; Bernstein et al. 1981). But the underlying cause(s) of the shifts, and the relative stability of the new community structure remain obscure (Mann 1977). Are the shifts simply a result of natural cycles in the relative abundance of predators and prey (North 1971; Rosenthal et al. 1974)? Or are they perturbation-related changes between alternate stable states (*sensu* Holling 1973; Sutherland 1974), requiring another perturbation or natural catastrophe to return the community to its original structure (Jones 1975; Pearse et al. 1977; Simenstad et al. 1978)? Shifts in the opposite direction (micro to macroalgal-dominance) have been observed in previously kelp-dominated communities as a result of pathological decimation of echinoid populations, even after periods of up to 12 years in the microalgal state (Pearse et al. 1977; Miller and Colodey 1983, K.H. Mann, personal communication). Such shifts have not been observed to occur naturally in communities in which the initial state is one of microalgal dominance (although they have been intimated, Lighty 1982).

Most coral reefs are characterized by microalgal-dominated communities (Dahl 1974; Marsh 1976). Although macroalgal assemblages do occur as permanent features on some coral reefs (Adey et al. 1977; Wanders 1976; Wilson and Marsh 1980), and may have profound effects on coral growth and reef development (Crossland 1982; Johannes et al. 1983), natural state changes have not been observed. Macroalgal dominance has been induced in coral reef habitats by the exclusion of grazing organisms (Ogden 1976; Lassay 1980), and by fertilization (Banner 1974). However, the persistence of the new algal community structure after the perturbation ends has not been demonstrated (but see Smith et al. 1981). I document here the persistence for one year of an apparently stable macroalgal community in a habitat that is usually microalgae-dominated, and provide circumstantial evidence that a shift occurred as a result of pollution

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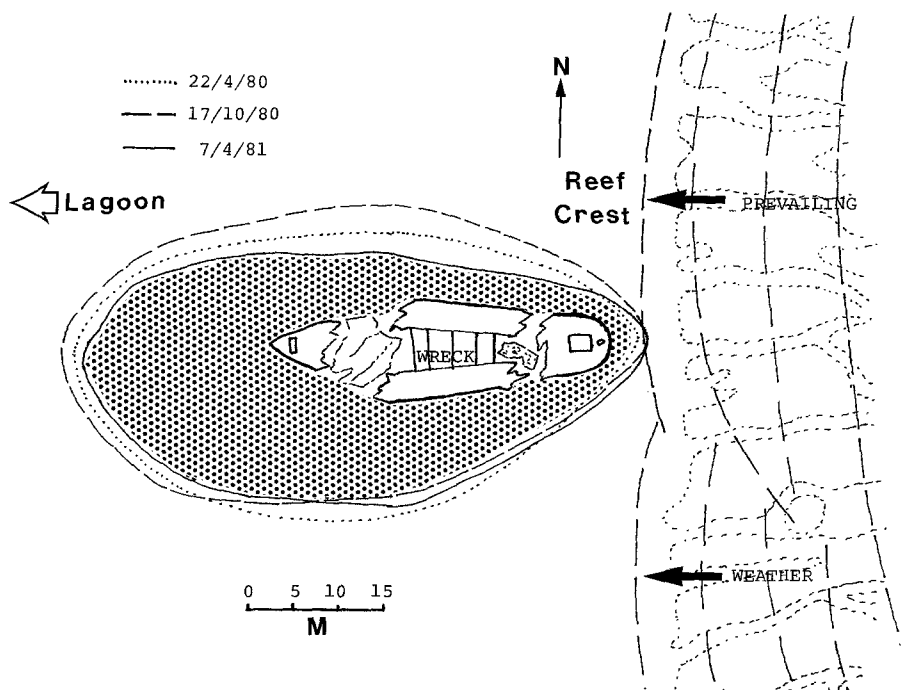


Fig. 1. Diagram of area on Myrmidon Reef dominated by *A. taxiformis*, as measured on three dates in relation to the ship wreck

Table 1. Chemical composition of a composite sample of Pozzalin, and a comparison of selected compounds in sediments and the water column within and outside the area affected by the shipwreck on Myrmidon Reef. Values are means (with standard deviations) of three samples per category. N.D. = No data

Components	Pozzalin (% of total)	Sediments		Water Column ( $\mu\text{M}$ )	
		Within	Outside	Within	Outside
SiO <sub>2</sub>	56	Nil	Nil	N.D.	N.D.
Al <sub>2</sub> O <sub>3</sub>	19	Nil	Nil	N.D.	N.D.
Fe <sub>2</sub> O <sub>3</sub>	8	N.D.	66 (22) ppm	<0.03	<0.03
Na <sub>2</sub> O	2	N.D.	N.D.	N.D.	N.D.
CaO	2	86 (2.4)%	86 (2.8)%	N.D.	N.D.
K <sub>2</sub> O	2	N.D.	N.D.	N.D.	N.D.
MgO	1	1.54 (0.21)%	1.52 (0.18)%	N.D.	N.D.
Loss on Ignition	9	0.18 (0.06)%	0.14 (0.07)%	N.D.	N.D.
N (total)	0.7	28.6 (7.4) $\mu\text{M}$	25.0 (10.2) $\mu\text{M}$	6.5 (3.8)	6.3 (3.1)
PO <sub>4</sub>	0.3	6.7 (3.7) $\mu\text{M}$	5.7 (2.9) $\mu\text{M}$	0.14 (0.04)	0.16 (0.04)

in an intensely grazed habitat. I suggest that the macroalgal community developed, and has persisted since the wreck (5 years) in the absence of any continuing pollution due to a perturbation-induced escape in size by a grazer-resistant macroalga.

## Methods and Results

On June 8th, 1976 the bulk carrier *M.V. Florida* ran aground on the windward (NE) edge of Myrmidon Reef (Lat. 18°15'S, Long. 147°24'E), on the outer margin of the Great Barrier Reef, Australia. The vessel came to rest just behind the submerged reef crest in 2–4 m depth (Fig. 1). A shallow (< 1 m) groove in the reef structure to seaward is the only visible legacy of structural damage to the reef resulting from the wreck. The cargo of 700 tonnes of crushed Pozzalin (a soft metamorphosed volcanic rock used in cement, Table 1) was spilled onto the reef surrounding the wreck as it broke up during the following weeks. Pozzalin is not soluble

in seawater, and the cargo was no longer visible at the wreck site after three months (B. Keogh, personal communication). Samples of the sediments and water column near the wreck, and outside the affected area were collected on October 17, 1980 and frozen for later analysis. The geochemical analyses were made by a commercial laboratory using standard techniques, while the nitrogen, iron and phosphorous determinations were made using the methods of Strickland and Parsons (1972).

I swam three transects across the reef on April 22, 1980 (4 years later), one through the wreck site, and one approximately 250 m on either side. The transition from reef crest to back reef is characterized by wave pounded, heavily cemented spur and groove topography supporting 38%–61% cover of live coral (Done 1982), and an extensive epilithic algal community consisting of a dense assemblage of filamentous, small foliose and crustose algae. Such microalgal communities are typical of sub-tidal coral reef habitats subjected to intense grazing (Bakus 1966; Wanders 1977; Hatcher 1983). The standing stock of herbivorous fish is very large (45 gms m<sup>-2</sup>) on these offshore reefs, and is composed primarily of non-territorial grazers (Williams and Hatcher 1983). Echinoid grazers are virtually absent (Borowitzka 1981; B. G. Hatcher, personal observation).

**Table 2.** Comparison of algal community structure on natural reef substrata outside the area affected by the wreck (control), within damselfish territories beyond the affected area (Territory), and within the area affected by the wreck (Wreck). Means and 95% confidence limits are given. \* = significantly > control; \*\* = significantly > territory and control, (*t*-test, S-N-K test,  $P=0.001$ ); N.B. = stoloniferous thalli only; N.D. = no data

Sample	Date	N	Ash-free dry wt.		Density	
			Epilithic algal community (mg cm <sup>-2</sup> )	<i>A. taxiformis</i> (%)	<i>A. taxiformis</i> (# cm <sup>-2</sup> )	Micrograzers (# cm <sup>-2</sup> )
Control	17/10/80	6	4.4 ± 2.3	0–	N.D.	N.D.
Wreck	17/10/80	6	20.1 ± 3.0*	81 ± 8	N.D.	N.D.
Control	22/9/81	7	4.5 ± 1.9	0.01 ± 0.01 (N.B.)	0.008 ± 0.011 (N.B.)	0.032 ± 0.025
Territory	22/9/81	7	8.0 ± 1.2*	0–	0–	0–
Wreck	22/9/81	7	22.0 ± 2.3**	78 ± 8	0.163 ± 0.047**	0.230 ± 0.131**

Imbedded within this habitat is a roughly elliptical area (approximately 0.15 ha) surrounding the wreck (located at the windward apex of the ellipse), which is dominated by the macrophytic, perennial red alga *Asparogopsis taxiformis* (Delile) Trevisan. The upright thalli of this stoloniferous plant form a dense overstory (1,200–2,100 branches m<sup>-2</sup>), extending 60–140 mm above the substrata (Table 2). Microalgae and encrusting corallines are poorly developed under the overstory, and live coral covers less than 1% of the area, with no colony exceeding 14 cm in diameter. I measured the extent of the macroalgal community on three occasions spanning 12 months in four directions from the wreck (Fig. 1). No significant change in the calculated elliptical area ( $\pm 15\%$ ), nor the appearance of the affected area was detected, although the location of the boundaries with respect to the wreck differed by as much as 5 m during the year.

On October 16–18, 1980 I haphazardly sampled segments of natural reef rock from within and outside the affected area by chiselling off about 100 cm<sup>2</sup> of dead coral rock, at the locations of a hammer thrown from a boat. The segments were placed in plastic bags, frozen, and returned to the lab where the epilithic algal community was analysed as in Hatcher and Larkum (1983). Briefly, all surface material was scraped from the substrata, freed of macroscopic epifauna, dried to constant weight, and ashed for 24 h at 495 °C to determine ash-free dry weight. The measurements were repeated 11 months later. In addition, samples were taken from within herbivorous damselfish territories (absent in the affected area), and counts of the number of *A. taxiformis* uprights and small invertebrates in samples were made at this time (Table 2). The standing crop of the epilithic algal community in the affected area was about five times greater than outside on both occasions, and about three times greater than that within fish territories. *A. taxiformis* occurred at high density within the wreck zone where it dominated the biomass, but was rare, and present only in stoloniferous form outside. Reproductive structures were observed, as well as the alternate, filamentous life form *Falkenbergia hildenbrandii* (Bornet) (Mitsuo 1960). Microinvertebrates (primarily amphipods and crabs) were much more abundant in the macroalgal-dominated community (Table 2).

## Discussion

The presence of a macroalgal community in this habitat is almost certainly related to the spill of Pozzalin. The shape and orientation of the affected area suggest a downstream plume from the wreck (Fig. 1). Larger spills of similar materials on windward coral reefs were rapidly dispersed (Dollar and Grigg 1981; Hudson et al. 1982). Only the stern section of the *M.V. Florida* remains, and there is no sign of the cargo nor its chemical constituents in either the sediments or the water column near the wreck (Table 1), indicating that there is no continuing

toxic or fertilization effect. The topography, substrata, water movement and turbidity of the affected area do not differ obviously from those of the surrounding habitat. Large predators were not observed within the wreckage, and herbivorous fish were consistently seen grazing microalgae from the wreckage itself, but never from the macroalgal-dominated, natural substrata.

How did the macroalgal community become established, and why has it persisted for at least seventeen months, and probably five years in an area of low ambient nutrient concentrations (Entsch et al. 1983 a), intensive herbivory (Hatcher 1982; G. P. Russ, in preparation) and in the absence of a continuing perturbation? I suggest that the Pozzalin spill served to temporarily enhance the growth of benthic algae within the affected zone by one or more of the following factors: (1) excluding grazers due to toxic, turbidity or increased predation effects (as discussed by Dollar and Grigg 1981), (2) increasing the availability of potentially limiting nutrients (Kinsey and Davis 1979; Hatcher and Larkum 1983; Entsch et al. 1983 b), (3) reducing competition with other benthic organisms (e.g. corals) by inhibiting their growth or killing them (Baker 1978; Dollar and Grigg 1981), (4) clearing and/or modifying a large area of the substrata in a manner, or at a time which favoured colonisation by a formerly rare alga (Glynn et al. 1964; Walsh 1983).

The resulting increase in the standing crop of the extant algal assemblage allowed a macroalga (*A. taxiformis*) which normally exists in grazer-resistant, prostrate or alternate life forms (sensu Slocum 1980; Hay 1981 a) in response to the algal production/grazing intensity relationship (sensu Montgomery 1980) in this habitat, to develop upright thalli. I suggest that the macroalgal-dominated community developed, and has persisted after the perturbation because: (1) A macroalga which had previously been consumed incidentally (i.e. along with the turfing algal community in which it was imbedded) by large herbivorous fish feeding non-selectively (Montgomery et al. 1981) became recognisable to grazers. These then avoided *A. taxiformis* due to its relative unpalatability (Tsuda and Bryan 1973; Norris and Fenical 1982), providing a size-related escape from

predation (sensu Lubcheno and Gaines 1981; Hay 1981 a). (2) The macroalga was able to inhibit the colonisation of (Connell and Slatyer 1977), and/or outcompete smaller forms for potentially limiting resources (e.g. light) due to its thallus morphology, which formed an overstorey (Littler and Littler 1980). (3) Micrograzers (sensu Brawley and Adey 1981 a) used the macroalga as shelter, and fed on potentially competing microalgae (Lobel 1980; Brawley and Adey 1981 b). The food-size dependent selectivity of grazers (item 1) may be of primary importance where preference is inversely related to thallus size, as it serves as a positive (destabilizing) feedback, facilitating shifts from micro to macroalgal-dominated communities. Shifts in the reverse direction also appear to involve positive feedbacks (Mann 1977; Bernstein et al. 1981).

Two alternative hypotheses to explain the local dominance of *A. taxiformis* around the wreck must be considered: (1) The wreck and the area of macroalgal dominance are not causally related, their co-occurrence being a chance event. (2) The perturbation is continuing due to the sustained release of some chemical other than those measured, associated with the wreck or its cargo. The macroalgal-dominated community is maintained by this regime and the epilithic algal community will return to the microalgal-dominated (original) state following the termination of the perturbation, as a result of physical attrition (e.g.: storm removal) and recolonisation by better competitors under conditions of intense grazing.

The wreck was not co-incidental with another obvious perturbation, such as a cyclone. The position and the shape of the area of macroalgal dominance in relation to the wreck, and the fact that the similar communities have not been observed on this reef make the first hypothesis highly improbable.

The chemical composition of the Pozzalin cargo (Table 1) does not include nutrients which are likely to selectively enhance the growth of *Asparagopsis* (Segot and Codomier 1981), nor compounds which are likely to be toxic to fish (Doudoroff 1957; Mckee and Wolf 1963). Furthermore, the major constituents of both the cargo and the hull (e.g., Fe), occur in oxidised states which are relatively non-reactive biologically (Stumm and Morgan 1970). The maintenance of elevated local concentrations of any compound for five years in an area of such high advection would require very rapid efflux from an unreasonably large mass of source material.

Finally, the relative stability of the macroalgal-dominated community must be considered. As no data on the composition and extent of the community is available for the first 4 years after the wreck, it is possible (but improbable) that the shift to macroalgal dominance occurred shortly before the community was discovered and has thus persisted for only 17 months. Alternatively, the original effect of the wreck may have been more extensive, and the affected area is contracting through the mechanism discussed in item 2) above (i.e. the community is very gradually returning to its original state). In this case

the macroalgal community may be but one stage in a successional sequence following the clearing of space by the wreck. The criteria for assessing the stability of the species composition (successional stage) of a community (as suggested by Connell and Slatyer 1977) are not fully met, in that the whole range of types and intensities of perturbations have not occurred during the observation period. However, an examination of meteorological data revealed a high frequency of the most likely destabilising perturbations: tropical cyclones. Four cyclones with wind strengths of greater than 70 kph passed within 220 km of Myrmidon reef between the date of the wreck and the first sample. A severe cyclone ("Freda": 972 mb, winds of up to 130 kph) passed directly over the reef between the second and third sample dates (Anonymous 1976–1983) without significantly altering the macroalgal community. Evidence from space-freeing perturbations on other coral reefs demonstrated that a well-defined algal succession takes place following the clearing of large areas: but the stage of macroalgal dominance lasts considerably less than 18 months after the perturbation terminates (Ogg and Koslow 1978; Pearson 1981; Walsh 1983). It is thus highly unlikely that the macroalgal-dominated community surrounding the wreck at Myrmidon reef is simply an ephemeral stage in a successional sequence.

Only time will test these hypotheses, and the conclusions are dependent on which definitions of "stability" and "perturbation" are used (Lewontin 1969). However, even if the community does not exhibit long term stability (due perhaps to the relatively small size of the effect), the mechanisms which allowed its development and persistence for even 5 years are worthy of note, and further study.

If my interpretation of this accidental perturbation is correct, then differences in benthic algal standing crop and community structure on coral reefs may not always be explainable simply in terms of the prevailing physical and/or biotic environment (e.g. grazer-control models; Wanders and Wanders-Faber 1974; Connor and Adey 1977; Van den Hoek et al. 1978; Montgomery 1980; Hay 1981 b), but rather by (often unknown) historical events (Doty 1971; Sutherland 1974; Simenstad et al. 1978). Recently, Lighty (Lighty and Macintyre 1980; Lighty 1982; see also: Walker et al. 1982) has provided evidence for alternate stable states for coral reefs. He suggests that a large scale shift from live coral to macroalgal dominance of a bank barrier reef ecosystem resulted from a geomorphological perturbation of local water temperature 3,500 years B.P. The macroalgal-dominated community persists, in the absence of a continuing perturbation.

A further implication of this study is that some forms of pollution on coral reefs, which may have apparently insignificant immediate effects (such as the clay spills reported by (Dollar and Grigg 1981; Hudson et al. 1982), may have significant long term secondary effects on community structure by precipitating a shift between alternate stable states.

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