

Biomechanics and mass mortality of erect bryozoans on a coral reef

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The bryozoan *Cigclisula* sp., is a heavily calcified erect species which occurs abundantly in the shallow sublittoral coral reef at Quilaluia Island, Quirimba Archipelago, northern Mozambique. It grows in an arborescent bilaminate form termed adeoniform on the undersides of coral heads or other available bioconstructed hard substratum. The geography and bathymetry of the area results in periodic high and complex current regimes often carrying water borne debris. If this periodic force overcomes the structural integrity of *Cigclisula* sp. either the outermost branches break or the colony topples at the base. The local population was dominated by young individuals: nearly 40% of the sample population had ten branches or fewer and less than 10% had more than 50 branches (these could be ascertained as young due to the lower proportion of damaged colonies with ≤ 10 branches; Figure 1). The only size group with no damaged specimens (branch breakage) were those with ≤ 5 branches. The mean proportion of branches broken significantly increased with increasing colony size. After one year a population of *Cigclisula* sp., initially comprising 30 colonies (encompassing the entire size spectrum of colonies), consisted of just one small specimen.

Erect bryozoans are an abundant feature of most shallow shelf faunas, particularly in temperate and polar regions. The variation in erect bryozoan morphology (in shallow water) is greatest in polar regions, and includes unilaminate and bilaminate sheets, arborescent unilaminate and bilaminate forms, flexible, rigid and 'rooted' forms (see Barnes, 1995a). In temperate waters heavily calcified sheets such as *Pentapora foliacea* and lightly calcified frond-like types such as *Flustra foliacea* are particularly abundant. In tropical regions, such as northern Mozambique, most bryozoans are cryptic and occur in refugia such as on the underside of coral heads and in caves. Encrusting forms are most abundant but arborescent unilaminate species with complex folding such as *Iodictyum* spp. and lightly calcified 'bushy' species such as *Scrupocellaria* spp. may be common.

Quilaluia Island (12°46'S 40°50'E), Mozambique (East Africa), is a small island with an estimated population of just 40 (mostly fishermen, see Barnes et al., 1998). It is almost entirely surrounded by a fringing coral reef, which although subject to very low anthropogenic disturbance, experiences complex currents of variable intensity (4 m tidal range) and periodic hyposalinity from river runoff. This has in the past (1965) resulted in localized catastrophic (>90%) coral mortality as well as severe effects on other marine taxa (J. Gessner & D. Stanwell-Smith, personal communication). Despite the extremes of current flow, salinity and heat experienced in the intertidal zone, initial studies have found high taxonomic diversity (Barnes, 1997, D.K.A.B., unpublished data). This is reflected in the diversity of shellfish species which are locally exploited in the intertidal zone by islanders (Barnes et al., 1998). The sublittoral zone of the region has remained virtually unstudied, except for a recent investigation into habitat diversity and resource use (Whittington & Stanwell-Smith, 1998).

Cigclisula sp., a rigid erect species which occurs abundantly in the shallow sublittoral at Quilaluia Island, grows in an arborescent bilaminate form often referred to as adeoniform (Brown, 1952). The growth of adeoniform morphotypes (by bifurcation

of branches) generally follows a regular pattern, which includes a number of features relating to colony strength (Cheetham et al., 1981). One such strengthening feature is thickening of the proximal part of branches as the distal part grows into the water column. Although Cheetham et al. (1981) described an increase in proximal branch thickening over geological time, Cheetham & Thomsen (1981) also found a decrease in material strength over a similar time. However, they also found an increase in mechanical resistance of adeoniform colonies through morphological changes. To date *in situ* observations have very rarely been made on adeoniform colonies with respect to breakage pattern and frequency. Here the branch number, normal and catastrophic breakage in a population of the adeoniform bryozoan *Cigclisula* sp. from Mozambique are described.

The erect bryozoan *Cigclisula* sp. was studied at Quilaluia Island, in the Quirimba Archipelago, northern Mozambique (for map see Barnes, 1997) during July 1996. The study site, a coral reef on the southern side of the island, steeply sloped from the intertidal zone to 16 m depth, where upon the bottom substratum was soft and the topography became shallow sloping. During the study period the current speeds ranged from zero to in excess of 2 ms^{-1} and were complex in terms of direction, on one occasion the current velocity and direction changed three times within a 30 min period. *Cigclisula* sp. did not occur in the top 5 m and was rare at 15 m ($0.2 \text{ colonies m}^{-2}$). The greatest density ($0.6 \text{ colonies m}^{-2}$) occurred at 10 m in coral interstices growing on dead coral, although colonies were also found growing on living bivalves (e.g. *Dendroostrea frons*). On 75, randomly selected, colonies a number of parameters were measured: (1) number of branches; (2) number of colonies with broken branches; and (3) number of broken branches on each colony. Thirty specimens, encompassing the range of branch number (all occurring in one particular location), were marked by tying a plastic numbered tag around the base using thin plastic twine. Collection of the specimens was then attempted one year later in 1997.

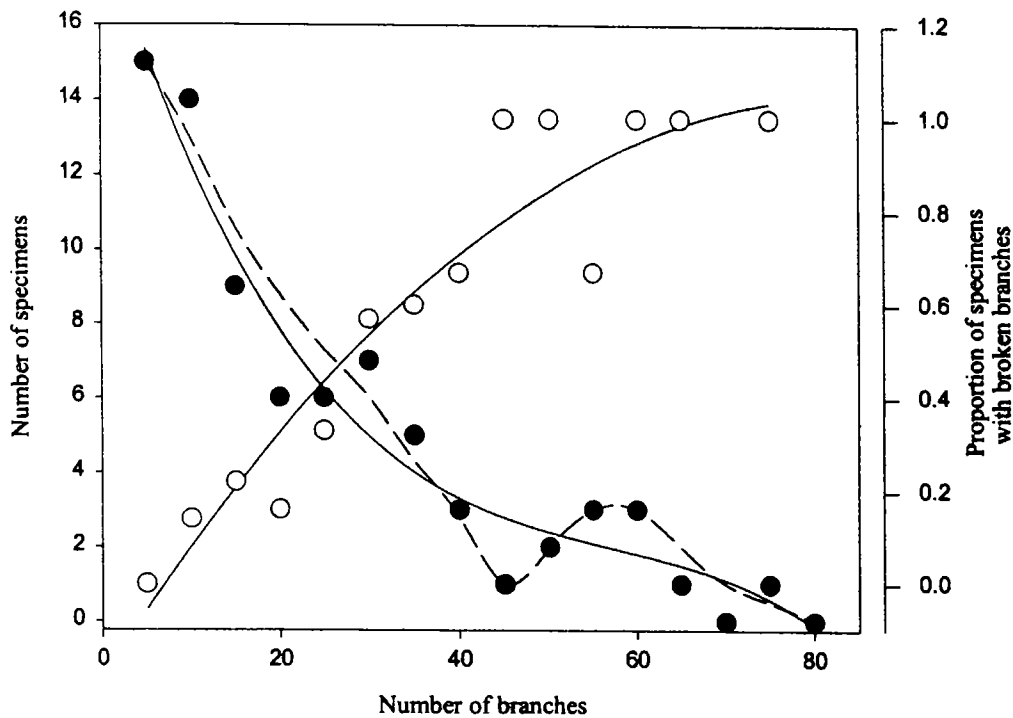


Figure 1. Morphology of *Cigclisula* sp. at Quilaluia Island. Number of specimens is illustrated (left scale) against number of branches (●) and proportion of damaged specimens (right scale) is also shown against branch number (○). Branch number is size-classed into multiples of five for ease of interpretation. Curves are fitted by eye.

The branch number frequency of the specimens of *Cigclisula* sp. observed at Quilaluia Island ranged from 1–75 (Figure 1). The height of specimens ranged from 5 to 70 mm and branch widths were approximately 4 mm wide irrespective of position or length. Nearly 40% of the sample population had ten branches or fewer and less than 10% had more than 50 branches. The only size group with no damaged specimens (branch breakage) were those with ≤ 5 branches. The majority of specimens with >20 branches were damaged. The mean proportion of branches broken significant increased (Figure 2) from 0–0.2 with increasing colony size (branch number). The breakages were generally restricted to the terminal endings of multiply divided branches, no regeneration was observed. After one year the population of *Cigclisula* sp., which had been tagged, consisted of just one small specimen.

The biomechanics of arborescent marine animal skeletons may be successful by either high resistance to breakage from current or particle transport or through fracture and regeneration from fragments. In the Antarctic marine environment, where erect bryozoans may be particularly abundant, breakage and regrowth has been well recorded (Winston, 1983). Growth and size of *Cellarinella watersi*, an Antarctic bryozoan with similar erect, heavily calcified and branching morphology, has been found to be current resistance restricted (Barnes, 1995b). Once colonies achieved a height of approximately 50 mm, either the distal branch tips broke off or the colony broke at the base and toppled. Growth from such fragments may then occur, a process which has also been recorded from fossil specimens (Cheetham et al., 1981). The breakage resistance of young colonies of many similar species has been calculated to be able to withstand currents of velocities of nearly 3 ms^{-1} but as colonies increase in size this value reduces considerably (Cheetham & Thomsen, 1981). Cheetham & Thomsen also calculated additional concentrated masses (such as water born particles, e.g. small stones or

coral fragments) which would cause breakage to distal tips. The most resistant colonies were found to withstand substantial masses up to 130 g.

The size structure of the Quilaluia Island *Cigclisula* sp. sample population was dominated by specimens with few branches (young colonies). Two possible interpretative curves are shown on Figure 1, the dashed line was added to include a possible second true peak of larger individuals. Large colonies persist at Quilaluia Island through particular local topography offering shelter as was also found in a shallow water Antarctic population of *Cellarinella watersi* (Barnes, 1995b). Some small, many medium sized and the majority of large individuals showed distal branch breakage. That such branch breakages occur on small (young) colonies is an indication of the high frequency (sub-yearly) of disturbance events. In addition, it also suggests a high minimum value to the magnitude of the forces involved. From the calculations of Cheetham & Thomsen (1981) this is either high water-borne masses, fast flow rates or both. Both high flow rates and substantial water-borne particles (small pieces of coral) were observed on two occasions during the study period.

Many erect bryozoans that live in environments subject to high flow rates have skeletons built of weaker materials or are lightly calcified and thus more flexible. However, for species capable of growth from fragments, a structural arrangement that results in frequent breakage can be an important aid to dispersal and colonization. This method of propagation has been noted as a major contributing factor to the high abundances of certain Antarctic species (Winston, 1983). Colonies of *Cigclisula* sp. with 40 or more branches had a mean of more than 10% breakage and up to 20% of branches were broken on the largest colony (Figure 2). Despite the high number of broken branches carried into the local water column, only one or two were seen on the substratum and neither showed signs of

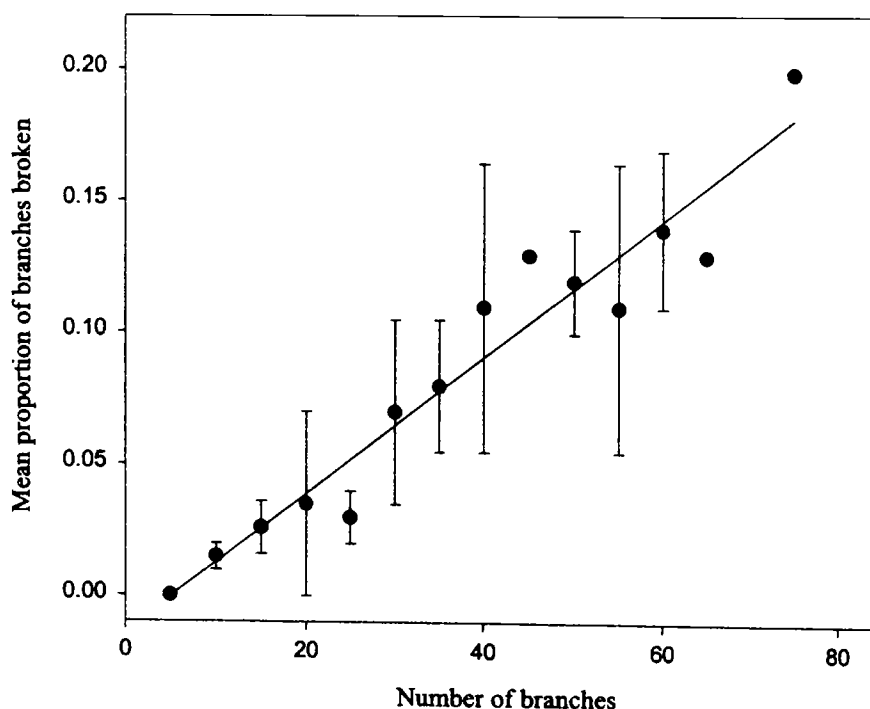


Figure 2. Proportion of branches broken with branch number in *Cigclisula* sp. The data are presented as mean with standard error. The regression shown has the equation, $y = -0.0134 + 0.0026x$ and the significance with ANOVA, $F = 165$, $P < 0.001$.

regeneration. All of the colonies seen at the Quilalua Island study site had normal ancestrulae origins. It is possible that large fragments such as branch tips are too easily removed by the local currents to settle and form new colonies (but this would require re-cementation). Most of the colonies of the comparable Antarctic species *Cellarinella watersi* studied close to the shallow-most upper limit (where strong currents are frequent) had also grown from normal origins (Barnes, 1995a,b). Colonies of the same species in deeper water, where generally water movement is probably less severe, have frequently grown from fragments (Winston, 1983). The growth (for which this experiment was initially designed to measure) and other life characteristics of *Cigclisula* sp. are unknown.

The mass catastrophic breakage, removing all but one of the 30 study colonies at their bases, may have been the result of several or just one major disturbance event. The uniformity of removal suggests that this event was probably an extremely high current regime. Large many branched colonies were, however, still present in topographical refugia and there were many new small specimens. It is possible, though unlikely, that the tags could have significantly increased the probability of breakage. With the possible exception of a few elongate branching demosponges the erect bryozoan *Cigclisula* sp. is probably the most susceptible of the Quilalua Island macrobiota to catastrophic dislodgement. Large scale catastrophic breakage of erect biota in the marine environment has been reported for a variety of taxa particularly after hurricanes. This is most dramatic, when the location and biota struck does not generally experience these conditions, such as the San Blas Islands in Panama (Wulff, 1995). Here the number of several species of erect sponges was halved through toppling whilst small sponge species increased. The domination of the Quilalua Island *Cigclisula* sp. population by few branched young individuals suggests high current disturbance events may be a relatively frequent phenomenon.

REFERENCES

- Barnes, D.K.A., 1995a. Sublittoral epifaunal communities at Signy Island, Antarctica. II. Below the ice foot zone. *Marine Biology*, **121**, 565–572.
- Barnes, D.K.A., 1995b. Seasonal and annual growth in erect species of Antarctic bryozoans. *Journal of Experimental Marine Biology and Ecology*, **188**, 181–198.
- Barnes, D.K.A., 1997. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: distribution, abundance and activity. *Marine Ecology Progress Series*, **154**, 133–142.
- Barnes, D.K.A., Corrie, A., Whittington, M., Carvalho, M. & Gell, F., 1998. Coastal resource use in the Quirimba Island Archipelago, Mozambique. *Journal of Shellfish Research*, **17**, 51–58.
- Brown, D.A., 1952. *The tertiary cheilostomatous Polyzoa of New Zealand*. London: British Museum (Natural History).
- Cheetham, A.H., Hayek, A.C. & Thomsen, E., 1981. Growth models in fossil arborescent cheilostome bryozoans. *Paleobiology*, **7**, 68–86.
- Cheetham, A.H. & Thomsen, E., 1981. Functional morphology of arborescent animals: strength and design of cheilostome bryozoan skeletons. *Paleobiology*, **7**, 355–383.
- Whittington, M.W. & Stanwell-Smith, D., 1998. The status of marine habitats in northern Mozambique. *Biodiversity and Conservation*, in press.
- Winston, J.E., 1983. Patterns of growth, reproduction and mortality in bryozoans from the Ross Sea, Antarctica. *Bulletin of Marine Science*, **33**, 688–702.
- Wulff, J.L., 1995. Effects of a hurricane on survival and orientation of large erect coral reef sponges. *Coral Reefs*, **14**, 55–61.

Submitted 8 September 1998. Accepted 9 November 1998.

