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NOTE

Long-term changes on coral reefs in booming populations of a competitive colonial ascidian

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ABSTRACT: A long-term study of the common coral reef spatial competitor *Trididemnum solidum* (van Name), a benthic colonial ascidian, showed a 900% increase in densities along the 84 km of fringing reef in Curaçao over 15 yr. The pattern of distribution along the coast did not change significantly and showed long-term effects of philopatry. This pattern relates to limited dispersal potential and the impact of the clonal ecological strategy of this modular organism. All hard reef substrata were overgrown but between 1978 and 1993 there was a significant increase in the number of ascidian colonies overgrowing dominant scleractinian corals such as *Montastrea annularis*.

KEY WORDS: Coral reef · Ascidian · Competition · Long-term change

Long-term records of population dynamics of benthic organisms are urgently needed to interprete changes in the marine environment. Such data are available to some degree for the temperate zones (e.g. Dörjes et al. 1987, Beukema 1989) but are very rare for tropical systems such as coral reefs. Most coral reefs are coastal systems and as such are subjected to all environmental changes connected with human population explosions along tropical coastlines (Buddemeier 1993, Wilkinson 1993). The few long-term data available for reefs are virtually restricted to scleractinian corals (e.g. Bak & Luckhurst 1980, Dollar & Tribble 1993, Hughes 1994, Bak & Nieuwland 1995). We report here on our observations over a 15 yr period on density and distribution of a compound ascidian *Trididemnum solidum* (van Name) over the 84 km fringing reef along the leeward coast of Curaçao (Netherlands Antilles). *T. solidum* is a colonial substratum-encrusting organism with a diameter of up to 30 cm. It is a highly mobile competitor for space on hard substratum, a possibly limited resource on coral reefs. It grows up to 10 cm mo^{-1} and shows a very flexible pattern of fission and fusion of colonies (Bak et al. 1981).

We studied aspects of the ecology of *Trididemnum solidum*, including the distribution along the coasts of the island in Curaçao in 1978. Since then, annual photographic records (Bak & Nieuwland 1995) and other observations have suggested a steady increase in densities and competitive impact of the ascidian over the years. The 3 questions we posed in 1993 were as follows: (1) has there been an increase in population density; (2) has there been a change in distribution pattern; and (3) has there been an increase in interactions with other benthic invertebrates?

To facilitate a comparison with the 1978 density and distribution data we employed the same survey method at the same localities in 1993. We recorded numbers of genets (clusters of separate colonies attached to the same area of substratum) and ramets (separate colonies) in 5 m wide belt transects running from 1.5 to 35 m depth perpendicular to the shore over the reef bottom. Such a definition of a genet is obviously only a minimum approximation of total genet number in the populations, but such data will reflect some of the dynamics of the fusion/fission processes. Type of substratum, such as rock with algal turf, crustose corallines, coral species or sponge, was recorded for each ascidian colony. A total of 42 sites was examined from west to east along the leeward coast of the island (Fig 1).

We found an enormous increase (Fig. 1) in the abundance of colonies in 1993 (paired samples t-test log transformed data, $t = 5.909$, $p < 0.001$). The overall number of colonies increased 900% (from 916 to 8272 colonies in the transects). Densities over the reef bottom increased all along the coast about 2 orders of

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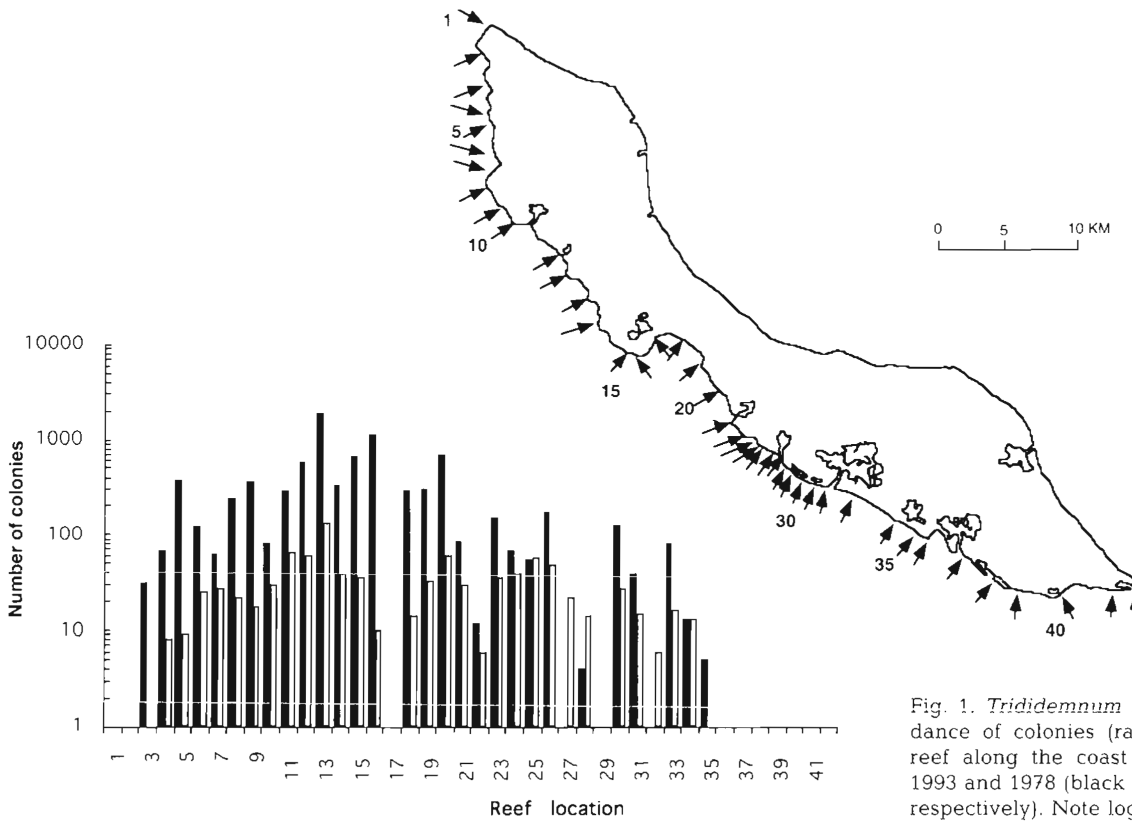

Fig. 1. *Trididemnum solidum*. Abundance of colonies (ramets) over the reef along the coast of Curaçao in 1993 and 1978 (black and white bars, respectively). Note log scale ordinate

magnitude (Fig. 2). This increase in ramet densities was paralleled in the number of genets, and the significant linear relation between ramet/genet numbers did not differ between the years (regression: $r^2 = 0.986$; ANOVA: $F_{1,53} = 3.22$, $p = 0.079$).

The pattern of distribution along the coast did not change significantly (paired samples *t*-test, logit transformed data, $p = 0.062$). The population spread a few hundred meters, or one transect site, to the east and the west (Fig. 1). The ascidians occur as a virtually uninterrupted population along the coast, absent only from some rubble slopes (Locations 17 and 27) and sites of extreme pollution such as down current of the island power plant and the mouth of the harbour

The ascidians practically do not occur on loose substrata such as coral rubble and sand. Coral rock with thin algal turfs is their preferred substratum. In 1978, 43% of all colonies occurred on rock, the remainder on living corals and other sessile animals. The much higher population density in 1993 resulted in a much higher occurrence of the ascidian on all available substrata but the absolute increase in number of colonies

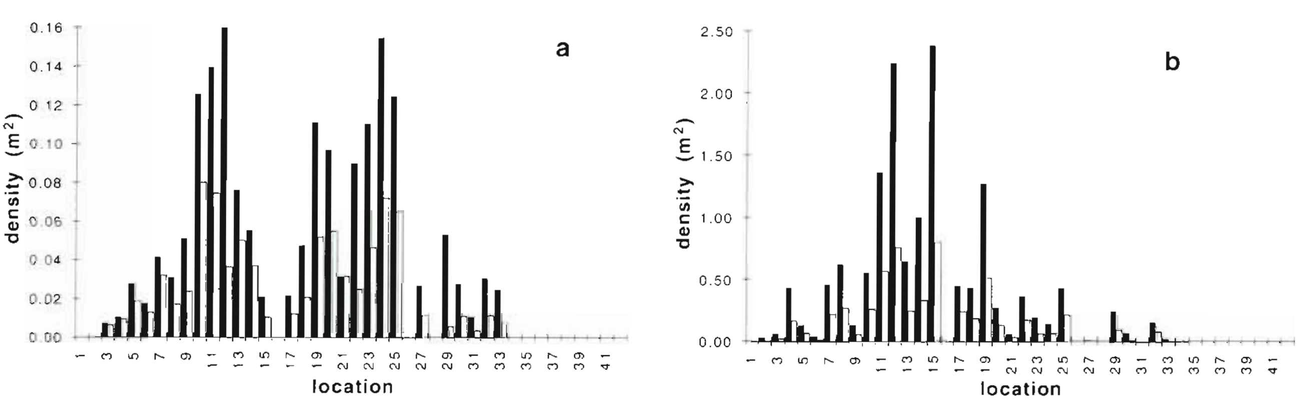

Fig. 2. *Trididemnum solidum*. Pattern and density of ramets and genets along the coast in (a) 1978 and (b) 1993. Black bars show ramet densities; white bars show genet densities. Note different ordinate scales

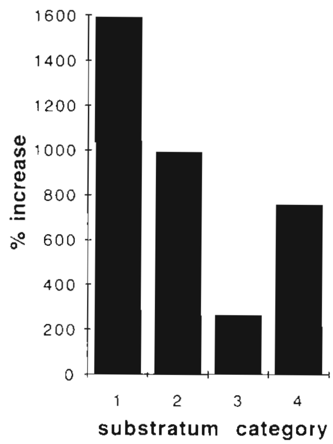

Fig. 3. *Tridemnum solidum*. Percentage increase in number of colonies of over different hard substratum types. (1) Dominant corals; (2) other corals; (3) other organisms; (4) coral rock and thin turf algae

was different for the different substratum categories ($G = 633.4$, df = 19, $p < 0.001$). The greatest increase in overgrowth was over the most common scleractinian corals (Fig. 3), with 45% of the colonies growing over *Agaricia agaricites, Eusmilia fastigiata* and *Montastrea annularis* (all 3 morphotypes) (Knowlton et al. 1992, Van Veghel & Bak 1993).

Apparently, the answers to our 3 research questions are as follows: (1) yes, there has been a tremendous increase in ascidian density; (2) the distribution shows no marked changes in pattern but the ascidian has spread a few hundred meters along the coast; and (3) yes, there is increased competition for space, in particular, with the most common coral species.

Life history traits such as the very short pelagic free-swimming period of the tadpole larvae, resulting in settlement in the vicinity of the parent colony (van Duyl et al. 1981), explain the limited spread of the population along the coast during the past 15 yr. The increase in ascidian density is caused by increased settlement of larvae, resulting in new colonies which subsequently undergo fission. It is not caused by increased fission of extant colonies, which would have resulted in a change in the ramet/genet ratio. *Trididemnum solidum* apparently competes very successfully with other sessile organisms for the available resources such as space and food. New space for settlement is frequently produced by small scale events (Bak & Luckhurst 1980), and ascidian tadpole larvae, produced daily throughout the year (van Duyl et al. 1981), are successful in such a habitat. Competition for space is facilitated by the fast growth rates, up to 14 cm linear growth per month, and the high rates of fission and fusion of colonies (Bak et al. 1981). *T solidum* is phototrophic as well as filter-feeding (Sybesma et al. 1981, Olson 1986), ingesting small bacteria (Bak, Joenje, Lambrechts unpubl.) and is well adapted to taking advantage of high bacterial densities, with up to 2×10^6 cells ml^{-1} (Bak & Nieuwland unpubl.) recently occurring along the coast. It is tempting to speculate that increased human activity results in a marine environment less favourable to corals, in which the ascidian would have a competitive advantage.

Recent reports suggest widespread degradation of coral reefs (Ginsburg & Glynn 1994). The events reported in the literature are major disturbances and spectacular disruptions of the state of the health of coral populations such as bleachings and large-scale mortality. Our report on change in densities of a very competitive coral reef benthic invertebrate highlights another kind of disturbance or non-equilibrium. Such change, though representing an enormous increase in the density of an ahermatype in hermatypic communities, is less conspicuous to the student of change in reefs and only obvious in the long-term perspective.

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