



Population dynamics of an association between a coral reef sponge and a red macroalga

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Abstract

Sponges are often as abundant as corals on tropical coral reefs and many species are symbiotic with algae. These associations may contribute significantly to reef primary productivity. This paper describes the first study ever made of the population biology of any of the known associations between sponges and macroalgae. Populations of the symbiotic association between the sponge, *Haliclona cymiformis* (Esper), and the red macroalga, *Ceratodictyon spongiosum* Zanardini, were studied in One Tree Lagoon, southern Great Barrier Reef. The association primarily occurs in areas where the substratum consists of dead coral rubble (rubble banks), at the edge of the lagoon, where it can reach a biomass of up to 270 g wet weight m⁻². Fragmentation is the primary mode of reproduction of the *Haliclona/Ceratodictyon* association at One Tree Reef. Although algal sporangia were frequently encountered during the summer, sperm cysts were infrequently found in the sponge, and oocytes and larvae were never observed. The size-frequency distribution of the clumps at the rubble bank sites was strongly skewed toward small individuals (longest branch length generally ≤ 80 mm). *Haliclona/Ceratodictyon* was also abundant at one site in the centre of the lagoon; at this site, which was not affected by strong currents or wave energy, the size-frequency distribution of the association was normal. Populations of the association at the rubble bank sites are very mobile, with intact clumps moved more than 30 cm per day under calm conditions and up to 1 m per day during rough weather. Survivorship of fragments or mobile clumps of the association is very high. At one site, the biomass of the association was not affected by two cyclones and at least one severe storm. At another site, up to 50% of the biomass of the population was lost following each of these storms, but the recovery of the biomass was largely complete within 9 months. The *Haliclona/Ceratodictyon* association has a rapid growth rate, of 8 mg (g wet weight)⁻¹ day⁻¹, which exceeds that of many other coral reef sponges, but it is within the range of growth rates reported for other species of marine macroalgae. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

On tropical reefs, the biomass of sponges often approaches or exceeds that of the reef-building corals (Rützler, 1978; Wulff and Buss, 1979), and on the coral reefs of the southern hemisphere, sponge–algal symbioses may contribute significantly to net primary productivity on the reefs on which they are found (Wilkinson, 1987; Cheshire and Wilkinson, 1991). Despite this abundance, there have been few quantitative assessments of coral reef sponge/algal populations.

A number of different associations between sponges and macroalgae have been described in the literature, including associations of sponges with green macroalgae (Weber Van Bosse, 1890) and several species of red macroalgae (Scott et al., 1984; Rützler, 1990), but there have been no studies of either the ecology or physiology of any of these associations. The symbiotic association between the haplosclerid sponge *Haliclona cymiformis* (Esper) (formerly *Sigmatocia symbiotica* Bergquist and Tizard), and the red macroalga *Ceratodictyon spongiosum* Zanardini, is common on shallow coral reefs of the Indo-West Pacific, where it has been described as being one of the most conspicuous organisms found in these areas (Morrissey, 1980; Vacelet, 1981; Price et al., 1984; van Soest, 1990). This symbiosis seems to be an obligatory association, as neither sponge nor alga has ever been identified growing independently or in association with other species (Morrissey, 1980; Ngan and Price, 1980). Most symbioses between plants and animals are considered to be mutualistic associations (Trench, 1979); however, it is not known if the sponge and alga derive mutual benefit from living in this particular partnership. Therefore, in this paper, we use the term symbiosis as defined by Gregory (1952) as ‘a system of cells and tissues composed of two genetically distinct cell types which proliferate harmoniously, resulting in a stable unit’.

The *Haliclona/Ceratodictyon* association consists of profusely branched, tightly interwoven algal ramuli, about 1 mm in diameter, which frequently anastomose to form the macrothallus, whose branches are about 1 cm in diameter (Fig. 1). The sponge grows over the surface of the algal ramuli and fills the spaces between them. Only the tips of the branches of the algal ramuli are free of sponge tissue. Because of the large amount of algal tissue found in the association, *Haliclona/Ceratodictyon* may make a major contribution to the benthic primary productivity in the areas in which it is found. As this association is both abundant and accessible, we chose to use it in this project, the first detailed study of the population dynamics of a sponge/macroalgal symbiosis, which forms part of a larger study of its biology and productivity.

The shallow fringing reefs where populations of *Haliclona/Ceratodictyon* are found are often areas of high turbulence where few other species of large, sessile organisms are able to survive. Constant water motion is of fundamental importance to the growth of marine sponges and algae, which need it for respiration and feeding or nutrient uptake; however, strong turbulence may suspend large volumes of sediments which can clog

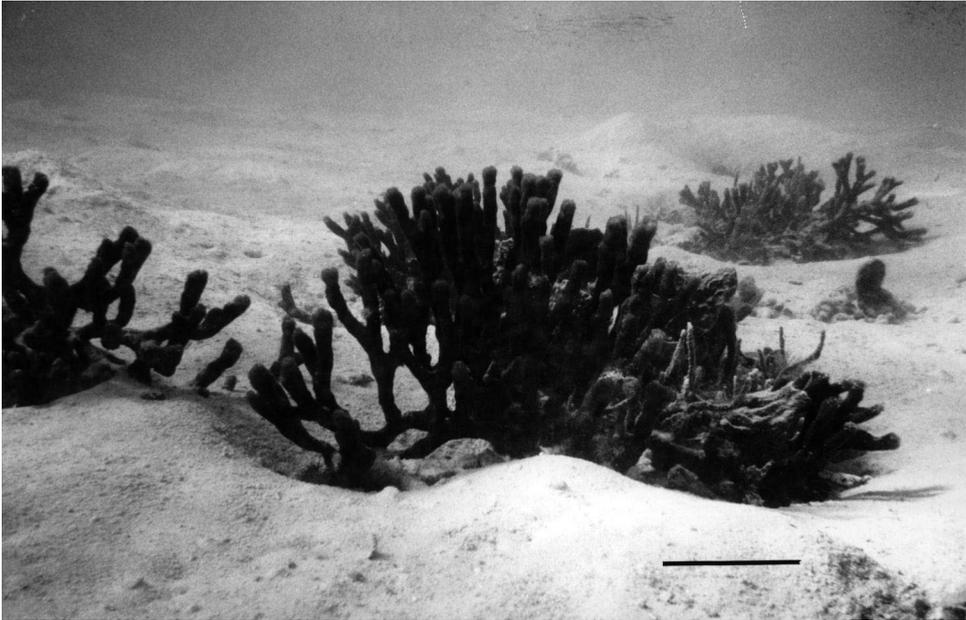


Fig. 1. The *Haliclona cymiformis*–*Ceratotidictyon spongiosum* association in its natural habitat at Ribbon Reef site 1, One Tree Lagoon, Great Barrier Reef (scale bar=10 cm).

sponge canals, and limit the amount of light received by algae. Smothering, as well as competition for space, food or light, may limit the survival of sessile marine organisms (Wilkinson and Vacelet, 1979).

Heavy turbulence may also fragment organisms, especially those with a branching or upright growth form (Wulff, 1986), thereby limiting the size to which most sponges and algae can grow (sponges: Reiswig, 1973; Johnson, 1992; Zea, 1993; algae: Mshigeni, 1978; Kilar and McLachlan, 1986b; Walters and Smith, 1994). As a consequence, the size-frequency distribution of a population may become skewed toward smaller organisms. As the *Haliclona*/*Ceratotidictyon* association is usually found in high energy environments, it was important to study the roles of fragmentation in determining the size frequency distribution of the populations and in the reproduction biology of the association.

Fragmentation may play an important ecological role in the propagation and dispersal of some species of sponges and algae. Asexual reproduction by fragmentation occurs commonly in a number of species of both sponges and algae. These fragments often survive very well, and in some species, virtually all recruitment into established populations is by asexually produced fragments (sponges: Wulff, 1986; Battershill and Bergquist, 1990; algae: Kilar and McLachlan, 1986a; Breeman and Hoeksema, 1987). Organisms with branching growth forms, such as the *Haliclona*/*Ceratotidictyon* association, are one group for which asexual reproduction by fragmentation may be an important mode of dispersion (Wulff, 1985).

Fell (1983) and Simpson (1984) have reviewed sexual reproduction in sponges, but

the reproductive biology of most species is quite poorly understood (Fromont, 1994), and no information is available on how sponge/algal symbioses are propagated from one generation to the next, following sexual reproduction.

This study is a quantitative assessment of the biomass of the association at different sites within the study area at One Tree Lagoon, Great Barrier Reef; it determines whether clumps of the association at different sites show different size-frequency distributions, and provides an estimate of the growth rate of the association. The reproductive biology of the association in One Tree Lagoon is evaluated, and the potential for fragments or propagules of the association to be transported to new sites, under the influence of water currents is also assessed.

2. Materials and methods

2.1. Study site

All field work was conducted at One Tree Reef (23° 30' S, 152° 06' E), southern Great Barrier Reef, between December 1989 and December 1994. Field trips to One Tree Reef were made during summer and winter each year. At One Tree Reef, the *Haliclona/Ceratodictyon* association is primarily found in three areas inside the reef crest which encloses One Tree Lagoon, where the substratum consists of dead coral rubble (rubble banks). Clumps of the association were relatively evenly distributed across these sites. Depending upon the state of the tide, these sites range in depth from 1 m to 3 m and they are affected by strong currents and strong turbulence, especially at high tide when the ocean swells break over the reef crest. Rubble Bank Sites 1 and 2 (RB 1 and RB 2) are ~100 m apart, and separated by areas of both rubble and sand. The third rubble bank site (RB 3) is ~550 m from RB 2, and is isolated from it by a wide sandy embayment bordered by a wall of living coral (Fig. 2). At all three of these rubble bank sites *Haliclona/Ceratodictyon* was the dominant macroscopic organism, particularly in the shallower waters close to the exposed reef crest. The association does not grow on the outside of the reef crest surrounding One Tree Lagoon.

At RB 1, the substratum slopes downward from the reef crest toward the centre of the lagoon at an angle of about 11°. At this site the band of rubble between the reef crest and the sandy lagoon floor is about 30 m wide. At RB 2, the band of rubble is only about 5 m wide and slopes downward at an angle of about 27°. RB 3 is almost level, the rubble covers an area of about 250 m², and is surrounded on three sides by walls of living coral. The fourth side is open to the lagoon and is the interface between the rubble and the sandy floor of the lagoon. At this site no clumps of the association are found within about 15 m of the rubble/sand interface.

In the centre of the lagoon, *Haliclona/Ceratodictyon* is found only in one small area, occupying about 100 m², toward the open end of a horseshoe-shaped area bounded by ribbon reefs. This site has a sandy bottom, through which a few pieces of rubble protrude. The site is approximately level, and is about 4 m deep at high tide. The ribbon reef site is not subject to wave-induced turbulence or strong tidal currents. At this site, other large species of sponges, such as *Phyllospongia* spp., and corals are common in

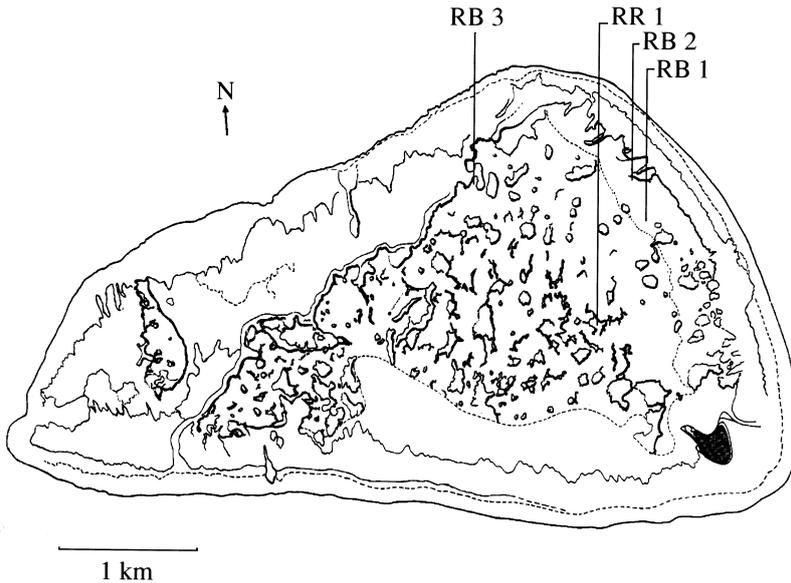


Fig. 2. Map of One Tree Lagoon showing the location of the study sites used in this project, which contained natural populations of the *Haliclona/Ceratodictyon* association; RB, rubble bank sites 1, 2, or 3; RR, ribbon reef site. Lines on the map indicate the position of ribbon reefs in the lagoon. The position of One Tree Island is indicated, as a shaded area, at the bottom right hand side of the map.

the middle of the enclosed area, but few are found close to the clumps of *Haliclona/Ceratodictyon* (Fig. 2).

2.2. Biomass determinations

The population density of the association was estimated by harvesting at ~6 month intervals at RB 1 and RB 2, between December 1989 and January 1994 to determine whether the biomasses of the populations of the association, or of its sponge and algal components were increasing/changing over time. Harvesting was not done at the site in the centre of the lagoon as the population at this site was too small to recover from repeated harvests.

A randomly selected area of 16 m² (area determined from preliminary sampling and a cost benefit analysis; Borowitzka, Hinde and Roberts, unpublished data) which had not previously been harvested, was cleared of the association at each sampling time. A strip measuring 2×8 m was sampled at each site; these strips were divided into eight subunits, each measuring 1×2 m. At RB 1, the area harvested was equivalent to about 1% of the total habitat occupied by the association. At RB 2, each sampling strip covered about 10% of the area containing populations of the *Haliclona/Ceratodictyon*. Each piece of rubble in these sampling areas was carefully examined for the presence of the association. When found, it was prised off the coral, using a knife or small screwdriver, and placed in a mesh bag.

After collection, the pieces of the association from each sampling area were cleaned of any adhering material, drained in a mesh bag for about 2 min and weighed to obtain the wet weight. Dry weight was determined by drying at 80°C for at least 24 h before weighing again. Ash-free dry weight was then determined by crushing the dried *Haliclona/Ceratodictyon* into a fine powder and taking a 1 to 2 g subsample. The subsample was placed in a clean, preweighed crucible and fired overnight (≥ 16 h) at 550°C in a muffle furnace. After cooling to room temperature, the ashed samples were reweighed and ash-free dry weights were calculated.

Results from the drying and ashing of intact clumps of *Haliclona/Ceratodictyon* were compared with those from isolated *C. spongiosum* which had been grown in unialgal culture. *C. spongiosum* was grown in culture according to the method described by Price et al. (1984), except that the alga was grown under an irradiance of 30 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, about half the irradiance used by Price et al. (1984). Five pieces of cultured *C. spongiosum* were ashed in the same way as intact pieces of the entire association.

Histological sections of the *Haliclona/Ceratodictyon* association were used to determine the relative proportions of algal and sponge tissue making up the intact association. After collection, the samples were fixed in marine Bouin's solution (Bancroft and Stevens, 1980), or, for long term storage, were transferred to 70% aqueous ethanol after fixation. The fixed samples were dehydrated through a graded series of aqueous ethanol solutions, and embedded in paraffin wax blocks. Sections were cut to a thickness of 10 μm , stained with either Mallory's triple stain for sponges or Mayer's haematoxylin-eosin (Bancroft and Stevens, 1980), and mounted in DePeX mounting medium. From each of 14 cross sectional areas of branch apices, from different clumps, four replicate fields were selected at random, and were individually analysed at 50 \times magnification using a Zeiss Axioplan microscope and Tracor Northern Image Analyser. Seven of these sections (one from each clump) were cut from clumps collected during summer, and seven from clumps collected during winter. The percentages of the total area covered by sponge and by alga were averaged over the four replicate fields examined from each section. Results were then analysed, using Student's *t*-test, to determine whether the relative proportions of the two tissue types changed seasonally.

2.3. Size-frequency distribution

As there was a higher degree of turbulence at the rubble bank sites than at the site in the centre of the lagoon, we tested the hypothesis that the size-frequency distribution of the rubble bank site would be skewed toward smaller clumps, while those in the centre of the lagoon would be normally distributed. Size-frequency distributions of the *Haliclona/Ceratodictyon* association were determined during the southern summer of 1993/1994 at each of the four sites in One Tree Lagoon. Three replicate surveys were made at each site. In each replicate, all clumps of the association within 50 cm on either side of a 20-m transect line were measured. The length of the longest branch of each clump of the association was measured, from the basal attachment of the clump to the tip of the branch.

The size-frequency distributions were compared between sites using a Kruskal–Wallis one factor ANOVA on ranks, and differences were located using Dunn's method. The Kolmogorov–Smirnov test for normality was used to determine the degree of skewness of the data collected for each site (Zar, 1984).

2.4. Reproduction

To determine the timing of sexual reproduction in the sponge, five branches of the *Haliclona/Ceratodictyon* association were collected at random, from each of the four sites, every month between August 1991 and September 1992. Sections cut from the apex, middle and base of the branches were fixed and prepared for histological examination as described previously for image analysis. The sections were examined by light microscopy for the presence of eggs or sperm cysts.

Since Fromont (1994) reported eggs and sperm cysts to be present in *H. cymiformis* collected from near Magnetic Island, central Great Barrier Reef (19° 9' S, 146° 50' E), during December and January, ~30 extra samples were collected from all sites during December 1994. These samples were cut longitudinally with a razor blade and the freshly cut surface was examined under a dissecting microscope for the presence of eggs or larvae, both of which are large enough (at maturity) to be seen under low magnification (Fromont, 1994).

Ceratodictyon spongiosum becomes fertile in summer and its reproductive structures can be seen with the naked eye (Price and Kraft, 1991). The reproductive status of the alga was, therefore, assessed each summer by visually examining 50 randomly selected clumps of the association found at the rubble banks. The percentage of the population bearing sporangial nemathecias was determined. No distinction was made between carposporangia and tetrasporangia.

2.5. Dispersal

The movement of clumps of *Haliclona/Ceratodictyon* was measured using two different methods to test the hypotheses that there is substantial movement of clumps of the association around the rubble bank sites, and that movement of the clumps occurs randomly in all directions. During June and December 1993 experiments were done at RB 1 and RB 3 to determine the rate at which clumps of the association were redistributed around a localised area. At each site, an area of 72 m² was divided into six smaller quadrats, each measuring 2×6 m. Each quadrat contained between 25 and 95 clumps of the association. All clumps of the association in three randomly chosen quadrats at each site were removed from the quadrats. All the clumps in the three remaining quadrats were tagged by pushing a stainless steel pin through a small piece of stiff, plastic tape and then through one of the branches of the association. Clumps from each of the three quadrats were distinguished by different coloured tags. The number of clumps in each quadrat was then recorded.

The quadrats were revisited every third day for a period of 15 days. The number of tagged clumps remaining in the tagged quadrats, and the total number of clumps (tagged

and untagged) which had appeared in the cleared quadrats were counted. The data were analysed using regression analyses (Zar, 1984).

A second study investigated the direction of dispersal and the distance moved by tagged clumps at the RB 1 site during an 11-day period of calm weather, and again after an additional 21 days of rough weather caused by a tropical cyclone. Three replicate groups of 10 clumps, each with multiple branches and an attachment to one or more small pieces of coral rubble (rubble weight >1 g), were collected from the site. The clumps were marked by threading coloured, plastic flagging tape through a branch of the association, using a large sewing needle. About 5 cm of tape was left protruding from each side of the branch. This tape was very light and flexible, so it did not become caught in the rubble and was not likely to alter the rate of current-induced movement by the clump. Each replicate group was marked using different coloured tape and the clumps, still attached to the rubble pieces, were placed at a point of origin marked by a tent peg flagged with the same coloured tape. The groups were placed along the same depth contour, separated by ~15 m. After 11 days, the distance from the point of origin and the net direction of movement were measured for each clump.

2.6. Growth

Estimates of growth rates were obtained from photographic records, taken during January and July 1994, of five small clumps of the association from the centre of the lagoon. From the January photographs, the combined length of all the branches in individual clumps was determined, and the total was multiplied by the known, mean weight of a piece of the association 1 cm in length (determined from 120 measurements). During the following field trip 7 months later the clumps were photographed again and a second weight was calculated for each clump. The difference between the two weights was divided by the number of days in the growth period, to give the average growth rate in g (wet weight) day⁻¹.

Several other methods for estimating the growth rate of the association were tested, including tagging branches and measuring increases in length from the tag to the tip, and buoyant weighing; however, these methods often damaged or killed the clumps. Measuring the maximum height and width of individual clumps at the rubble banks, and taking photographs of clumps along permanent transects to measure growth at the rubble bank sites were also unsuccessful, as strong currents often fragmented the clumps or moved them out of the study area.

3. Results

3.1. Biomass

Results of biomass harvesting at RB 1 supported the hypothesis that the standing stock of the *Haliclona/Ceratodictyon* association increased over time between December 1989 and January 1994. This increase occurred despite the fact that at least one severe storm (October 1990) and two tropical cyclones (March 1992 and January 1994)

passed almost directly over One Tree Lagoon during this period. The mean biomass of the association increased (t -test, $P=0.001$), from 6.2 g dry weight m^{-2} (37.2 g wet weight m^{-2}) to 25 g dry weight m^{-2} (150 g wet weight m^{-2}) over the 50-month study period (Fig. 3a).

In contrast, at RB 2, where the band of coral rubble between the reef crest and the lagoon floor was only about 5 m wide, the hypothesis was not supported. There were at least two marked declines in the biomass of the association. These declines in biomass were recorded soon after the passing of the October 1990 storm and the March 1992 cyclone. After these events, the recovery of the sponge population at this site was quite rapid, but the biomass tended to remain at the same mean level, around 18 g dry weight m^{-2} , during the periods between the storms (Fig. 3b).

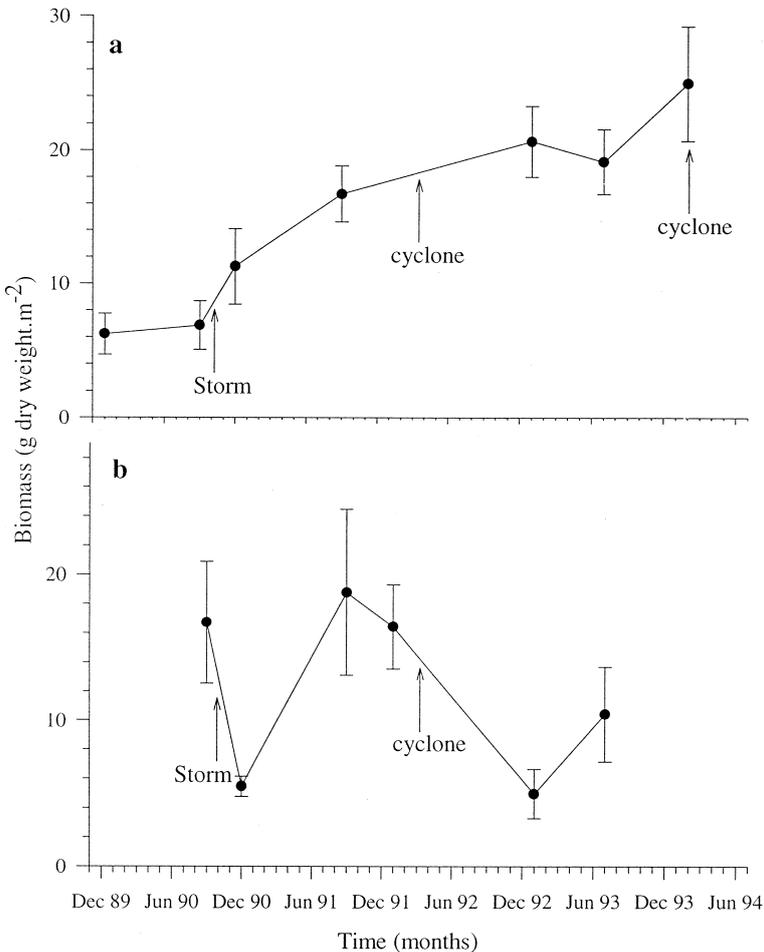


Fig. 3. The biomass (g dry weight m^{-2}) of *Haliclona/Ceratodictyon* collected from an area of 16 m^2 at (a) RB 1 and (b) RB 2. Collections were made from December 1989 to January 1994 (mean \pm S.D.; $n=8$).

The wet weight of *Haliclona/Ceratodictyon* was 5.9 ± 1.1 times the dry weight (mean \pm S.D., $n = 105$). The dry weight to ash-free dry weight ratio was $1.5 \pm 0.2:1$ following incineration at 550°C , and the intact association had an ash content of $32.8 \pm 5.1\%$. No statistically significant differences were found between any of the weight ratios of the clumps collected from the two sites. The wet weight to dry weight ratio of cultured *C. spongiosum* was $7.86 \pm 2.49:1$ and the dry weight to ash-free dry weight ratio was $1.6 \pm 0.3:1$ (mean \pm S.D., $n = 5$). The cultured alga had an ash content of $35.2 \pm 10.9\%$.

There was significantly more algal tissue than sponge tissue in the association (t -test, $P < 0.0001$). A mean of $41.6 \pm 5.6\%$ (mean \pm S.D.; $n = 14$) of the cross sectional area was occupied by the alga, compared with only $12.9 \pm 1.6\%$ occupied by the sponge. Some of the remaining 'empty' area may have resulted from damage to the association during fixation and sectioning, but it is likely that the most of this area was occupied by the sponge aquiferous system. A small proportion of this area was also occupied by polychaete worms; the area taken up by these worms was not measured. The ratio of algal to sponge tissue, 3.2:1, did not vary with season.

3.2. Size-frequency distribution

At all four sites, the longest branches of 99% of the measured clumps were in the range of 10 to 120 mm. At each of the three rubble bank sites the size-frequency distributions of the sponges were strongly skewed to the left (Fig. 4a–c), indicating that, at these sites, individual clumps of the association tend to be small, with the longest branch less than 80 mm long (Kolmogorov–Smirnov test, $P < 0.0126$). At the site in the centre of the lagoon, where there was less mass water movement, the size-frequency distribution of the sponges was normal (Kolmogorov–Smirnov test, $P = 0.206$) (Fig. 4d). These results supported the hypothesis that the maximum size of the clumps of the association is influenced by the degree of turbulence to which the clumps are exposed.

A one-factor analysis of variance showed that there were no significant differences in mean branch length between the four sites. The mean lengths of the longest branch ranged from 50 to 57.3 mm at all sites.

3.3. Reproduction

Sperm cysts were found in about 5% of the clumps, between December and March, but no oocytes or larvae were observed in any of the histological sections of the *Haliclona/Ceratodictyon* association, whether collected from the centre of the lagoon or the rubble bank sites, at any time of year. Although both mature eggs and larvae are large enough to be visible under a dissecting microscope (Fromont, 1994), examination of longitudinally cut branches of the association collected from all sites during the summer of 1993/94 did not reveal any sponge reproductive products. Periodic sampling since then has never shown any sponge eggs or larvae either.

Algal reproductive structures are, however, common during the summer. Up to 84% of the clumps of *Haliclona/Ceratodictyon* at the rubble bank sites had sporangial nematocelia (with either carposporangia or tetrasporangia) during December and January in each year.

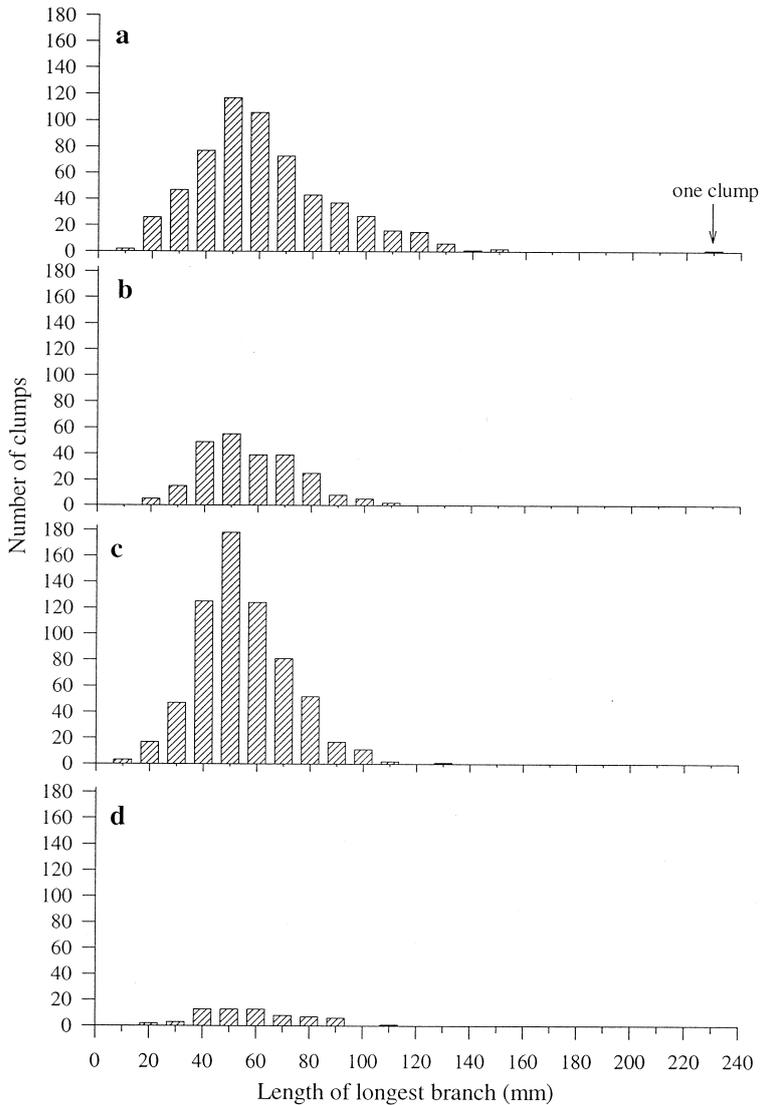


Fig. 4. Size-frequency distribution of the *Haliclona/Ceratodictyon* association within an area of 60 m^2 , at the sites of each of the four major populations in One Tree Lagoon; (a) RB 1, (b) RB 2, (c) RB 3, and (d) RR 1. The data shown are the lengths of the longest branch in each clump.

3.4. Dispersal

Over a period of 15 days, between 12 and 40% of the tagged clumps were lost from each of the quadrats at RB 3. The mean rate of loss from this site was equivalent to $0.044 \pm 0.013 \text{ clumps m}^{-2} \text{ day}^{-1}$ ($1.5 \pm 1\%$ of the population per day; mean \pm S.D., $n = 3$)

in summer, while in winter the mean rate of loss from the quadrats was equivalent to 0.087 ± 0.021 clumps $m^{-2} day^{-1}$ ($1.4 \pm 0.2\%$ of the population per day). At RB 1, between 4 and 22% of the tagged sponges were lost from the quadrats over the 15-day study period, at a mean rate of loss of 0.036 ± 0.026 clumps $m^{-2} day^{-1}$ ($0.8 \pm 0.6\%$ of the population per day) during summer, and 0.06 ± 0.025 clumps $m^{-2} day^{-1}$ ($1.2 \pm 0.2\%$ of the population) during winter (Fig. 5a and b).

The number of clumps which were moved back into the cleared quadrats after 15 days ranged from 1 to 11 at RB 3, equivalent to a mean rate of 0.03 ± 0.03 clumps gained $m^{-2} day^{-1}$ during summer. During winter, between 0 and 8 clumps were moved into the cleared quadrats at a mean rate of 0.04 ± 0.02 clumps gained $m^{-2} day^{-1}$. At RB 1, between 6 and 14 clumps were counted in the cleared quadrats after 15 days, at a mean

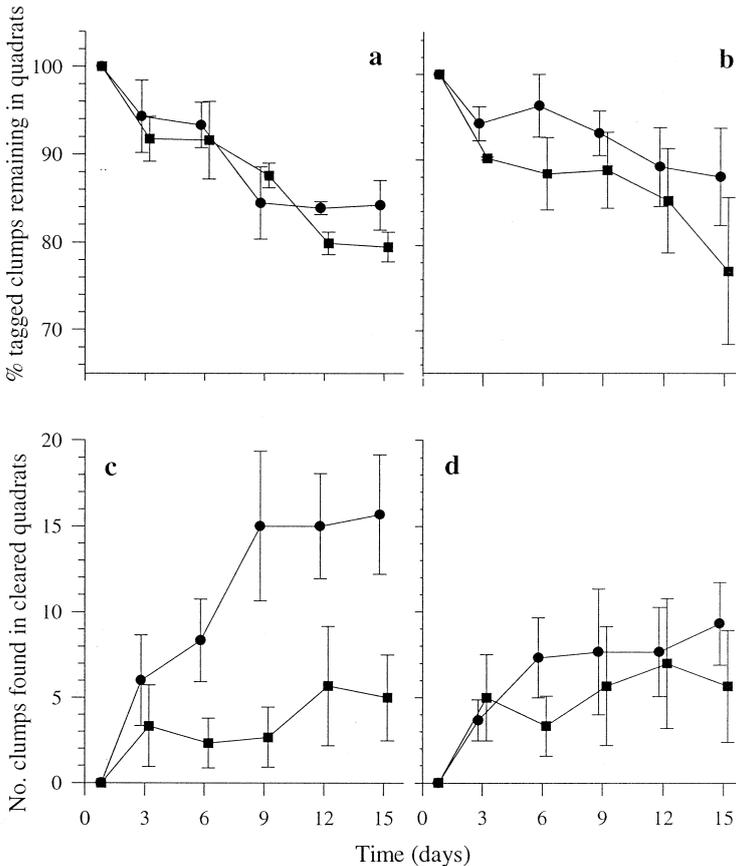


Fig. 5. The percentage of tagged clumps of *Haliclona/Ceratodictyon* which remained in the marked quadrats over 15 days during (a) July 1993 (winter) and (b) December 1993 (summer), and the number of clumps which were carried into cleared quadrats by the action of currents over 15 days during (c) July 1993 and (d) December 1993 at RB 1 (●) and RB 3 (■) (means \pm S.E.; $n = 3$).

rate of 0.05 ± 0.02 clumps gained $\text{m}^{-2} \text{day}^{-1}$ during summer; while during winter, between 10 and 22 clumps were moved into the cleared quadrats at the mean rate of 0.09 ± 0.03 clumps gained $\text{m}^{-2} \text{day}^{-1}$ (Fig. 5c and d). These results support the hypothesis that there is substantial movement of the clumps around the rubble bank sites.

Intact clumps of the *Haliclona/Ceratodictyon* association were moved up to 3.76 m in 11 days in calm conditions (Fig. 6). During this time, five of the clumps used in this experiment had formed secure attachments to large pieces of coral and were considered to have become immobile under calm weather conditions. After an additional 21 days of rough weather caused by a tropical cyclone, clumps were found up to 24 m from the initial point of origin. As only 18 of the 30 tagged clumps were recovered after this period, it is likely that some were transported even further, outside the area searched.

The hypothesis that clumps of the association are moved randomly around the site was not supported. The direction of dispersal of the clumps was generally southerly, corresponding to the direction of the prevailing current flow across the reef (Frith, 1981). Only one clump was found a short distance north of the point of origin.

3.5. Growth

All five clumps used to measure the growth rates of the association were estimated to weigh between 10 and 12 g at the start of the experiment, when they had either three or four branches. Photographic records of these clumps showed a mean increase in branch length of 0.38 mm day^{-1} , which is equivalent to $\sim 91 \text{ mg wet weight day}^{-1}$ for each clump, or $0.0083 \text{ g (g wet weight)}^{-1} \text{ day}^{-1}$, or 3.5 cm year^{-1} linear growth, totalled over all the branches; or a doubling time of about 120 days, over a period of 192 days from January to July 1994. This increase in weight corresponded to at least a 250% increase in the mass of the association over this period.

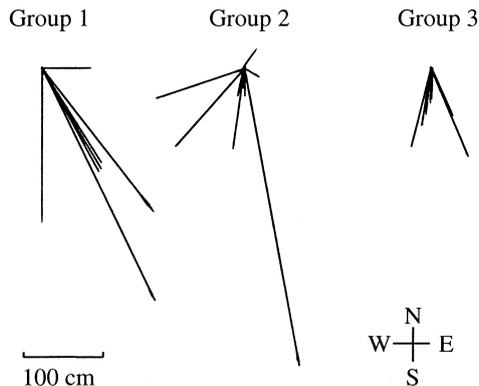


Fig. 6. The distances and directions that members of three replicate groups of 10 tagged clumps were moved by the action of currents at RB 1, over a period of 11 days. The point of origin for each group is the point from which all the lines in each group diverge (scale bar = 100 cm).

4. Discussion

The biomass of the *Haliclona/Ceratodictyon* association at One Tree Reef is comparable to some of the highest biomasses of both sponge and red algal populations found in coral reef lagoons. At 3 m depth the maximum biomass of this association (25 g dry weight m^{-2} ; Fig. 3a) was similar to the maximum biomass (~ 30 g dry weight m^{-2}) of at least two species of sponges (which lacked algal symbionts) on a shallow Jamaican reef (Reiswig, 1973). The mean biomass of *Haliclona/Ceratodictyon* per unit area (160 g wet weight m^{-2}) was also greater than two of the four most prominent dictyoceratid sponge species (~ 50 g wet weight m^{-2} for each species) examined by Wilkinson (1987) at Flinders Reef flat, Great Barrier Reef. On coral reefs, algae are generally inconspicuous, occurring as turfs or as symbionts within animal tissues. Large species of red algae in particular are very rare in coral reef lagoons, but biomasses of up to 700 g m^{-2} wet weight have been reported for the brown alga *Sargassum* sp. at Magnetic Island, northern Great Barrier Reef (Vuki and Price, 1994). The *Haliclona/Ceratodictyon* association therefore provides a means for the establishment of an abundant and mature population of red algae, in an environment where they are otherwise rare. The large biomasses of the algae also make a significant contribution to the primary productivity of the fringing reefs of One Tree Lagoon (Trautman, 1997) and possibly other reefs on which they are found.

The variation in biomass between the two rubble bank sites appears to be primarily due to differences in the physical environment, in particular, the area available for colonization by the association; this hypothesis will be investigated in a later paper. At the larger of the rubble bank sites, sponges which were fragmented or detached during rough weather probably had a greater chance of remaining in the wide zone of coral rubble between the reef crest and the sandy floor of the lagoon, which acts as a substratum for the growth of the association. At the other rubble bank site the scouring of the substratum during rough weather probably swept many clumps of the association out of the narrower rubble bank zone into a sandy area where they were likely to be smothered by sediments. More than 50% of the standing stock of *Haliclona/Ceratodictyon* was lost from this site during one severe storm, and again during a later cyclone. However, the *Haliclona/Ceratodictyon* population at One Tree Reef recovered rapidly after these storms (in about 7 months). In contrast, Wulff (1995) reported the loss of about 25% of the sponge biomass on a shallow Caribbean reef during a hurricane. These populations took at least 2 years to regain their pre-hurricane biomasses. The rapid recolonization by the *Haliclona/Ceratodictyon* association may have been partially attributable to the algal symbiont, *C. spongiosum*, as algae have been shown to be able to rapidly recolonize denuded substrata in coral reef ecosystems (Mshigeni, 1978).

The ash content of *Haliclona/Ceratodictyon* (about 33% of the dry weight) is at the low end of the range previously recorded for other shallow water sponge species (31 to 62%) (Reiswig, 1973). Cultured pieces of isolated *C. spongiosum*, had an ash content similar to that of the intact association ($35.2 \pm 10.9\%$ of the dry weight; mean \pm S.D., $n=5$). This ash content is within the range reported for other species of non-calcified algae (18 to 63%; Bosler and Hay, 1996). Since there is little difference between the ash weight of the intact association and the isolated alga, it can be inferred that an extremely

small proportion of the dry weight of this sponge is composed of inert skeletal material, such as spicules or sand grains, and strongly suggests that the sponge tissue primarily relies on the algal thallus for structural support. The lack of sponge skeletal material may also make the association more prone to being damaged during rough weather.

At the rubble bank sites the size-frequency distribution of *Haliclona/Ceratodictyon* was strongly skewed toward smaller individuals, with the majority of the clumps having a maximum branch length of 5 cm (Fig. 4a–c). This may be due largely to the effects of water movement. It was noted in the field on several occasions that larger clumps of the association were broken, usually at the point of emergence of a branch. Rapid water movement may either snap off the branches directly, or cause clumps growing on loose pieces of rubble to be broken by being rolled over in the currents. The rarely encountered larger clumps found at these sites were invariably found in deeper water attached to large, immobile pieces of coral rubble. Similarly, Reiswig (1973) reported that within a population of a species of *Mycale* in Discovery Bay, Jamaica, individuals grow to maturity only when they are attached to stable substrata within a deep basin. In the centre of One Tree Lagoon (RR 1), which is relatively unaffected by strong currents or high wave energy (Frith, 1981; Trautman, 1997), the sizes of the clumps in the population were normally distributed (Fig. 4d), supporting the model that the skewed distribution at the rubble bank sites is largely due to water movement.

High energy environments may also have an effect on the reproductive biology of the organisms that inhabit them, and *H. cymiformis* has many of the life-history characteristics found in species which live in disturbed environments (Ayling, 1980; Johnson, 1992). At Magnetic Island, small females of *H. cymiformis* are less likely to be gravid than large females and the larvae are large and are brooded (Fromont, 1994). Even though algal sporangia were found on up to 84% of the population of *Haliclona/Ceratodictyon* at the rubble bank sites in One Tree Lagoon during each summer, the paucity of sperm cysts found and the complete lack of oocytes and larvae in the clumps examined during this research suggests that sexual reproduction is rare in *H. cymiformis* in these populations. Thus, at One Tree Reef, most or all reproduction of the sponge (and therefore of the association) must occur asexually, by fragmentation.

Our observations on the reproductive biology of the *Haliclona/Ceratodictyon* association agree with those of Price and Kraft (1991) and Fromont (1994), who proposed that sexual reproduction of the algal and sponge partners in this symbiosis occurs completely independently of one another. Since re-establishment of the symbiosis has never been observed, it is assumed that it must occur soon after the release of the sponge and algal propagules (Price and Kraft, 1991; Fromont, 1994). Further investigation is required to determine how the symbiosis is propagated by sexual reproduction (and/or algal spore production), how often sexual reproduction occurs, and its importance to populations of *Haliclona/Ceratodictyon* at different locations on the Great Barrier Reef, and between disturbed and undisturbed habitats.

Monitoring of the dispersal of both fragments and intact clumps of *Haliclona/Ceratodictyon* at the rubble bank sites revealed constant and often substantial redistribution of the clumps occurring within each site (Fig. 5a and b). Repopulation of cleared areas occurred extremely rapidly. In one 12-m² quadrat almost 50% of the original number of clumps was found within the area only 15 days after the quadrat had been

cleared (Fig. 5c and d). In a similar experiment conducted by Wulff (1991) in Guigala Tupo, Panama, repopulation of an area cleared of sponges was substantially slower, although differences in the physical environments between One Tree Lagoon and the Panamanian reef may account for the differences in repopulation rates. In contrast to the results presented here, on the Panamanian reef it took a year to repopulate an area of 7.5 m² to a density of approximately half that which occurred before clearing.

The net distances which intact clumps of *Haliclona/Ceratodictyon* were moved (Fig. 6) were similar to those reported by Wulff (1985) for three species of branching sponges over a similar length of time, in San Blas, Panama. However, the sponges monitored by Wulff were single branches only, whereas all the pieces of the association used in the experiments described here had multiple branches and were attached to small pieces of coral rubble. This would have made the clumps substantially heavier and less liable to move, even though the larger size of the clumps would have presented a greater surface area on which the force of water currents could act. Therefore the forces acting upon clumps of the *Haliclona/Ceratodictyon* association on the rubble banks at One Tree Lagoon appear to be significantly greater than those in San Blas.

The pieces of the *Haliclona/Ceratodictyon* association which formed secure attachments to the rubble were invariably found in slight depressions in the rubble, as noted for other species of sponges by Wulff (1985), and Battershill and Bergquist (1990). This effect of microtopography possibly decreases fragment mortality by enforcing a kind of passive habitat selection into areas where the effects of currents may be somewhat reduced (Nowell and Jumars, 1984).

In One Tree Lagoon, the *Haliclona/Ceratodictyon* association appeared to have a high rate of growth but a size distribution which was skewed toward smaller specimens. It is likely that these growth traits are influenced by the physical characteristics of the habitat in which the sponge is found, primarily the turbulent nature of the rubble bank sites.

It was extremely difficult to determine the rate of growth of the *Haliclona/Ceratodictyon* association without damaging it. In light of these difficulties, the estimated rate of growth presented here for a clump of the association weighing in the order of 11 g, 91 mg wet weight day⁻¹ (about 0.83% growth day⁻¹; 15 mg dry weight day⁻¹; 3.5 cm year⁻¹ linear growth, totalled over all the branches; doubling time of about 120 days), can only be considered to be approximate. The maximum rate of growth for this association is likely to be somewhat higher, as the growth measurements reported here were taken in autumn and winter, rather than summer, when growth rates are likely to be at their maximum. Compared to other species of coral reef sponges this growth rate is high; Hoppe (1988) measured linear growth rates for three species of sponges which ranged from 0.7 to 2.4 cm year⁻¹. The doubling times reported for three species of Caribbean sponges by Wulff (1985) were between 275 and 730 days, while Wilkinson and Cheshire (1988) estimated doubling times ranging from 232 to 304 days for five species of sponges in Jamaica. Two of the sponges studied by Wilkinson and Cheshire (1988), *Ircinia felix* and *Verongula ardis*, contained small populations of symbiotic cyanobacteria. These two species showed the fastest growth rates, and it was suggested that the increased growth over the other species may have been due to supplementary nutrition from the symbionts. This is also likely to be the case for the *Haliclona/*

Ceratodictyon association, although transfer of photosynthate from the alga to the sponge would be likely to reduce the growth rate of the alga.

The rate of growth of the *Haliclona/Ceratodictyon* association is somewhat lower than that of other species of red macroalgae, including *Eucheuma* sp. (Dawes et al., 1993; Mollion and Braud, 1993) and *Gracilaria* sp. (Beer and Levy, 1983), where increases in the size of the algal thallus of between 1.4 and 20% day⁻¹ have been reported. However, the rates reported for these other commercially grown species are maximum rates, where the algae are in the early stages of growth, and have been maintained under ideal growth conditions. As the clumps of *Haliclona/Ceratodictyon* measured here were probably not under ideal conditions (measurements were made during autumn/winter), it is difficult to make comparisons with other species of algae at this stage.

The two species in this association may influence each others' growth rates, as the alga rarely protrudes more than 2 mm from the tips of the branches. However, it is not clear which of the partners limits the growth rate of the clumps.

There is often an inverse relationship between the size and/or age of a sponge and its growth rate (Reiswig, 1973; Wilkinson, 1988). This is also true for at least some species of red algae (Beer and Levy, 1983). However, in some instances, the effects of size on growth may be confounded by other factors. For instance, the growth rates of three species of branching sponges measured by Wulff (1990) remained unchanged following fragmentation, even though two or more smaller individuals had taken the place of the larger one. Small intact clumps were always used in attempts to measure the growth rate of the *Haliclona/Ceratodictyon* association; but it was impossible to determine whether these clumps were derived directly from larvae (i.e. the clumps were young) or from the fragmentation of larger clumps (i.e. the clumps were old, but small in size due to fragmentation). Therefore the effect of age on the growth rate of the *Haliclona/Ceratodictyon* association cannot be reliably determined from the data presented here.

This is the first detailed study of the ecology of a sponge/macroalgal symbiosis. Our results show that populations of the *Haliclona/Ceratodictyon* association have one of the highest biomasses per unit area recorded for either shallow water sponges (with or without symbiotic algae) or red algae on coral reefs. As the association grows faster than many other sponge and algal species, and ~70% of the biomass of each clump is made up of algal tissue, this association is also likely to contribute significantly to the primary productivity of the reefs on which it is found.

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