

Persistence and coexistence of a nonsymbiotic coral in open reef environments

(*Tubastraea micrantha*/growth/abundance/competition/predator avoidance)

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ABSTRACT In the Republic of Belau (western Caroline Islands), the nonsymbiotic stony coral *Tubastraea micrantha* (Ehrenberg) occurs commonly on open reef habitats that are dominated by symbiotic corals. This observation calls into question the often-held view that nonsymbiotic corals are restricted to cryptic environments because of their inability to compete successfully for space with rapidly growing symbiotic corals. In this study, we investigated aspects of the biology of *Tubastraea* that might account for its coexistence and persistence on the reef. Our results indicate that despite low calcification rates, linear skeletal extension for *Tubastraea* is surprisingly rapid for a nonsymbiotic species and comparable to those of many symbiotic corals. This factor, coupled with *Tubastraea*'s resistance to direct competitive dominance (i.e., by aggressive interactions) and avoidance of predation, promotes its coexistence with symbiotic species. The relative importance of these biological interactions in different coral communities leads to predictions corroborated by observed patterns of local distribution and abundance.

Since the Triassic Period scleractinian corals have been among the dominant contributors to carbonate accretions in tropical shallow-water marine environments (1, 2). The most obvious corals on modern reefs are symbiotic (hermatypic) species; nonsymbiotic (ahermatypic) corals do not usually contribute to reef formation and generally occupy cryptic or deepwater habitats and seldom achieve large-growth forms, except at higher latitudes or depths where physical conditions preclude symbiotic forms (3-5).

The relative predominance of symbiotic corals in shallow tropical reef environments is usually attributed to two factors: first, the influence of the endosymbiotic algae (zooxanthellae) in enhancing calcification (6-8) and growth (9) and in directly contributing photosynthetically derived reduced carbon (10-12) and second, the effect of differential predation (e.g., sea urchins and fishes) on other benthic reef organisms (mainly algae) which potentially compete for open space (13, 14). Although nonsymbiotic corals would also benefit from the effects of differential predation, the absence of endosymbiotic algae presumably places them at a direct disadvantage with respect to calcification, growth, and phototrophically derived nutrition, parameters potentially important either directly or indirectly to the acquisition and maintenance of living space on open reef environments. The validity of this assumption, however, has not been tested.

Here we report the occurrence of a nonsymbiotic coral, *Tubastraea micrantha* (Ehrenberg) in open reef environments dominated by symbiotic corals. We address the question of how *T. micrantha* is able to coexist with symbiotic corals in reef environments where living space is often a limiting resource.

The ability of a coral to persist on the reef is due to a combination of factors, among which are its growth rate, resistance to competitive attack by neighboring corals, avoidance of predators, and ability to withstand destructive physical forces (15-17). We experimentally evaluate the importance of these factors and show that their potential efficacy in promoting coexistence varies between reef environments. Further, we discuss factors that may impose ecological constraints limiting the evolutionary success of nonsymbiotic species in open reef environments.

METHODS

Study Areas and Organisms. The study was conducted in the Republic of Belau (Palau) (Caroline Islands; 134° 30' E, 7° 20' N). Study sites were located on reefs bordering channels that connect the lagoon to the open sea (inner reefs) and on reefs just inside the outer barrier reef (outer reefs). Coral communities at these sites are equally well developed, with high abundances of symbiotic corals present. Species composition, however, contrasts markedly; outer reefs are dominated by fast-growing corals, such as branching and tabular acroporids, whereas inner reefs are dominated by slower-growing poritid corals (Table 1). The major coral predator, the Crown-of-Thorns seastar *Acanthaster planci* (L.) occurs at low densities on outer reefs but is moderately abundant on inner reefs. Both areas, however, are periodically subjected to high densities of *Acanthaster*, resulting in catastrophic mortality to acroporid and other nonporitid corals (18, 19).

The dark olive-green to black, erect-branching colonies of *T. micrantha* were found at depths of 1-20 m below the mean low-water level, usually in regions subject to strong tidal currents but protected from direct assault by ocean waves (Fig. 1). A daily tidal excursion of 2 m results in extensive water movement which provides a continuous supply of particulate food. *T. micrantha* was observed in open, well-illuminated areas of the reef and never found in caves or other cryptic habitats. Some colonies achieve enormous size; one colony was nearly 2.5 m high with a basal diameter of 20 cm. The abundance of *T. micrantha* is higher on inner reefs than on outer reefs, and colonies on inner reefs achieve significantly larger sizes than those on outer reefs (Table 1).

Sampling Procedures. The abundances of *Tubastraea* and *Acanthaster* at various reef sites at a depth of 1-20 m were estimated by counting the number of individuals occurring within 0.5 m on either side of a 100 m long plastic transect line laid haphazardly on the reef parallel to a depth contour. The percentage cover of living coral was determined by photographic analyses of 0.25-m² quadrats taken at randomly determined points along a 100 m long transect.

Calcification and Linear Growth Rate. Calcification rates were measured by using the ⁴⁵Ca²⁺ method (6, 7). Experiments were conducted simultaneously on excised 5-cm branch tips of *T. micrantha* and *Acropora* cf. *A. pulchra* (a

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Table 1. Distribution and abundance of *T. micrantha*, the coral predator *A. planci*, and symbiotic corals on two reef sites off Koror, Republic of Belau

	<i>T. micrantha</i> colonies			<i>A. planci</i> , individuals per 100 m ²	Acroporids, absolute % cover	Poritids, absolute % cover	Total coral cover, %
	No./100 m ²	Mean height, cm	Height range, cm				
Inner reefs	6.1 ± 1.2 (12)	55.2 ± 2.9 (152)	6–175	0.14 ± 0.01 (12)	10.8 ± 2.1 (52)	55.6 ± 4.6 (52)	66.4 ± 3.8
Outer reefs	1.7 ± 0.8 (12)	36.9 ± 2.7 (80)	4–106	0 (10)	53.6 ± 2.3 (50)	4.3 ± 1.1 (50)	57.9 ± 1.9
Significance	<i>P</i> < 0.01	<i>P</i> < 0.001		<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.001	<i>P</i> = 0.35

Values represent means ± SEMs. The number of 100-m² transects surveyed for density estimates of *T. micrantha* and *A. planci* are indicated in parentheses. Percentage cover is based on 0.25-m² quadrats. Differences between sites were evaluated using the Mann-Whitney U-test statistic with percentages transformed using \sin^{-1} transformation.

branching form). Incubations were conducted in separate 500-ml water-jacketed containers at 28°C in filtered seawater to which ⁴⁵Ca²⁺ was added to give an initial activity of 1 μCi/ml (1 Ci = 37 GBq). In all cases, formalin-fixed specimens (after exhaustive washing to remove fixative) were used as controls for ⁴⁵Ca²⁺ exchange. Exchange never accounted for more than 5% of the ⁴⁵Ca²⁺ incorporated. The symbiotic *Acropora* were illuminated at 700 μeinsteins (1 einstein = 1 mole of photons) per m² per sec. Incorporated ⁴⁵Ca²⁺ was measured by liquid scintillation spectrometry (Beckman Model LS-6800) and quantified in terms of mg of tissue protein (20).

To estimate the rate of linear skeletal extension, colonies of *T. micrantha* and five symbiotic corals were stained *in situ* with alizarin red (21). Several colonies of *T. micrantha* were also tagged for direct time-course measurements. Plastic cable ties were positioned several centimeters from the branch tips (3 per colony, 19 colonies) as a reference point for subsequent measurements. Colonies were stained on May 21, 1983, and initial measurements on tagged branch tips were taken on June 14–16, 1983. Both stained and tagged branch

tips were collected and measured with vernier calipers to within 0.1 mm on July 26, 1983. Annual growth increments were extrapolated from these measurements. The data yielded from the two techniques were not significantly different ($F_{1,21} = 1.32$, $P > 0.25$) and thus were pooled for analysis.

Aggressive Interaction Experiments. Experiments were conducted in the field, and observations of naturally occurring interactions were recorded to assess competitive abilities resulting from physical contact between *T. micrantha* and the more abundant symbiotic corals. In the experimental design, heterospecific pairs, representing six coral species with five replicates and conspecific controls, were placed within tentacular contact on June 20, and the resulting interactions were scored on July 24, 1983. A colony inflicting tissue damage to an adjacent colony was judged to be a winner, and that receiving damage, the loser. The data for naturally occurring interactions represent a summary of independent field observations made over a 2-month period (June–July 1983). We did not ascertain the mechanism by which one coral was able to inflict tissue damage; however, several possibilities have been described (22, 23).

Predation Experiments. We conducted a series of choice/nonchoice predator-prey experiments with *T. micrantha* and five predominant species of symbiotic corals to assess the relative susceptibility of *T. micrantha* to predation by *A. planci*. Coral colonies of approximately equal surface area (one colony each of six coral species) were placed equidistant in outdoor cement raceways (4 m long × 2 m wide × 1 m deep) with a single seastar for two weeks [6 trial runs; disc diameter of seastars, 33.6 ± 2.0 cm (mean ± SEM, $n = 6$)]. Two separate 6-week trials were conducted in which seastars were provided only with colonies of *T. micrantha*. In addition, daily observations on the feeding activity of 10 *A. planci* were recorded over an 8-day period at Rmegethu Reef (an inner reef site).

RESULTS

Calcification and Linear Growth Rates. In both *T. micrantha* and *Acropora* cf. *A. pulchra*, the rate of ⁴⁵Ca²⁺ incorporation into the skeleton decreased with distance from the apical polyp (6, 7). As expected for a nonsymbiotic species, *T. micrantha* calcified at rates [16.7 ± 4.9 μg Ca²⁺/mg of protein per hr (mean ± SD, $n = 5$)] that were 16–20% those for *Acropora* [83.7 ± 9.2 ($n = 5$)] within the first 2 cm of the actively accreting branch tips. This 5-fold difference was consistent over the entire 5-cm length of the branches.

Because rapid growth can lead to competitive displacement by overtopping (15, 17), an ecologically important aspect of growth that is not necessarily positively correlated to calcification is linear growth. *Tubastraea* grew at an average rate of 3.8 ± 0.83 cm/yr ($n = 22$), a rate 5–6 times faster than that previously recorded for a nonsymbiotic coral (5). Our measured growth rate for *Acropora echinata* was 5.2 ± 0.89 cm/yr ($n = 24$). Although lower than the growth rate

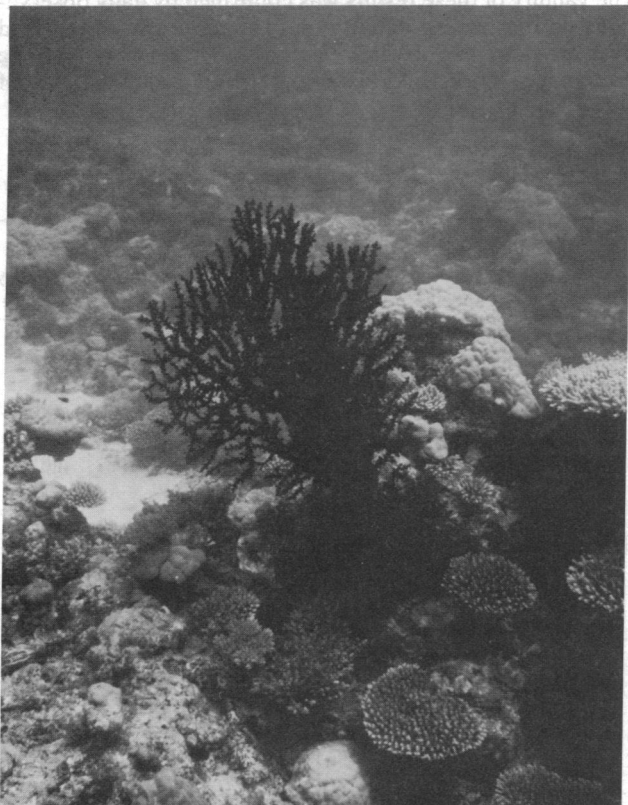


FIG. 1. *T. micrantha* in growth position at 10-m depth on the reef slope at Augulpelu Reef, near Koror, Belau.

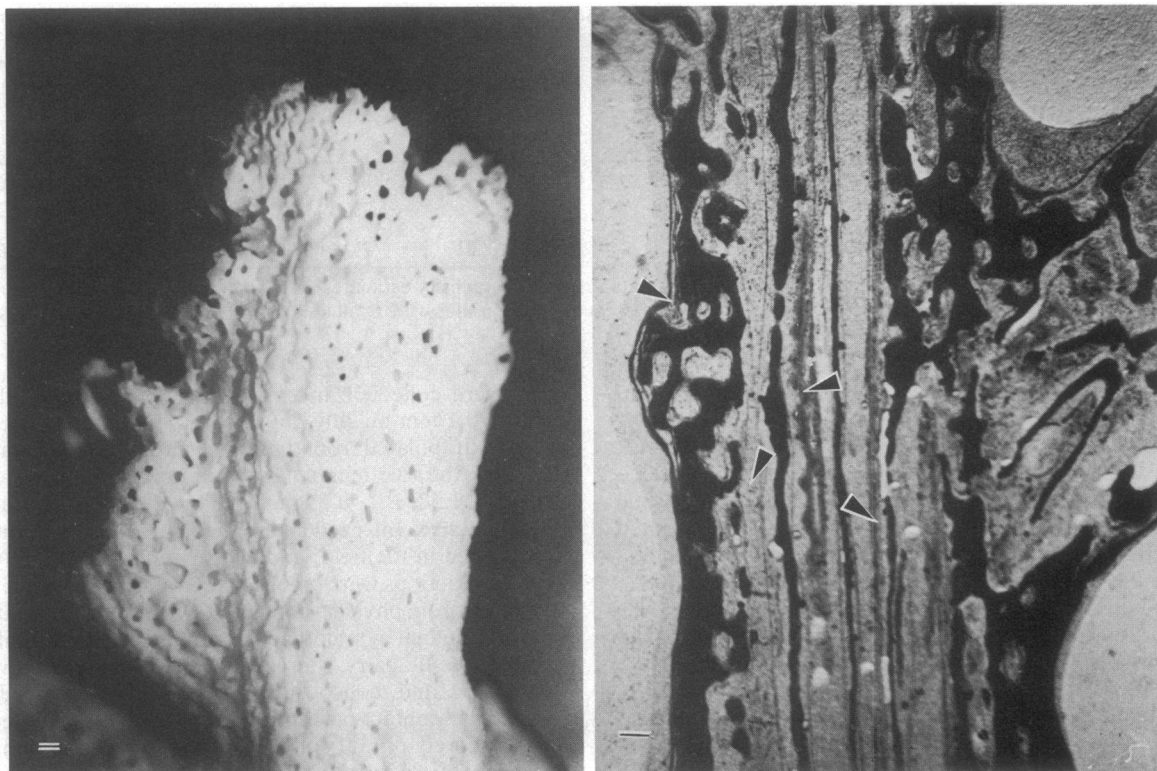


FIG. 2. (Left) Light micrograph of apical portion of the skeleton of *T. micrantha*, illustrating the high porosity of the skeleton. (Bar = 1 mm.) (Right) Light micrograph of a thin-ground longitudinal section of *T. micrantha*, illustrating the deposition of tissue and skeleton. The dark perforated components represent the aragomitic skeleton. Arrowheads indicate animal tissue. (Bar = 1.2 mm.)

of *A. echinata* and predominant acroporids on outer reef environments (ref. 9, p. 214), the growth rate of *T. micrantha* was equal to or greater than the three poritid species which dominate inner reef habitats [Table 1; *Porites andrewsi*, 3.5 ± 0.55 cm/yr ($n = 46$); *P. lutea*, 1.3 ± 0.20 cm/yr ($n = 15$); and *P. (Synaraea) iwayamensis*, 3.8 ± 0.68 cm/yr ($n = 15$)]. Comparisons of *Tubastraea* with all three poritid species indicate significant differences in growth (Kruskal-Wallis test, $P < 0.05$).

How is rapid linear skeletal extension reconciled with low calcification rates? Examination of histological sections of decalcified tissues and of thin-ground sections with tissue and skeleton in place revealed that the animal tissue pervades much of the skeleton (Fig. 2). Rapid extension is possible because skeletal material is spread out to form a thin scaffolding to accommodate rapid proliferation of tissue. Further along the colony, toward the base, the skeleton becomes denser as the primary cavities become secondarily filled in, so that the bases of large colonies are very dense and robust.

Aggressive Interactions. A summary of the results of experimentally induced pairwise comparisons and observations on naturally occurring interactions is presented in Table 2. These data indicate that *T. micrantha* is capable of withstanding the attack of or actually inflicting damage on the predominant symbiotic corals on inner reefs. Conversely, two predominant corals on outer reefs, *Acropora hyacinthus* and *Montipora* spp., demonstrate a marked tendency to inflict damage on the tissues of *T. micrantha*. Thus, these data indicate an aggression hierarchy with acroporids $>$ *T. micrantha* $>$ poritids. This hierarchy is consistent with observed patterns of abundance of *Tubastraea* on inner and outer reefs.

Predation Experiments. Results of the predator/prey choice experiments unequivocally indicate that *A. planici* has a preference for acroporids and pocilloporids over poritid

corals (Table 3). *T. micrantha* was never attacked, even after 6 weeks exposure to the seastars in nonchoice experiments. The validity of these results was confirmed by daily observations on the feeding activity of 10 *Acanthaster* in the field over an 8-day period. The electivity indices show a strong preference for acroporids (+0.71) and an avoidance of

Table 2. Experimental and naturally occurring interspecific interactions between *T. micrantha* and several symbiotic corals

Opponent species	<i>T. micrantha</i>			Binomial probability ($P = 0.5$)
	Wins	Losses	No inter-action	
Experimental pairwise comparisons				
<i>Pocillopora damicornis</i>	2	1	2	0.50
<i>Acropora echinata</i>	2	2	1	0.68
<i>Porites andrewsi</i> *	4	0	1	0.06
<i>Porites lutea</i> *	5	0	0	0.03
<i>Porites (Synaraea) iwayamensis</i> *	0	1	4	—
Naturally occurring interactions				
<i>Acropora hyacinthus</i> †	2	12	3	0.006
<i>Montipora</i> spp.†	0	8	0	0.003
<i>Pocillopora robusta</i>	8	0	2	0.003
<i>Stylophora mordax</i>	2	2	0	0.68
<i>P. andrewsi</i> *	4	0	0	0.06
<i>P. lutea</i> *	10	0	0	0.001
<i>P. (S.) iwayamensis</i> *	6	2	0	0.03
<i>Millepora tenera</i> *	6	0	0	0.015

See text for definitions of win and loss.

*Predominant on inner reefs.

†Predominant on outer reefs.

Table 3. Results of prey-choice experiments with *Acanthaster*

	Order of attack in six independent experiments			
	1st	2nd	3rd	Not attacked
Preferred				
<i>Acropora echinata</i>	5	1	0	0
<i>Pocillopora damicornis</i>	1	3	1	1
Nonpreferred				
<i>Porites lutea</i>	0	1	2	3
<i>P. (S.) iwayamensis</i>	0	1	2	3
<i>P. andrewsi</i>	0	0	1	5
Avoided				
<i>T. micrantha</i>	0	0	0	6

Daily observations over a 2-week period recorded the sequence of attack in six independent experiments. In two separate trials conducted with *Tubastraea* only, no colonies were attacked after 6 weeks.

poritids (-0.97) and *T. micrantha* (-1.0) in 179 observed feeding bouts (24).

DISCUSSION

Although we could not assess the reproductive potential and recruitment rates of *T. micrantha* and, hence, cannot address the role of these factors on the distribution of this coral, our results strongly indicate that coexistence of *T. micrantha* with symbiotic corals and its abundance on open reef environments are made possible by the combination of its relatively rapid growth, aggressive competitive abilities, and resistance to predation by *Acanthaster*.

If coexistence is determined by growth rate and aggressive ability, then *T. micrantha* is competitively equal or superior to the poritid corals that dominate inner reef habitats. In areas dominated by acroporid corals, *T. micrantha*, by virtue of its slower growth and inability to avoid tissue destruction by acroporids, would persist only if another force controlled the acroporid population in a selective manner. Our observations show that *A. planci* does not prey on *T. micrantha*, but catastrophic predation by *A. planci* is known to reduce local populations of acroporids to zero (18). Full recovery of decimated reef areas is estimated to take 10–20 years (18, 25), adequate time for vertically growing colonies of *T. micrantha* to attain a size sufficient to avoid overgrowth by acroporid corals. We saw evidence, however, that laterally extending acroporids that made contact with the bases of colonies of *T. micrantha* inflicted tissue damage. These areas were subsequently invaded by several excavating invertebrates whose boring weakens the colony and eventually results in its collapse (26, 27). These events probably limit the abundance of *T. micrantha* on outer reefs. Thus, although it may attain a refuge in size from competitive overtopping, *Tubastraea*'s long-term persistence in this environment may be dependent on the compensatory mortality that occurs during periodic population explosions of *A. planci*.

In spite of the long geological history of coral reefs, *T. micrantha* appears to be the only nonsymbiotic coral to assume an open reef existence where symbiotic species predominate (28). *T. micrantha*'s success in this environment can be attributed not to any single factor but rather to a combination of physiological attributes and ecological circumstances. Despite low rates of calcification, *T. micrantha* has a rapid linear growth rate and erect morphology which can prevent competitive overtopping. The trade-off for a coral possessing rapid linear growth with a low calcification rate, however, is vulnerability to mechanical destruction (29). *Tubastraea*'s erect morphology, oriented perpendicular to the direction of water flow, is hydrodynamically unstable

and leads to frequent fragmentation of branches (unpublished data). Although this can be potentially advantageous for purposes of asexual reproduction (30), examination of broken pieces lying at the base of living colonies indicates that the regenerative capabilities of fragments are limited, if present at all. It is likely that the persistence of *Tubastraea* in protected and semiprotected open habitats in Belau is related, at least in part, to the rare occurrence of typhoons or storms severe enough to cause extensive damage to corals (31). In general, the costs associated with assuming a rapid growth form may impose severe limitations on the ecological and evolutionary success of corals unable to withstand damage from physical perturbations or regenerate rapidly from fragmentation. This factor, perhaps, accounts for the relative paucity of nonsymbiotic corals in most open reef environments.

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