

## REPORT

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## The role of colony morphology and substratum inclination in the success of *Millepora alcicornis* on shallow coral reefs

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**Abstract** *Millepora* species are conspicuous members of shallow coral reefs where they occupy a variety of substrata and produce morphologically complex skeletons. This study focuses on the roles of growth on vertical and horizontal surfaces and the production of encrusting bases and branches (a “sheet-tree” morphology) for the success of the *Millepora alcicornis* on coral reefs. The effects of inclination were investigated by comparing the size and growth rates of *M. alcicornis* on vertical and horizontal surfaces at 3–5 m depth, in St. John, US Virgin Islands. The consequences of morphological complexity were investigated by comparing polyp density, chlorophyll content and biomass between encrusting bases and branches; the role of branches in asexual reproduction was also quantified. Colonies on vertical surfaces had larger encrusting bases, longer perimeters and lower densities of branches compared to those on horizontal surfaces. Growth rates also varied significantly between surfaces, largely because colonies on horizontal surfaces shrank in area while those on vertical surfaces increased in area, albeit slowly. Branches were not specialized in comparison to encrusting bases in terms of the density of dactylozooids and gastrozooids, chlorophyll content and biomass, but they were effective asexual propagules. During one storm, 79% of the branches were removed from colonies of *M. alcicornis*, and 4% attached to the substratum to produce new colonies at a density of  $\approx 0.5$  colonies.m<sup>-2</sup>. Anecdotal observations suggest that such storms rarely damaged encrusting bases on vertical surfaces, but often destroyed those on horizontal surfaces. Thus, the encrusting bases on vertical surfaces are likely to be large because of greater age rather than faster growth, while those on horizontal surfaces are likely to be small because they are relatively

young and short lived. These findings suggest that the success of *M. alcicornis* is a result, in part, of the beneficial consequences of their “sheet-tree” morphology, that supports: (a) slow growth and resistance to wave damage of encrusting bases on vertical surfaces, and (b) the use of branches as asexual propagules.

**Key words** Structure · Growth · Morphology · Fire coral · *Millepora*

### Introduction

Calcareous hydrocorals in the genus *Millepora* produce conspicuous colonies on shallow coral reefs throughout the world (Boschma 1948; deWeerd 1984). In some locations they contribute to reef construction (Adey and Burke 1977), become spatially dominant (Witman 1988, 1992) and play a central role in community ecology (Lewis 1989) similar to that of zooxanthellate scleractinians (Sheppard 1982). However, despite the ecological prominence of *Millepora*, their biology has received relatively little attention compared to the sympatric scleractinians. Therefore, there is much to learn about *Millepora* (e.g., Lewis 1989; Frank et al. 1995; Vago et al. 1998), including how they achieve success in shallow coral reef environments where space typically is a limiting resource (Jackson 1977).

Some parallels can be drawn between the biology of *Millepora* and scleractinian corals (e.g., Schonwald et al. 1987, 1997), because of the possible functional convergence between these taxa (Lewis 1989). Both the Milleporina and the Scleractinia share a common body plan (Brusca and Brusca 1990) and members of both orders contain symbiotic dinoflagellates. The symbionts of *Millepora* support autotrophy, nutrient recycling and light-enhanced calcification (Achituv and Mizrahi 1996; Schonwald et al. 1997), as they do in scleractinians (Muller-Parker and D’Elia 1996).

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Additionally, both coral orders produce morphologically complex, calcareous skeletons that display a high degree of phenotypic plasticity (deWeerd 1981; Bruno and Edmunds 1997; Vago et al. 1998). Regardless of these similarities, the *Milleporina* and the *Scleractinia* belong to classes that diverged as early as the Pre-Cambrian (Conway Morris 1993), and differ in a number of ways including the presence of medusae and polymorphic polyps in most hydrozoans but not in anthozoans (Brusca and Brusca 1990). The life-history characteristics of *Millepora* will be shaped, in part, by their pelagic medusae, while their defense and feeding will be affected by the polymorphism and arrangement of the defensive dactylozooids surrounding the feeding gastrozooids (de Kruijf 1975).

*Millepora* also differs from scleractinians in the habitats where it is most successful and the morphological strategy it exploits. For example, in the Caribbean *Millepora* species are most abundant in shallow, turbulent environments (Lewis 1989), where the *Scleractinia* are limited to species with wave-resistant morphologies (Sheppard 1982; Sebens and Done 1992). In such locations *Millepora* can exploit available substrata through directional overgrowth (e.g., Wahle 1980) and the use of branches in asexual reproduction (Lewis 1991). Branches are an integral component of the morphological strategy of most *Millepora* species, and are formed typically as outgrowths from thin, encrusting bases (deWeerd 1981; Vago et al. 1998). Extensive "sheet-tree" morphologies are not common among scleractinians in the Caribbean (*Acropora palmata* provides one notable example) or other colonial, marine invertebrates (Jackson 1979), and may be important to the success of *Millepora*. This study focuses on the potential benefits of the "sheet-tree" morphology of *Millepora*, with the goal of understanding how the *Milleporina* achieve success on shallow coral reefs.

The shallow fringing reefs of St. John, US Virgin Islands, are similar to those found throughout the northeast Caribbean (Edmunds et al. 1990), and support large populations of *Millepora complanata* and *M. alcicornis*. The reef structure is dominated by rock walls (Witman 1992) and boulders made of metamorphosed volcanic rock (Donnelly 1966). The encrusting bases of *M. complanata* and *M. alcicornis* can cover up to 65% of this substratum (Witman 1988, 1992), and individual colonies can spread several meters and produce a dense forest of branches (e.g., Fig. 2 in Witman 1988). Although colonies grow on a diversity of substrata, the largest are found on rocky surfaces inclined vertically rather than horizontally (P.J. Edmunds, personal observation). This study was designed to address three questions using *M. alcicornis* as an example of a *Millepora* that exploits a "sheet-tree" morphology:

1. Are there beneficial consequences to growing on vertical or horizontal surfaces in terms of growth rate and colony size?

2. Are there differences in the polyp density, chlorophyll content or biomass of encrusting bases and branches that might make it advantageous to produce one structure instead of another?

3. Do branches play a functionally important role in asexual reproduction? The ability of *Millepora* to grow by aggressively covering other taxa (*sensu* Wahle 1980) was not investigated explicitly because this strategy was exhibited rarely by *M. alcicornis* on the shallow reefs of St. John.

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## Methods

Research was completed at the Virgin Islands Environmental Resource Station, located in Great Lameshur Bay on the south coast of St. John. Colonies of *Millepora alcicornis* growing on vertical and horizontal surfaces (15 colonies for each orientation) were monitored for a year to quantify size and growth as a function of inclination. Polyp density, chlorophyll content, and biomass were compared between encrusting bases and branches to determine whether there are functional consequences to producing these structures. An opportunity to determine whether broken branches have a role in asexual reproduction was created by Hurricane Gilbert in 1988.

### Colony size and growth

Colony size was determined from the area and perimeter length of the encrusting bases, together with the number and length of branches. Because changes in colony size can be a result of the growth of encrusting bases and/or branches, growth rates were measured in three ways: (1) the change in area of encrusting bases, (2) the change in length of branches, and (3) the proliferation of branches. To determine the effect of inclination on *Millepora alcicornis*, sizes and growth rates were compared among 15 colonies selected arbitrarily on vertical and horizontal surfaces (total of 30 colonies). All colonies were tagged to allow relocation, and were situated between 3 and 5 m depth at the Tektite site within Great Lameshur Bay.

The area and perimeter of encrusting bases were obtained by digitizing photographs taken in 1987 and 1988. Photographs were taken using a Nikonos V camera and strobe that were held perpendicular to the substratum; a 0.5 × 0.5 m quadrat was included in each frame to provide a scale. The growth rates of encrusting bases were calculated from the change in area and were expressed per colony ( $\text{cm}^2 \cdot \text{y}^{-1}$ ). It is difficult to quantify branches of *Millepora alcicornis* because they are complex structures that originate from a basal point of attachment, furcate distally to produce multiple growing points, and can fuse with adjacent branches. Therefore, a single branch was defined as the sum of all the growing points attached to its base, and branch length was taken as the distance between the site of attachment and the tip of the growing points. Because each branch usually had many growing points, multiple length measurements were obtained for each branch. The number of branches on each colony was counted in the photographs taken in 1987 and 1988, and was used to calculate both the density of branches ( $\text{branches} \cdot \text{m}^{-2}$  of encrusting base) and their growth rates normalized per colony ( $\text{branches} \cdot \text{colony}^{-1} \cdot \text{y}^{-1}$ ) and per area of encrusting base ( $\text{branches} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ ). The linear growth of branches was calculated by measuring their length in 1987 and 1988 using vernier calipers. The length to every growing point was measured on small colonies, but a haphazardly selected subsample of growing points ( $n = 45$  per colony) was measured on colonies with numerous branches. The change in length was used to calculate linear growth ( $\text{mm} \cdot \text{y}^{-1}$ ).

Colony sizes were compared between vertical and horizontal surfaces using the 1987 values of the area and perimeter of the encrusting bases, together with the density and length of branches. Growth rates were compared between surfaces using the changes occurring between 1987 and 1988 in the area of the encrusting base, the density of branches and their length. To test the null hypothesis of no difference in colony size between horizontal and vertical surfaces more rigorously, additional colonies were measured in 1998. These colonies were selected at random on horizontal and vertical surfaces between 3 and 5 m depth; randomization was accomplished by selecting the first colony encountered after swimming blindly for two fin strokes. The maximum and minimum diameters of the encrusting bases were recorded, and colony size was calculated as the average of the two values.

#### Polyp density, chlorophyll content and biomass

To identify differences between encrusting bases and branches, their polyp density and chlorophyll content were measured on fragments collected from each of 10 colonies on horizontal surfaces at 3–5 m depth. Additional pieces were collected from different colonies at the same depth for the determination of biomass. These variables were selected because polyp density provides a measure of the defense and feeding capabilities, chlorophyll content provides an indication of photosynthetic capabilities, and biomass provides a measure of living tissue that is independent of calcareous structures.

Polyp density was assessed as the number of pores in the skeleton. A dissecting microscope was used together with mini-quadrats (1 cm<sup>2</sup>,  $n = 3$  on each piece) to count the large gastropores and the small dactylopores. Biomass was determined by fixing fragments in 5% formalin, decalcifying in 10% HNO<sub>3</sub>, and cutting triplicate samples of the tissue layer (each 1 cm<sup>2</sup>) and drying them to a constant weight at 60 °C. Polyp density and biomass were expressed per cm<sup>2</sup>. Chlorophyll a content was measured by extracting fragments in 100% acetone overnight (4 °C) and calculating concentrations according to Jeffrey and Humphrey (1975). The surface areas of the extracted fragments were obtained by counting the total number of gastropores and dividing by the mean gastropore density for encrusting bases or branches as necessary (obtained from different fragments as described); chlorophyll a content was expressed as µg.cm<sup>-2</sup>. Gastropore density was used to determine surface area because gastropores were uniformly distributed on the surface of the encrusting bases and branches.

#### Fragmentation

In 1988 Hurricane Gilbert (September 9 to 11) damaged many colonies of *Millepora alcicornis* and provided the opportunity to quantify the role of broken branches in asexual reproduction. The number of broken branches was determined on October 7, 1988, by taking color photographs of 0.25-m<sup>2</sup> areas on each of 12 colonies at 3 m depth. Colonies were photographed as encountered while swimming along the depth contour. Because recently broken branches leave white scars that are visible in photographs, branch loss was estimated as the number of scars as a percentage of scars plus attached branches. This generated a conservative value since some branches and branch scars were not visible in planar photographs, and because multiple fragments can be derived from a single scar.

To determine the survivorship of broken branches, fragments were censused between December 1988 and April 1989 using 1-m<sup>2</sup> quadrats placed contiguously along the 3 m, 6 m and 10 m depth contours. Fragments were identified by their irregular shape and were recorded as attached or unattached. Attached fragments spread tissue and skeleton over the substratum that prevented their movement when touched lightly. To determine if there was a relationship

between substratum type and attachment, the substratum under the fragments was categorized as rock, sand or conspecific. Fragments were recorded as unattached if they were not secured to the substratum, irrespective of whether they were alive (tissue present) or dead. Fragments that had been broken before Hurricane Gilbert and that had been lying on the reef longer than the 3 to 7 months between the storm and the surveys were excluded from the analyses. Fragments that had been formed by earlier storms were recognized by the absence of a fresh fracture site, heavy growths of encrusting taxa, or by their complete overgrowth by *Millepora* tissue from attached colonies.

#### Statistical analyses

Statistical analyses were completed with Systat 5.2. As several dependent variables were used to compare colonies between vertical and horizontal surfaces (independent variable I), and between encrusting bases and branches (independent variable II), multivariate and univariate statistics were used wherever possible to test the null hypothesis of no difference between the levels of each independent variable. First, MANOVA was used to examine the overall effect of the independent variable and, where this was significant, ANOVA was completed for each dependent variable. Bonferroni adjustments ( $\alpha'$ ) were used to detect significant univariate effects with an overall type I error rate of 0.05 (Tabachnick and Fidell 1996). Data were log-transformed as necessary and then tested for normality (Kolmogorov-Smirnov test,  $\alpha = 0.05$ ) and homoscedasticity ( $F_{max}$  test) before proceeding with the MANOVAs and ANOVAs.

Biomass was compared between the encrusting bases and branches using a *t*-test. To determine whether growth rates were related to the initial area of the colonies, or whether areal growth was related to the initial perimeter length of the colonies, correlation analyses were used with Bonferroni adjustments ( $\alpha'$ ). The results were used to determine whether the area or perimeter should be used as covariates in the analysis of growth.

The number of branch fragments generated by Hurricane Gilbert that were found attached or detached were compared among substrata using a contingency table (23; attached/detached versus substratum type) and  $\chi^2$  analyses; data were pooled by depth as heterogeneity  $\chi^2$  analysis (Zar 1996) showed that the data were homogeneous (heterogeneity  $\chi^2 = 2.896$ ,  $df = 4$ ,  $0.750 > P > 0.500$ ). To determine the relative success of fragments attaching to each substratum type, the percentages attaching on each substratum were compared among substrata with a Kruskal-Wallis test.

## Results

### Colony size and growth

In 1987 colonies of *Millepora alcicornis* ranged in area from 287 to 4357 cm<sup>2</sup> on vertical surfaces, and from 99 to 852 cm<sup>2</sup> on horizontal surfaces; their perimeters ranged from 80 to 710 cm, and from 54 to 216 cm, respectively. Branch densities ranged from 46 to 422 branches.m<sup>-2</sup> on vertical surfaces, and from 148 to 611 branches.m<sup>-2</sup> on horizontal surfaces. Branch length was less variable, ranging from 22 to 61 mm on vertical surfaces and from 35 to 104 mm on horizontal surfaces (Fig. 1). MANOVA completed with all 4 measures of size showed that inclination had a significant effect on colony size (Wilks'  $\lambda = 0.507$ ,  $F = 6.078$ ,  $df = 4,25$ ,  $P = 0.001$ ). The subsequent ANOVAs ( $\alpha' = 0.014$ ) showed that inclination had a significant effect on area

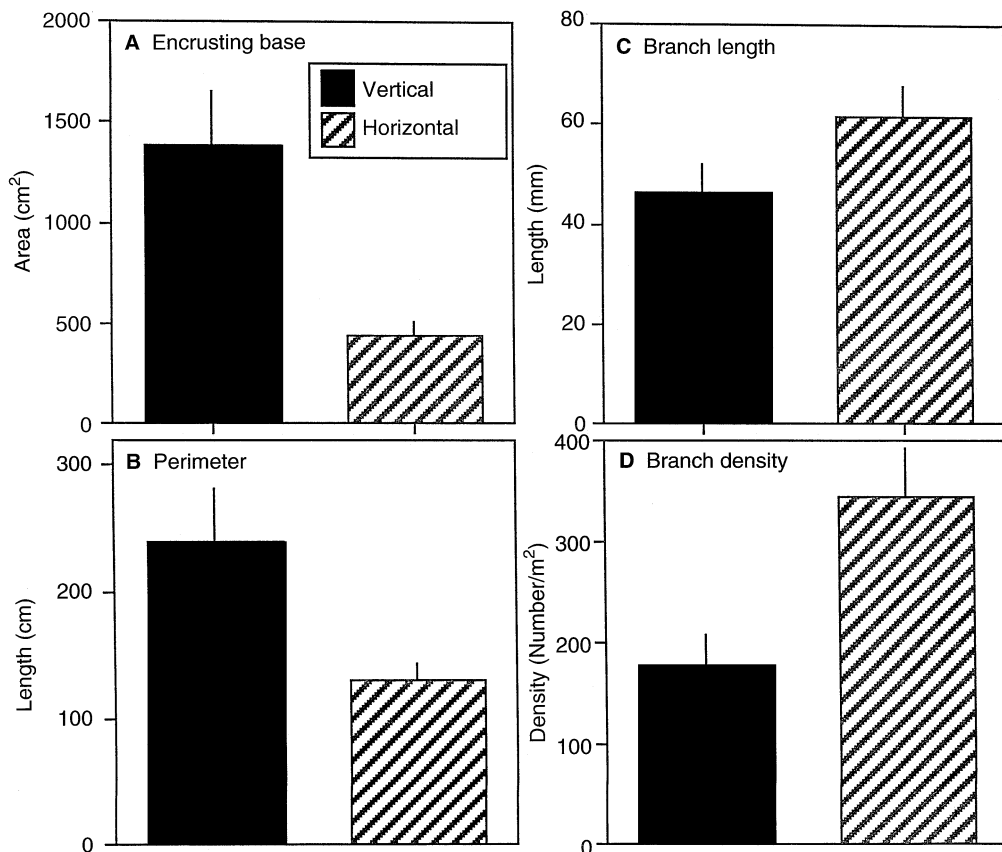
( $F = 17.554$ ,  $df = 1,28$ ,  $P = 0.000$ ), perimeter ( $F = 7.776$ ,  $df = 1,28$ ,  $P = 0.009$ ) and branch density ( $F = 10.721$ ,  $df = 1,28$ ,  $P = 0.003$ ), but not branch length ( $F = 5.009$ ,  $df = 1,28$ ,  $P = 0.033$ ). Thus colonies on vertical surfaces had larger areas, longer perimeters and fewer branches than those on horizontal surfaces (Fig. 1). The surveys completed in 1998 confirmed this trend by showing that colonies on vertical surfaces were  $37.6 \pm 2.9$  cm in diameter (mean  $\pm$  SE,  $n = 81$ ) but on horizontal surfaces they were  $19.7 \pm 1.3$  cm in diameter (mean  $\pm$  SE,  $n = 80$ ); colony sizes were significantly different between surfaces ( $t = 5.578$ ,  $df = 159$ ,  $P < 0.001$ ).

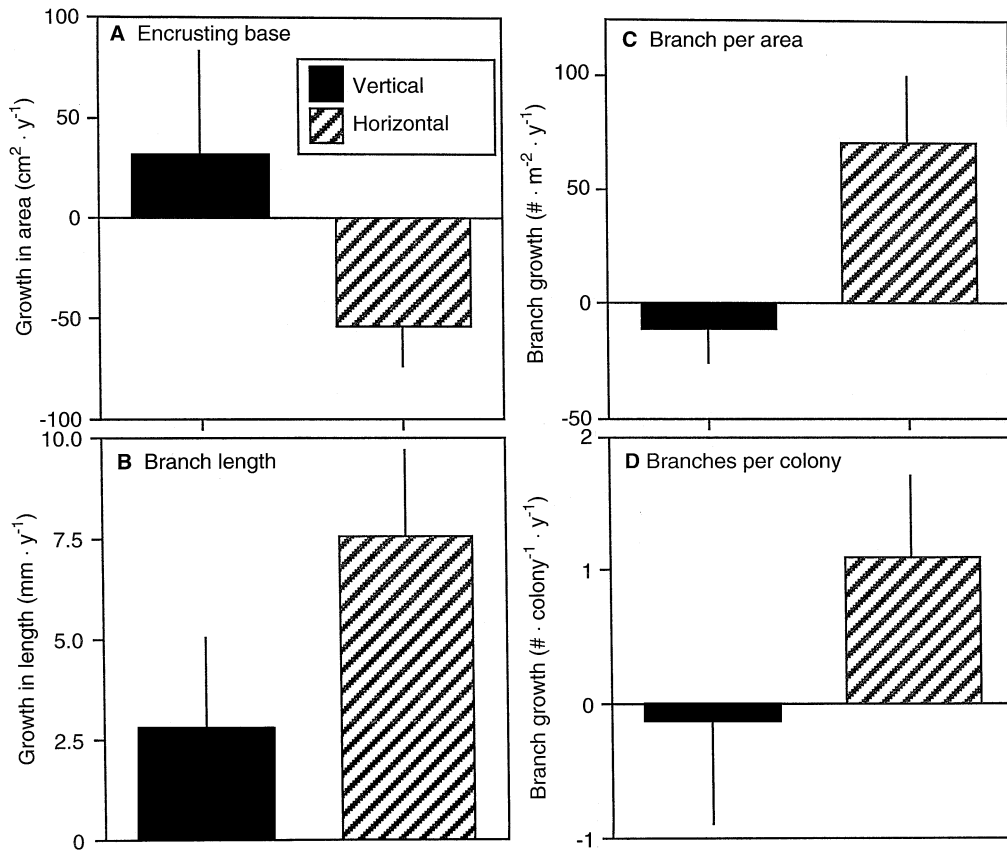
Between 1987 and 1988 the tagged colonies changed area, branch length and branch density, although the direction of the changes varied (Fig. 2). As a result of partial mortality seven of the 15 colonies on vertical surfaces, together with 12 of the 15 colonies on horizontal surfaces, decreased in area while the remainder increased in area. Thus, while some colonies increased in area by as much as  $478 \text{ cm}^2 \cdot \text{y}^{-1}$  on vertical surfaces and  $112 \text{ cm}^2 \cdot \text{y}^{-1}$  on horizontal surfaces, others shrank by as much as  $295 \text{ cm}^2 \cdot \text{y}^{-1}$  and  $139 \text{ cm}^2 \cdot \text{y}^{-1}$ , respectively. Similarly, increases and decreases were recorded in branch characteristics. A mean of  $10.0 \pm 1.0\%$  ( $\pm$  SE,  $n = 30$  colonies) of all branches were lost through breakage (not significantly different between surfaces,  $t = 1.194$ ,  $df = 28$ ,  $P = 0.243$ ), but new branches were added at rates of up to seven

branches.colony $^{-1} \cdot \text{y}^{-1}$  on vertical surfaces and six branches.colony $^{-1} \cdot \text{y}^{-1}$  on horizontal surfaces. When branch proliferation was normalized to the surface area of the encrusting bases, the values were larger and more variable (Fig. 2) because the encrusting bases were  $< 1 \text{ m}^2$  in area and also changed over time.

Although the areas of the 15 colonies on vertical and horizontal surfaces varied 15- and 9-fold in 1987, respectively, the initial size had no effect on growth rates. None of the measures of growth were significantly correlated with colony area, or the log of the colony area, on either vertical or horizontal surfaces ( $r \leq |0.61|$ ,  $P > 0.04$ ,  $n = 15$  for each comparison except for branch density on horizontal surfaces where  $n = 14$ ,  $\alpha' = 0.013$ ). Additionally, growth of the encrusting bases was not significantly correlated with perimeter length for colonies on either surface ( $r \leq |0.53|$ ,  $P > 0.07$ ,  $n = 15$  for each comparison,  $\alpha = 0.050$ ). Therefore, the initial areas or perimeters of the encrusting bases were not used as covariates in the comparison of growth rates between surfaces.

**Fig. 1A–D** Comparison of the size of colonies of *Millepora alcicornis* on vertical and horizontal surfaces at 3 to 5 m depth in St. John: **A** The area of encrusting bases; **B** the perimeter length of encrusting bases; **C** the length of branches, and **D** the density of branches per area of encrusting base. Values displayed are mean  $\pm$  SE;  $n = 15$  for all variables





**Fig. 2A–D** Comparison of growth rates of *Millepora alicornis* on vertical and horizontal surfaces at 3 to 5 m depth in St. John: **A** Growth of the encrusting bases; **B** growth in length of branches; **C** branch proliferation per area of encrusting base, and **D** branch proliferation per colony. Values displayed are mean  $\pm$  SE; all sample sizes were 15 except for branches per area on horizontal surfaces ( $n = 14$ ), where the statistical outlier of 1,885 branches.  $m^{-2} \cdot y^{-1}$  was excluded from all analyses. Linear growth of branches was obtained by averaging individual measurements for each colony so that each colony provided one statistical replicate; these determinations are based on a total 324 branches on vertical colonies and a total of 299 branches on horizontal colonies

MANOVA completed with all four measures of growth showed that inclination had a significant effect on growth rates (Wilks'  $\lambda = 0.652$ ,  $F = 3.203$ ,  $df = 4, 24$ ,  $P = 0.031$ ). The subsequent ANOVAs ( $\alpha' = 0.014$ ) showed that inclination had no significant effect on the growth of the encrusting bases ( $F = 2.150$ ,  $df = 1, 27$ ,  $P = 0.154$ ), branch proliferation per colony ( $F = 0.930$ ,  $df = 1, 27$ ,  $P = 0.344$ ), branch proliferation per area ( $F = 6.092$ ,  $df = 1, 27$ ,  $P = 0.020$ ) or the growth in branch length ( $F = 2.245$ ,  $df = 1, 27$ ,  $P = 0.146$ ). However, based on the low significance level of the univariate analysis of branch proliferation per area, the multivariate effect of inclination on growth rate was probably a result of the rapid increase in the number of branches relative to the area of the encrusting base for colonies on horizontal surfaces (Fig. 2).

#### Polyp density, chlorophyll content and biomass

Polyp density, chlorophyll content and biomass were similar in encrusting bases and branches (data not shown), and there were no significant difference between these structures in either their multivariate characteristics (i.e., dactylozoid density, gastrozoid density, and chlorophyll a content) (MANOVA: Wilks'  $\lambda = 0.815$ ,  $F = 1.212$ ,  $df = 3, 16$ ,  $P = 0.337$ ) or biomass ( $t = 1.032$ ,  $df = 13$ ,  $P = 0.321$ ). Biomass was not included in the MANOVA as it was measured on separate pieces of *Millepora alicornis*. Because there were no significant differences between encrusting bases and branches, the data were pooled to describe the polyp density, chlorophyll content and biomass of *M. alicornis*. Overall, there were  $34.1 \pm 1.4$  gastrozooids. $cm^{-2}$  ( $n = 20$ ) and  $169.4 \pm 9.8$  dactylozooids. $cm^{-2}$  ( $n = 20$ ) arranged with  $\approx 5$  dactylozooids surrounding each gastrozoid; the dry tissue biomass was  $4.6 \pm 0.4$  mg. $cm^{-2}$  ( $n = 15$ ) and contained  $5.76 \pm 0.59$   $\mu g$ . $cm^{-2}$  of chlorophyll a.

#### Fragmentation

After Hurricane Gilbert passed by St. John, the density of branches and branch scars on *Millepora alicornis* at 3 m depth was  $19 \pm 3$  per  $0.25 m^2$  of substratum (mean  $\pm$  SE,  $n = 12$  quadrats), and a median of 79%

**Table 1** Contingency table displaying the number of branch fragments of *Millepora alcicornis* that were attached or detached from the substratum as a function of substratum type. Expected values are shown in parentheses. The fate of the branches was not independent of the substratum type ( $\chi^2 = 358.921$ ,  $df = 2$ ,  $P < 0.001$ ).

	Substratum type			Total
	Rock	<i>Millepora alcicornis</i>	Sand	
Attached	51 (125)	105 (25)	6 (13)	162
Detached	912 (838)	84 (165)	94 (87)	1,090
Total	963	189	100	1,252

(range 56%–100%) were removed by the hurricane. Overall, 1,252 fragments of *M. alcicornis* were found ( $n = 100$  quadrats; 189 were lying on conspecifics, 963 on rock and 100 on sand). Thirteen percent were attached to the underlying substratum; 8.4% to conspecifics, 4.1% to rock and 0.5% to sand. All other fragments were unattached. Therefore Hurricane Gilbert produced at least 0.5 colonies of *M. alcicornis* per  $m^2$  of substratum (from 4.1% of 1,252 fragments in 100 quadrats).

The number of fragments that were attached or detached depended significantly on the substratum on which they landed (Table 1). Attachment occurred in 56% of fragments found on living conspecific ( $n = 42$  quadrats), 5% of fragments on rock ( $n = 77$  quadrats) and 6% of fragments on sand ( $n = 19$  quadrats). Substratum-specific attachment was significantly higher on *M. alcicornis* than on other substrata (Kruskal-Wallis test,  $H = 80.694$ ,  $P < 0.001$ ).

## Discussion

On the shallow reefs of St. John, the sizes and growth rates of *Millepora alcicornis* differed significantly between vertical and horizontal surfaces. Colonies had larger encrusting bases with longer perimeters and lower densities of branches on vertical surfaces. The analysis of growth rates suggests that these differences were a result of poor growth performance (i.e. reduction in area) on horizontal surfaces rather than rapid growth on vertical surfaces. Although there was no evidence that the branches were specialized for a specific purpose through changes in polyp density, chlorophyll content or biomass, there was a strong indication of their role in asexual reproduction. Together with the overall slow growth of encrusting bases on vertical surfaces (see Wahle 1980; Frank et al. 1995), and the mortality of the small colonies on horizontal surfaces during storms (P.J. Edmunds personal observation), the present results suggest that the success of *Millepora* in this habitat is related to: (a) the slow growth and resistance to wave damage of encrusting bases on

vertical surfaces, and (b) the use of branches as asexual propagules.

Previous studies suggest that the success of *Millepora* can be attributed to rapid growth (Wahle 1980), the overgrowth of adjacent taxa (Wahle 1980; Müller et al. 1983; Lewis 1996), resistance to wave stress (Witman 1992), asexual reproduction (Lewis 1991, 1996), the potential for autotrophy (Schonwald et al. 1997) and voracious zooplanktivory (Lewis 1992). The present study underscores the importance of colony shape in the success of *Millepora*, specifically the use of a “sheet-tree” morphology in a turbulent and spatially heterogeneous environment. Complex and plastic morphologies are well known in both the Scleractinia (e. g., Bruno and Edmunds 1997) and the Milleporina (deWeerd 1981; Lewis 1989; Vago et al. 1998), but evidence of their adaptive value is rare (e.g., Bruno and Edmunds 1997). In *M. alcicornis* the “sheet-tree” morphology appears to have a number of beneficial consequences. Whether or not it is adaptive can only be determined by quantifying fecundity as a function of morphology, and demonstrating how morphology arose through natural selection for its present role (Koehl 1996).

One reason for the slow growth of encrusting bases of *Millepora alcicornis* in this study (see Wahle 1980; Frank et al. 1995) may be that lateral spreading was inhibited by the algal turf that surrounded most of the colonies. Algal turf can inhibit the growth of other sessile taxa including scleractinians (Birkeland 1977), and it is possible that rapid growth of *M. alcicornis* is achieved only when algal turf is removed by processes such as grazing (Carpenter 1986) or storms. Because horizontal surfaces are characterized by high growth rates of algal turf and elevated sedimentation (Birkeland 1977; Rogers et al. 1984), competition with algal turf and sediment burial might account for the reduction in area of encrusting bases on horizontal surfaces (Fig. 2). Such effects are likely to be chronic rather than acute and, therefore, could routinely inhibit the growth of *M. alcicornis* on horizontal surfaces. The large colonies on vertical surfaces are likely to be a result of age rather than growth effects, because the growth rates of encrusting bases (Fig. 2) did not differ significantly between surfaces.

Branching morphologies are found in a wide variety of taxa and have a number of selective advantages. These include roles in competitive interactions, zooplanktivory, mass transfer, the interception of light, and asexual reproduction (Porter 1976; Jackson 1979; Highsmith 1982; Patterson 1992; Sebens et al. 1997). In *Millepora alcicornis* branches were not structurally specialized. However, their function may change with size (Koehl 1996). For example, branches increase the total number of polyps and the volume of water that is sampled for food particles, without requiring an increased commitment to spreading over the substratum (Jackson 1979). Under ecologically relevant flow

conditions the branches of *M. alcornis* probably capture more zooplankton than the encrusting bases (Sebens 1997), and may also exhibit increased photosynthetic rates because of the enhanced mass transfer associated with cylindrical, branching morphologies (Patterson 1992). It is possible that branches assume a greater role in asexual reproduction as they grow in length and increase their chances of breakage (Denny et al. 1985).

The small size and decrease in size observed for *Millepora alcornis* on horizontal surfaces suggests that these colonies turn over relatively fast, yet the sexual recruits to support this flux are found rarely (Bak and Engel 1979). Asexual reproduction provides a potential mechanism to support this turnover. Although only a small percentage (4%) of the branches broken from *M. alcornis* form new colonies, the potential for proliferation by this method is high (at least 0.5 colonies.m<sup>-2</sup> from a single event). This is because of the large number of fragments produced and the resistance to damage of the encrusting bases that produce them. For example, a colony on a vertical surface has between 2 and 59 branches and can lose the majority (79%) in a single storm; branches can be replaced at a maximum rate of seven branches.y<sup>-1</sup> and, with an average length of 46 mm (Fig. 1), will be formed fully within <17 months (the fastest growth rate was 33 mm.y<sup>-1</sup>). Although the average growth rates of branches are lower, and branch length, density and growth rates differ between surfaces (Fig. 2), over a decadal (or longer) time scale asexual reproduction is likely to play an important role in the population structure of *M. alcornis*. If the large colonies on vertical surfaces live for lengthy periods, produce numerous branches and subsequently lose them by breakage, then it is possible that the vertical colonies provide a source of asexual recruits to horizontal surfaces. One prediction of this hypothesis is a clonal population structure and a reduced genetic diversity among colonies on horizontal substrata. Testing of this hypothesis will require the application of molecular genetic techniques, but the high frequency with which branch fragments of *M. alcornis* fuse to conspecifics (fusion occurred in 56% of branches landing on conspecific; see also Lewis 1991) may provide some evidence of extensive clonal proliferation (Müller et al 1983; Niegel and Avise 1983).

This study addresses three questions pertaining to the potential mechanisms that are exploited by *Millepora alcornis* to achieve success on the shallow reefs of St. John. As the ultimate goal was to gain insights into the reasons for the success of the Milleporina, then it is important to know whether (if at all) the present results have general application? Three lines of evidence suggest that the present findings have broad application to other *Millepora* spp. First, the encrusting bases and upright branches that characterizes *M. alcornis* are found also in virtually every species of

*Millepora* (Lewis 1989; Vago et al. 1988). Second, the trait values for *M. alcornis* are similar to those previously reported for *Millepora* spp. including the linear growth of branches (Strömberg 1975; Witman 1988), the net annual growth of encrusting bases (Hughes 1989; Witman 1992), polyp density (deWeerd 1984), chlorophyll a content (Schonwald et al. 1987), and the tissue biomass (calculated from Schonwald et al. 1997). Finally, the habitats favored by *M. alcornis* in St. John are similar to those favored by *Millepora* spp. worldwide (Lewis 1989).

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## References

- Adey WH, Burke RB (1977) Holocene bioherms of Lesser Antilles – Geologic control of development. In: Frost SH, Weiss MP, Saunders JB (eds) Reefs and related carbonates – ecology and sedimentology. Am Assoc Petrol Geol Tulsa 4: 67–81
- Achituv Y, Mizrahi L (1996) Recycling of ammonium within a hydrocoral (*Millepora dichotoma*) - zooxanthellae-cirripede (*Savignium milleporum*) symbiotic association. Bull Mar Sci 58: 856–860
- Bak RPM, Engel MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent community. Mar Bio 54: 341–352
- Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc 3rd Int Coral Reef Symp, Miami 1: 15–21
- Boschma H (1948) The species problem in *Millepora*. Zool Verh Leiden 1: 3–115
- Bruno JF, Edmunds PJ (1997) Clonal variation for phenotypic plasticity in the coral *Madracis mirabilis*. Ecology 78: 2177–2190
- Brusca RC, Brusca GJ (1990) Invertebrates. Sinauer, Sunderland, Massachusetts, p 922
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecol Monogr 56: 345–363
- Conway Morris S (1993) The fossil record and the early evolution of the Metazoa. Nature 361: 219–225
- Denny MW, Daniel TL, Koehl MAR (1985) Mechanical limits to size in wave-swept organisms. Ecol Monogr 55: 69–102
- Donnelly TF (1966) Geology of St. Thomas and St. John, US Virgin Islands. Geol Soc Am Mem 98: 85–176
- Edmunds PJ, Roberts DA, Singer R (1990) Reefs of the north-eastern Caribbean I. Scleractinian populations. Bull Mar Sci 46: 780–789
- Frank U, Brickner I, Rinkevich B, Loya Y, Bak RPM, Achituv Y, Ilan M (1995) Allopathic and xenogenic interactions in reef-building corals may induce tissue growth without calcification. Mar Ecol Prog Ser 124: 181–188

- Highsmith RC (1982) Reproduction by fragmentation in corals. *Mar Ecol Prog Ser* 7: 207–226
- Hughes TP (1989) Community structure and diversity of coral reefs: The role of history. *Ecology* 70: 275–279
- Jackson JBC (1977) Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *Am Nat* 980: 743–767
- Jackson JBC (1979) Morphological strategies of sessile animals. In: Larwood G, Rosen BR (eds) *Biology and systematics of colonial organisms*. Academic Press, London, pp 499–555
- Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem Physiol Pflanzen* 167: 191–194
- Lewis JB (1989) The ecology of *Millepora*. *Coral Reefs* 8: 99–107
- Lewis JB (1991) Testing the coral fragment size dependent survivorship hypothesis in the calcareous hydrozoan *Millepora complanata*. *Mar Ecol Prog Ser* 70: 101–104
- Lewis JB (1992) Heterotrophy in corals: zooplankton predation by the hydrocoral *Millepora complanata*. *Mar Ecol Prog Ser* 90: 251–256
- Lewis JB (1996) Spatial distribution of the calcareous hydrozoans *Millepora complanata* and *Millepora squarrosa* on coral reefs. *Bull Mar Sci* 59: 188–195
- Koehl MAR (1996) When does morphology matter? *Ann Rev Ecol Syst* 27: 501–542
- Kruijf HAM de (1975) General morphology and behaviour of gastrozooids and dactylozooids in two species of *Millepora* (Milleporina, Coelenterata). *Mar Behav Physiol* 3: 181–192
- Müller WEG, Maidhof A, Zahn RK, Müller I (1983) Histoincompatibility reactions in the hydrocoral *Millepora dichotoma*. *Coral Reefs* 1: 237–241
- Muller-Parker G, D'Elia CF (1996) Interactions between corals and their symbiotic algae. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, New York, pp 96–113
- Neigel JE, Avise JC (1983) Clonal diversity and population structure in a reef-building coral, *Acropora cervicornis*: Self-recognition analysis and demographic interpretation. *Evolution* 37: 437–453
- Patterson MR (1992) A chemical engineering view of cnidarian symbioses. *Am Zool* 32: 56–582
- Porter JW (1976) Autotrophy, heterotrophy and resource partitioning in Caribbean reef-building corals. *Am. Nat.* 110: 731–742
- Rogers CS, Fitz HC, Gilnack M, Beets J, Hardin J (1984) Scleractinian coral recruitment patterns at Salt River Submarine Canyon, St. Croix, US Virgin Islands. *Coral Reefs* 3: 69–76
- Schonwald H, Aчитuv Y, Dubinsky Z (1987) Differences in the symbiotic interrelations in dark and light coloured colonies of the hydrocoral *Millepora dichotoma*. *Symbiosis* 4: 171–184
- Schonwald H, Dubinsky Z, Aчитuv Y (1997) Diel carbon budgets of the zooxanthellate hydrocoral *Millepora dichotoma*. *Proc 8th Int Coral Reef Symp, Panama* 1: 939–946
- Sebens KP (1997) Adaptive responses to water flow: morphology, energetics, and distribution of reef corals. *Proc 8th Int Coral Reef Symp, Panama* 2: 1053–1058
- Sebens KP, Done T (1992) Water flow, growth form and distribution of scleractinian corals: Davies reef (GBR), Australia. *Proc 7th Int Coral Reef Symp, Guam* 1: 557–568
- Sebens KP, Witting J, Helmuth B (1997) Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). *J Exp Mar Biol Ecol* 211: 1–28
- Sheppard CRC (1982) Coral populations on reef slopes and their major controls. *Mar Ecol Prog Ser* 7: 83–115
- Strömberg T (1975) Skeleton growth of the hydrocoral *Millepora complanata* Lamarck in relation to light. *Limnol Oceanogr* 21: 100–104
- Tabachnick BG, Fidell LS (1996) *Using multivariate statistics*. Harper Collins, New York, p 880
- Vago R, Aчитuv Y, Vaky L, Dubinsky Z, Kizner Z (1998) Colony architecture of *Millepora dichotoma* Forskal. *J Exp Mar Biol Ecol* 224: 225–235
- Wahle CM (1980) Detection, pursuit, and overgrowth of tropical gorgonians by milleporid Hydrocorals: Perseus and Medusa revisited. *Science* 209: 689–691
- Witman JD (1988) Effects of predation by the fireworm *Hermodice carunculata* on milleporid hydrocorals. *Bull Mar Sci* 42: 446–458
- Witman JD (1992) Physical disturbances and community structure of exposed and protected reefs: a case study from St. John, US Virgin Islands. *Am Zool* 32: 641–654
- Weerdt WH de (1981) Transplantation experiments with Caribbean *Millepora* species (Hydrozoa, Coelenterata), including some ecological observations on growth forms. *Bijdr Dierk* 51: 1–19
- Weerdt WH de (1984) Taxonomic characters in Caribbean *Millepora* species (Hydrozoa, Coelenterata). *Bijdr Dierk* 54: 243–262
- Zar JH (1996) *Biostatistical analysis*. Prentice Hall, New Jersey p 662