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Tube-dwelling coral symbionts induce significant morphological change in *Montipora*

Gerick S. Bergsma

Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA,
Email. bergsma@lifesci.ucsb.edu

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Abstract

Several groups of tube-dwelling coral symbionts induce the formation of long, finger-like branches (“fingers”) on *Montipora* corals in the lagoons of Moorea, French Polynesia. We surveyed the prevalence and taxonomic diversity of these symbionts across the northern lagoons of Moorea, and documented the length and density of the finger structures on coral colonies. We found that the symbionts, which include gammarid amphipods and chaetopterid polychaete worms that were not previously known to associate with scleractinian corals, dramatically alter coral skeletal morphology, and may alter coral biology and reef ecology.

Keywords: *Montipora*, gammarid amphipod, chaetopterid polychaete, vermetid snail, coral morphology

1. Introduction

Symbioses compose a diverse array of direct species interactions that have wide ranging effects on symbionts’ biology and demography. These effects can include induced changes in species’ morphology. For example, induced morphological changes are commonly recognized in plants, often resulting from compensatory or redirected plant growth in response to herbivory, or from direct modification by symbiotic organisms such as leaf-rolling or gall-making insects (Shorthouse and Rohfritsch, 1992; Ohgushi, 2005). Symbiont induced morphological changes are likely common in a number of systems, and are important because of their potential to impact primary producers and providers of biogenic habitat. However, little attention has been given to identifying the diversity of organisms that induce morphological changes and the degree to which these changes alter biological and ecological processes.

Reef-building corals form close associations with many organisms, establishing symbioses that alter coral growth and productivity (Zann, 1980; Castro, 1988). The mutualism between corals and zooxanthellae is the best known example, with photosynthetic endosymbiotic protists providing much of the coral’s energy (Halldal, 1968). Epibiotic organisms, such as worms, mollusks and crustaceans, also frequently associate with corals, and can change the size and shape of colonies by directly modifying coral growth (Abelson et al., 1991), boring into the coral skeleton (Scott and Risk, 1988) or forming tubes that are subsequently overgrown by the coral (Liu and Hsieh, 2000). Organisms such as these that alter coral growth or morphology have the potential to greatly impact coral biology and reef ecology.

In the lagoons of Moorea, French Polynesia, several species of symbiotic tube-dwelling invertebrates induce morphological changes in their host corals. Such infestations occur in several genera of corals, but are most common in species of *Montipora*, where symbionts induce the formation of long, finger-like branches (Fig. 1a). These structures, termed “fingers” to differentiate them from autogenic coral branches, are ubiquitous on *Montipora* spp. throughout the lagoons, and add considerable three-dimensional structure to encrusting or plating colonies.

This study documents the abundance and diversity of tube-dwelling epibiotic symbionts that induce aberrant skeletal structures in *Montipora* and the effects of these associations on coral colony morphology. Colony morphology has important repercussions on coral growth, reproduction and survival (Highsmith, 1980; Helmuth and Sebens, 1993), so symbiont-induced morphological change may greatly affect coral biology and condition. Because of coral’s importance as a foundational species within its community, morphological changes that involve increased structural complexity may also have community impacts. The added structure may provide structural refuge for reef fish and invertebrates, modify interactions with predators or competitors, or alter insolation or water flow around the coral. In this manner, the symbionts may act as ecosystem engineers (*sensu* Jones et al., 1994), altering the physical environment around *Montipora* and indirectly affecting other reef organisms.

2. Methods

Divers conducted surveys to assess the taxonomic diversity of symbionts inhabiting *Montipora* and document their distribution in the northern lagoons of Moorea, French Polynesia during the Austral winter of 2004. Corals were surveyed along three 2 m wide band transects that extended from the reef crest to the shore in the Vaipahu (17°28'37"S, 149°50'6"W), Teharoa (17°28'16"S, 149°47'10"W), and Maharepa (17°28'25"S, 149°48'47"W) sectors of the lagoon. Transect lengths varied according to the width of the lagoon, and ranged from 655 to 850 m. A GPS was used to record the distance to the reef crest for each colony encountered along each transect. The presence of coral fingers was also documented for each colony, and symbionts were collected for identification.

Tube-dwelling worms and amphipods were initially identified in the laboratory. Symbionts were collected by detaching the finger they inhabited at the base and were transported and maintained within their tubes. Organisms were kept in a flow-through seawater system at the UC Berkeley Richard B. Gump South Pacific Research Station until processing. They were expelled from their tubes using backpressure created by administering seawater to the base of the tube with a syringe and hypodermic needle. Needles were selected to be just large enough to fit into the tube, usually #20–22 for polychaete and amphipod tubes. Once expelled, organisms were relaxed in a solution composed of 50% seawater and 50% isotonic magnesium chloride, and observed through a 10–40× stereo-zoom dissecting microscope.

Preliminary identification of coral symbionts to family was conducted at the field station using electronic taxonomic keys: POLiKEY for polychaetes (Glasby and Fauchald, 2003), and World Crustacea for amphipods (Lowry and Springthorpe, 2001). Voucher specimens were preserved in 70% EtOH. Polychaetes were sent to Gustav Paulay at the Florida Museum of Natural History and amphipods to James Thomas at Nova Southeastern Oceanographic Center, and identified to genus. The amphipods were monospecific, and likely represent a previously undescribed species (J. Thomas, pers. communication). Molluskan symbionts were infrequently encountered, and typically were deeply embedded within the corals. They were therefore not extracted due to the excessive coral damage necessary to remove them. Mollusks were identified as precisely as possible *in situ* with visible external features using photographic guides (Colin and Arneson, 1995; Gosliner et al., 1996).

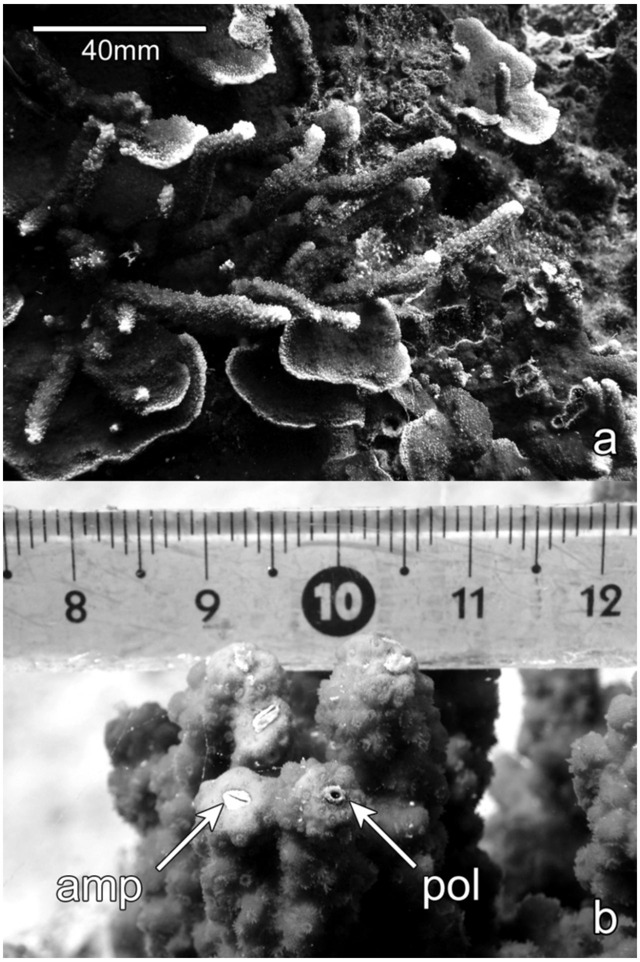

Figure 1. a: Symbiont-induced finger structures extend from a plating *Montipora* colony. b: Tips of coral fingers showing tube apertures for gammarid amphipods (amp) and chaetopterid polychaete worms (pol). Amphipod tubes were oval in cross section with slit-like apertures, and did not extend beyond the coral surface. Worm tubes were round in cross section with round apertures, and extended 1–4 mm beyond the surface of the coral. Numbers on scale in photograph are centimeters.

Individual *Montipora* colonies were easily distinguished, but the taxonomy of *Montipora* is poorly resolved and species level identification could not be made in the field. However, the most common species encountered in surveys were probably *M. aequituberculata* and *M. hispida* (P. Edmunds, pers. communication), though several other species may have been represented (e.g., *M. spumosa*, *M. grisea*, *M. efflorescens*, *M. tuberculosa*, and *M. verrucosa*; Veron and Stafford-Smith, 2000). For the purpose of surveys and subsequent analysis, all corals were identified to genus.

The percent cover of *Montipora*, the morphometrics of coral colonies and fingers, the density of fingers, and the relative abundance of different symbionts were documented in a second series of surveys during the Austral winter of 2007. Twenty 50 m transects ranging in depth from 1 to 2.5 m were conducted on snorkel and SCUBA in both back reef and fringing reef habitats in the Aroa (17°28'26"S, 149°46'40"W), Teharoa, Maharepa, Vaipahu, Tiahura (17°29'15"S, 149°54'0"W) and Ahuru (17°30'0"S, 149°55'15"W) sectors of the lagoon. Percent cover of *Montipora* was calculated from benthic point contact surveys, with points spaced at 1 m intervals along each transect (i.e., 50 pts per transect), that provided estimates of the cover of non-living substrate, living corals and algae.

The length and width of *Montipora* colonies intersected by transects were then measured using a measuring tape. The length was recorded as the maximum basal diameter of the coral, and the width recorded as the maximum diameter perpendicular to the length. Fingers on each colony were selected by haphazardly placing a 10×10 cm quadrat on the surface of the coral, and the number of fingers within the quadrat was used to estimate the finger density on the colony. The length and basal diameter of each finger was measured using a small ruler.

The colonies were then surveyed for symbionts, and the tube-dwelling taxa associated with each colony were recorded. Symbiont tube size and shape differed among taxa, with mollusks exhibiting 10–15 mm round (gastropod) or figure-eight (bivalve) shaped apertures, polychaetes exhibiting 1–2 mm wide round apertures, and amphipods exhibiting 1–2 mm wide oval or slit-like apertures (Fig. 1b). Therefore, following initial identification in the laboratory, symbionts could be identified to class *in situ* using tube structure. Fingers that had no visible tube aperture were dissected to determine whether they had been previously inhabited by a symbiont.

To explore the relative effect of the altered morphology on colony topography, surface area and volume of *Montipora* colonies were approximated from recorded measurements using standard geometric shapes. Colony length and width measurements were used to approximate colony basal area as an ellipse, and finger height and diameter measurements were used to approximate finger surface area and volume as the upper surface and volume of a cone. Colony basal area, finger surface area and finger density were used to approximate the total surface area of colonies with fingers, and colony basal area, average finger height and finger volume were used to approximate the volume of water within the 3-dimensional structure formed by fingers (interstitial volume) as a hemiellipsoid minus the volume of the fingers. Error estimates were excluded from the reported results because the error introduced by the geometric approximations is unknown and probably far greater than the error introduced from the measured parameters. Extrapolations to lagoon-scale effects were calculated using lagoon areas estimated from aerial photographs using the image analysis program *ImageJ* (Rasband, 2005).

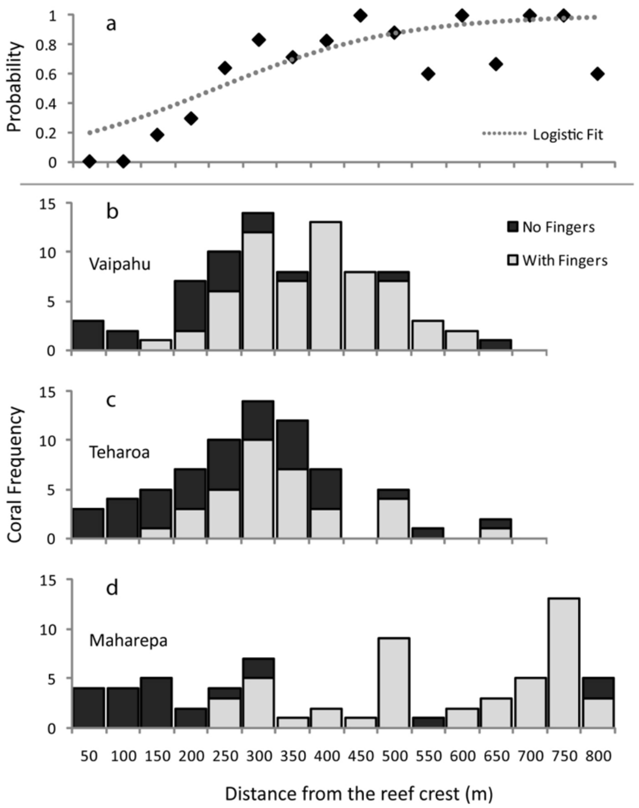

Figure 2. a: Probability that *Montipora* possess symbiont fingers across the lagoon for 50 m bins from combined data for three lagoons. The dotted line shows the fit from a logistic regression. b–d: Stacked column histograms showing the frequency of occurrence of *Montipora* colonies with and without fingers in 50 m bins for the Vaipahu (b), Teharoa (c) and Maharepa (d) lagoons.

3. Results

The surveys revealed that *Montipora* was ubiquitous throughout the northern lagoons of Moorea, and that symbiont-induced fingers were common and widespread. *Montipora* was the second most common genus of coral, after *Porites*, and accounted for approximately 11% of total substrate cover and 34% of live coral cover. *Montipora* colonies with fingers were present in all of the lagoons, and of 218 colonies encountered on the surveys, 65.1% possessed at least two fingers that were at least 20 mm in length. The frequency of colonies with fingers changed across the width of the lagoons (Logistic Regression, $\chi^2_{(1, n=218)} = 59.69$, $p<0.0001$), with fingers nearly absent

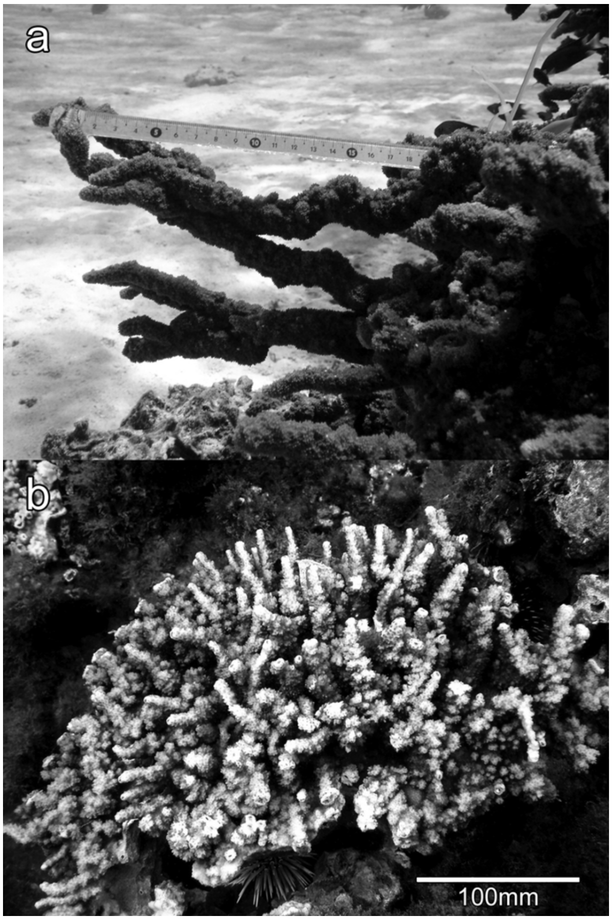

Figure 3. a: Fingers commonly extend beyond 100 mm in length, with the longest observed fingers reaching 210 mm. The longest fingers frequently have multiple branches, with tube apertures at the tip of each branch. Numbers on scale in photograph are centimeters. b: Many corals are heavily colonized by symbionts, with fingers covering the entire surface of the colony. The gross morphology of such colonies resembles that of autogenously branching corals.

near the reef crest, then becoming increasingly common until the mid-lagoon and fringe reefs where approximately 80% of colonies possessed fingers (Fig. 2). Most *Montipora* colonies without symbionts were morphologically similar, exhibiting encrusting or plating growth forms. No colonies were encountered exhibiting branching morphologies in the absence of symbionts.

Of the 2,300 fingers surveyed, 94.1% had active symbiont tubes in them and 5.4% had uninhabited tubes that were revealed upon dissection. Only 0.5% lacked evidence that they had been previously inhabited by symbionts. Fingers averaged 39 ± 0.48 mm (mean ± SE) in length and 13 ± 0.16 mm (mean ± SE) in basal diameter, with fingers reaching lengths up to 210 mm (Fig. 3a). Colonies possessing fingers had a mean finger density of 10.36 ± 0.37 fingers per 100 cm^2 of coral area (mean ± SE), with densities reaching as high as 45 fingers per 100 cm^2 (Fig. 3b).

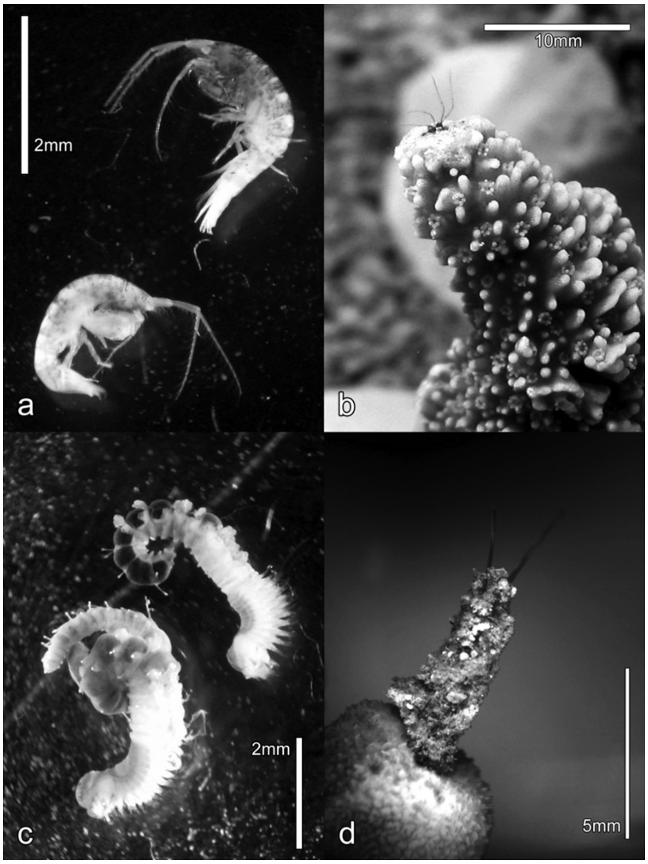

Figure 4. a: Tube dwelling gammarid amphipods (*Gammaropsis* sp.) removed from their tubes. b: An amphipod emerges from its tube at the tip of a coral finger to feed. c: Tube dwelling chaetopterid polychaete worms (*Spiochaetopterus* sp.) removed from their tubes. d: A worm extends its feeding appendages from its tube at the tip of a coral finger.

Several symbiont species were commonly found associated with fingers in *Montipora*, including gammarid amphipods (*Gammaropsis* sp.; Fig. 4a, b), chaetopterid worms (*Spiochaetopterus* sp.; Fig. 4c, d), and vermetid snails (*Dendropoma* spp.; Fig. 5a). Of these, amphipods were the most abundant and were present on 93.4% of *Montipora* colonies possessing fingers and on 89.0% of individual fingers surveyed. Chaetopterids were present on 29.2% of colonies and 9.3% of fingers, and vermetids were present on 2.0% of colonies and 1.4% of fingers. Infestations by multiple (e.g., two or more) symbiont species occurred on 26.5% of colonies, but only 0.3% of individual fingers harbored multiple species of symbionts. Fingers inhabited by amphipods and worms were similar in size and shape, while fingers inhabited by vermetids were typically shorter and wider. Boring bivalves (possibly *Lithophaga* sp.) were also observed to form fingers on one *Montipora* colony (Fig. 5b), but none were encountered during the surveys.

Fingers dramatically altered colony topography, and added 3-dimensional structure to the reef landscape. The

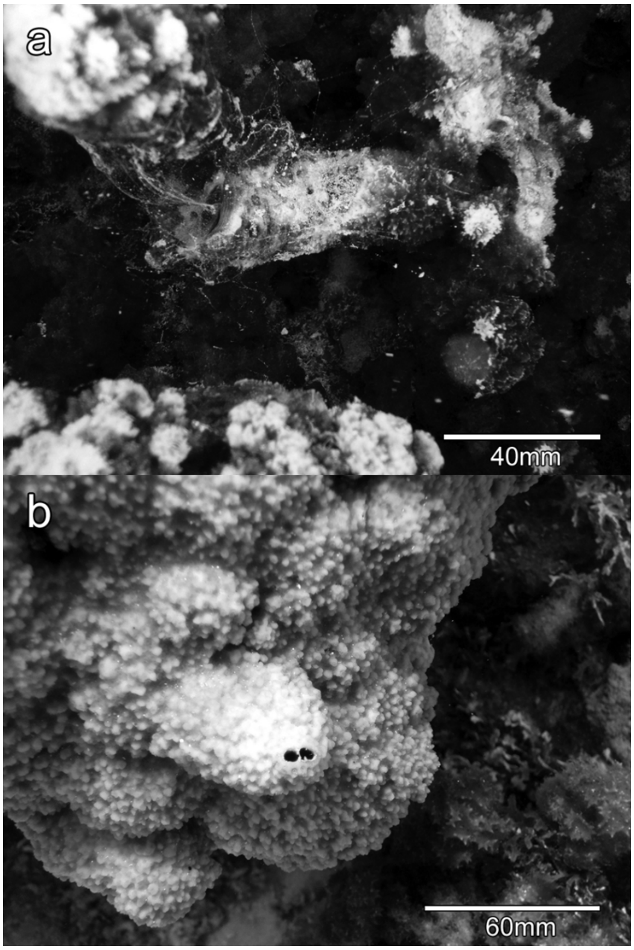

Figure 5. a: A *Montipora* finger formed by a vermetid snail. Vermetids typically form shorter, stouter fingers than do either amphipods or worms. b: A *Montipora* finger formed around a boring bivalve's siphons.

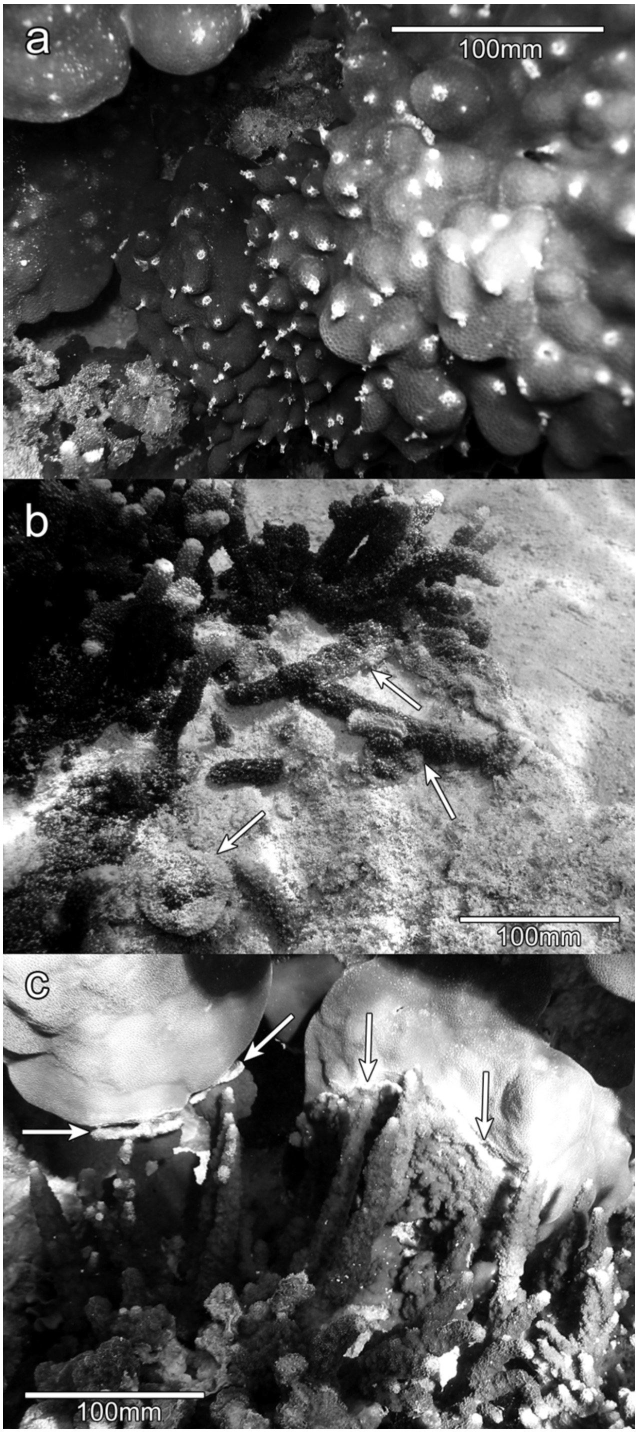

Figure 6. a: Stout conical structures formed by polychaete worms on a massive *Porites* coral colony. b: A *Montipora* colony where several fingers have become detached. Arrows indicate instances where broken fingers have reattached to the substrate and continue to grow. c: A *Montipora* colony competing with a *Porites* colony for space. Arrows indicate instances where fingers growing from the *Montipora* have formed plates above the *Porites* colony or have begun to overgrow it.

mean colony basal area, which approximates the surface area of fingerless plating or encrusting colonies, was 1,150 cm^2. Fingers added 217 cm^2 in surface area to fingered colonies of the same length and width, a 19% increase. The mean volume of fingers on a colony, an estimate of the skeletal material added to the colony, was 206 cm^3, and the mean interstitial volume of colonies with fingers, a measurement of space available to coral associated organisms, was 2,780 cm^3. Given that *Montipora* comprises 11% of total cover and 65.1% of *Montipora* exhibit fingers, it is estimated that fingers add approximately 135 cm^2 of coral tissue, 128 cm^3 of skeletal material, and 1,730 cm^3 of interstitial coral volume per square meter of lagoon area. The Vaipahu lagoon, the largest in the study, is approximately 2,500 m^2 in area, of which about 20% consists of large sand patches. Assuming the remaining 80% is amenable to *Montipora* growth, this translates to an estimated lagoon-wide increase of 192 liters of skeletal material, 2,600 liters of interstitial space, and over 20 square meters of coral surface, an area equivalent to 176 average sized colonies of plating or encrusting *Montipora*, due to the presence of symbionts.

4. Discussion

While polychaetes (Peyrot-Clausade, 1974), mollusks (Zuschin et al., 2001) and crustaceans (Castro, 1976; Patton, 1976) frequently associate with corals, commonly as active coral borers (Hutchings, 1986; Scott and Risk, 1988; Scott et al., 1988; Hutchings and Peyrot-Clausade, 2002), this study presents two novel symbioses. Gammaridean amphipods and chaetopteridean worms were both commonly encountered in association with *Montipora*. To my knowledge, this is the first report of either amphipods or chaetopterids inhabiting live scleractinian corals, though amphipods have been previously observed living on octocorals (Kumagai and Aoki, 2003).

The associations of amphipods and chaetopterids with *Montipora* are potentially important because the interaction results in profound structural changes for the host. The longest finger inhabited by amphipods was 210 mm long, and the longest finger inhabited by a chaetopterid was 122 mm long. These are considerably longer than the 50 mm lengths reported for otherwise identical structures formed by spionids on *Montipora* in Taiwan (Liu and Hsieh, 2000). Montipora fingers also dwarf similar structures formed by symbionts on other coral genera. On Moorea, polychaete infestations of *Porites* and *Millepora* produce stout conical structures 15–30 mm in length (Fig. 6a). These are almost identical to the 5–25 mm worm "cones" reported on *Porites* by Wielgus et al. (2002) in the Red Sea, and larger than the several millimeter long worm "spines" reported on *Millepora* by Lewis (1998) in the Caribbean. The greater length of the finger structures in *Montipora* is likely due to its fast growth and morphological plasticity. Liu and Hsieh (2000) observed a similar pattern in Taiwan, where spionid worms were observed to induce finger-like structures in *Montipora* but not in *Porites*. Fingers appear to form when coral encrusts the tube produced by the symbionts, and symbionts must continually extend their tubes to avoid overgrowth by rapidly growing *Montipora*. This results in longer structures than are seen on other coral genera; slower-growing, massive coral species do not exhibit the well-developed fingers observed on *Montipora*.

Vermetid snails and boring bivalves also both commonly infest a variety of coral genera (Kleemann, 1980; Colgan in Smalley, 1984), and are important bioeroders in Moorea (Peyrot-Clausade et al., 1992). The observations presented here, however, are again unique in the extent of the skeletal modifications induced in their hosts. Boring bivalves commonly alter coral morphology by excavating coral skeletal material (Goreau et al., 1972; Scott and Risk, 1988), but have also been reported to produce "chimney" structures on *Montipora* when calcareous siphons are overgrown by coral (Kleemann, 1980). The chimneys described by Kleemann are smaller, but otherwise identical to the fingers formed by bivalves in French Polynesia (Fig. 5b). Vermetids are generally considered coral competitors or parasites, and they alter coral morphology by reducing coral growth (Zvuloni et al., 2008). On massive or branching corals, this typically yields reduced structural complexity. On *Montipora*, however, the tube produced by the gastropod is overgrown by coral, forming finger-like structures and enhancing structural complexity.

The species of *Montipora* encountered in Moorea do not appear to branch without symbionts present, as almost all fingers surveyed had a symbiont tube, and no colonies were found with a branching morphology in the absence of symbionts. Symbionts, therefore, appear to be responsible for the addition of considerable material and habitat structure to the reef. The coral area and volume approximations illustrate this; fingers increased coral surface area and volume, and therefore living coral tissue and skeletal material, on fingered colonies relative to fingerless corals of similar length and width. Similarly, the additional interstitial volume arising from the 3-dimensional structure of the corals represents novel habitat for coral associated fish and invertebrates.

These approximations are clearly very course and rely on a number of untested assumptions. For example, the estimated increase in area due to fingers assumes that the presence of fingers does not alter basal area growth, and that the growth of fingers and the growth of the colonies on which they are found are additive. Morphometric surveys were conducted in mid-lagoon patch reefs and fringing reefs where *Montipora* is common and presumably grows well, so measured parameters also may not be representative of *Montipora* throughout the lagoons. The geometric approximations used are likely to be conservative estimates of actual coral areas and volumes, but they assume that the corals are on flat surfaces, clearly a flawed assumption for corals that encrust rugose reefs. Nonetheless, these approximations are instructive in that they provide some understanding of the relative magnitude of these morphological changes. Given the commonness of *Montipora*, the high rate of infestation across the lagoons, and the size and density of the structures produced, the presence of the symbionts may be an important factor impacting the ecology of corals and coral associated organisms.

Symbionts dramatically alter the morphology of *Montipora* corals and could subsequently be either advantageous or deleterious to their host corals. Indwelling coral symbionts, for example, have been shown to reduce skeletal strength (Scott and Risk, 1988), increase nutrient availability (Mokady et al., 1998), and increase photosynthetic potential in their hosts (Wielgus and Levy, 2006). Furthermore, coral size and structure are known to impact coral feeding, reproduction and survival (Highsmith, 1980; Helmuth and Sebens, 1993), indicating that changes in structure could impact *Montipora's* growth, fecundity and mortality.

There is anecdotal evidence that these changes in structure do affect coral ecology. Fingers were frequently encountered that had been detached from their parent colony, evidence that symbionts may reduce *Montipora's* ability to withstand physical disturbance. However, detached coral fingers are able to survive and reattach to form new colonies (Fig. 6b). Fragmentation of coral colonies is recognized as an important mechanism for asexual coral reproduction and dispersal (Highsmith 1982), but has not previously been attributed to the presence of coral symbionts. Morphological changes may also affect corals' ability to utilize resources and compete for space. Competitive interactions between *Montipora* and other corals have been observed where fingers extend from a *Montipora* colony towards a competing colony and then grow plates that overgrow or shade the competitor (Fig. 6c). These observations indicate that symbiont-induced growth forms may enhance reproductive potential and competitive ability of *Montipora* in Moorea.

Corals are foundational to tropical reef ecosystems, so symbionts are also likely to indirectly affect many other reef organisms (Wootton, 1994). Coral growth and morphology drive reef accretion (Montaggioni, 2005), productivity (Hatcher, 1988), and the structural complexity of reef habitats (Holbrook et al., 2002). Processes altering coral morphology will therefore impact the availability of food and habitat for reef organisms. Many reef organisms, for example, consume coral, and changes in coral growth or survival will impact food availability and accessibility for coral predators (Aeby, 2002). Similarly, organisms altering physical structure in their environment alter habitat availability for other organisms (Jones et al., 1994; Bertness et al., 1999). Coral structure has been shown to drive local diversity and abundance of fishes and invertebrates (Vytopil and Willis, 2001; Holbrook et al., 2002; Idjadi and Edmunds, 2006), so symbiont induced structural changes may alter reef diversity and community structure. Similar interactions may occur anywhere biogenic habitat drives species diversity and abundance; identifying and evaluating the impacts of symbiont induced morphological changes could therefore enhance our understanding of the roles of diversity and species interactions in these ecosystems.

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REFERENCES

Abelson, A., Galil, B.S., and Loya, Y. 1991. Skeletal modifications in stony corals caused by indwelling crabs: Hydrodynamical advantages for crab feeding. *Symbiosis* **10**: 233–248.

Aeby, G.S. 2002. Trade-offs for the butterflyfish, *Chaetodon multicinctus*, when feeding on coral prey infected with trematode metacercariae. *Behavioral Ecology and Sociobiology* **52**: 158–165.

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R., and Ingraham, A.O. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* **80**: 2711–2726.

Castro, P. 1976. Brachyuran crabs symbiotic with scleractinian corals: A review of their biology. *Micronesica* **12**: 99–110.

Castro, P. 1988. Animal symbioses in coral reef communities: A review. *Symbiosis* **5**: 161–184.

Colin, P.L. and Arneson, C. 1995. *Tropical Pacific Invertebrates: A field guide to the marine invertebrates occurring on tropical Pacific coral reefs, seagrass beds and mangroves*. Coral Reef Press, Beverly Hills, CA, 296 pp.

Glasby, C.J. and Fauchald, K. 2003. POLiKEY Version 2. Australian Biological Resources Study, Canberra.

Goreau, T.F., Goreau, N.I., and Yonge, C.M. 1972. On the mode of boring in *Fungiacava eilatensis* (Bivalvia: Mytilidae). *Journal of Zoology* **166**: 55–60.

Gosliner, T.M., Behrens, D.W., and Williams, G.C. 1996. *Coral Reef Animals of the Indo-Pacific: Animal life from Africa to Hawai'i exclusive of the vertebrates*. Sea Challengers, Monterey, CA, 288 pp.

Halldal, P. 1968. Photosynthetic capacities and photosynthetic action spectra of endozoic algae of massive coral *Favia*. *Biological Bulletin* **134**: 411–424.

Hatcher, B.G. 1988. Coral reef primary productivity: A beggar's banquet. *Trends in Ecology & Evolution* **3**: 106–111.

Helmuth, B. and Sebens, K. 1993. The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **165**: 251–278.

Highsmith, R.C. 1980. Passive colonization and asexual colony multiplication in the massive coral *Porites lutea* Milne Edwards and Haime. *Journal of Experimental Marine Biology and Ecology* **47**: 55–67.

Holbrook, S.J., Brooks, A.J., and Schmitt, R.J. 2002. Variation in structural attributes of patch-forming corals and in patterns of abundance of associated fishes. *Marine and Freshwater Research* **53**: 1045–1053.

Hutchings, P.A. 1986. Biological destruction of coral reefs: A review. *Coral Reefs* **4**: 239–252.

Hutchings, P.A. and Peyrot-Clausade, M. 2002. The distribution and abundance of boring species of polychaetes and sipunculans in coral substrates in French Polynesia. *Journal of Experimental Marine Biology and Ecology* **269**: 101–121.

Idjadi, J.A. and Edmunds, P.J. 2006. Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. *Marine Ecology Progress Series* **319**: 117–127.

Jones, C.G., Lawton, J.H., and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.

Kleemann, K.H. 1980. Boring bivalves and their host corals from the Great Barrier Reef. *Journal of Molluscan Studies* **46**: 13–54.

Kumagai, N.H. and Aoki, M.N. 2003. Seasonal changes in the epifaunal community on the shallow-water gorgonian *Melithaea flabellifera*. *Journal of the Marine Biological Association of the United Kingdom* **83**: 1221–1222.

Lewis, J.B. 1998. Reproduction, larval development and functional relationships of the burrowing, spionid polychaete *Dipolydora armata* with the calcareous hydrozoan *Millepora complanata*. *Marine Biology* **130**: 651–662.

Liu, P.J. and Hsieh, H.L. 2000. Burrow architecture of the spionid polychaete *Polydora villosa* in the corals *Montipora* and *Porites*. *Zoological Studies* **39**: 47–54.

Lowry, J.K. and Springthorpe, R.T. 2001. Amphipoda: Families, Version 1. Australian Museum, Sydney.

Mokady, O., Loya, Y., and Lazar, B. 1998. Ammonium contribution from boring bivalves to their coral host – a mutualistic symbiosis? *Marine Ecology Progress Series* **169**: 295–301.

Montaggioni, L.F. 2005. History of Indo-Pacific coral reef systems since the last glaciation: Development patterns and controlling factors. *Earth-Science Reviews* **71**: 1–75.

Ohgushi, T. 2005. Indirect interaction webs: Herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution and Systematics* **36**: 81–105.

Patton, W.K. 1976. Animal associates of living reef corals. In: *Biology and Geology of Coral Reefs*. Vol. 3. Jones, O.A. and Endean, R., eds. Academic Press, New York, pp. 1–37.

Peyrot-Clausade, M. 1974. Ecological study of coral reef cryptobiotic communities: An analysis of the polychaete cryptofauna. *Proceedings of the Second International Coral Reef Symposium* **1**: 269–283.

Peyrot-Clausade, M., Hutchings, P., and Richard, G. 1992. Temporal variations of macroborers in massive *Porites lobata* on Moorea, French Polynesia. *Coral Reefs* **11**: 161–166.

Rasband, W.S. 2005. *ImageJ*. US National Institutes of Health, Bethesda, MD, http://rsb.info.nih.gov/ij/.

Scott, P.J.B. and Risk, M.J. 1988. The effect of *Lithophaga* (Bivalvia: Mytilidae) boreholes on the strength of the coral *Porites lobata*. *Coral Reefs* **7**: 145–151.

Scott, P.J.B., Reiswig, H.M., and Marcotte, B.M. 1988. Ecology, functional morphology, behavior, and feeding in coral- and sponge-boring species of *Upogebia* (Crustacea: Decapoda: Thalassinidea). *Canadian Journal of Zoology* **66**: 483–495.

Shorthouse, J.D. and Rohfritsch, O. 1992. *Biology of Insect-Induced Galls*. Oxford University Press, New York, 296 pp.

Smalley, T.L. 1984. Possible effects of intraspecific competition on the population structure of a solitary vermetid mollusk. *Marine Ecology Progress Series* **14**: 139–144.

Veron, J.E.N. and Stafford-Smith, M. 2000. *Corals of the World*. Australian Institute of Marine Science, Townsville, 1382 pp.

Vytopil, E. and Willis, B.L. 2001. Epifaunal community structure in *Acropora spp.* (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity. *Coral Reefs* **20**: 281–288.

Wielgus, J. and Levy, O. 2006. Differences in photosynthetic activity between coral sections infested and not infested by boring spionid polychaetes. *Journal of the Marine Biological Association of the United Kingdom* **86**: 727–728.

Wielgus, J., Glassom, D., Ben-Shaprut, O., and Chadwick-Furman, N.E. 2002. An aberrant growth form of Red Sea corals caused by polychaete infestations. *Coral Reefs* **21**: 315–316.

Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**: 443–466.

Zann, L.P. 1980. *Living Together in the Sea*. TFH Publications, Neptune, NJ, 416 pp.

Zuschin, M., Hohenegger, J., and Steininger, F.F. 2001. Molluscan assemblages on coral reefs and associated hard substrata in the northern Red Sea. *Coral Reefs* **20**: 107–116.

Zvuloni, A., Armoza-Zvuloni, R., and Loya, Y. 2008. Structural deformation of branching corals associated with the vermetid gastropod *Dendropoma maxima*. *Marine Ecology Progress Series* **363**: 103–108.