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The vermetid gastropod *Dendropoma maximum* reduces coral growth and survival

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Coral reefs are one of the most diverse systems on the planet; yet, only a small fraction of coral reef species have attracted scientific study. Here, we document strong deleterious effects of an often overlooked species—the vermetid gastropod, *Dendropoma maximum*—on growth and survival of reef-building corals. Our surveys of vermetids on Moorea (French Polynesia) revealed a negative correlation between the density of vermetids and the per cent cover of live coral. Furthermore, the incidence of flattened coral growth forms was associated with the presence of vermetids. We transplanted and followed the fates of focal colonies of four species of corals on natural reefs where we also manipulated presence/absence of vermetids. Vermetids reduced skeletal growth of focal corals by up to 81 per cent and survival by up to 52 per cent. Susceptibility to vermetids varied among coral species, suggesting that vermetids could shift coral community composition. Our work highlights the potential importance of a poorly studied gastropod to coral dynamics.

Keywords: coral growth; coral survival; *Dendropoma maximum*; vermetid gastropod

1. INTRODUCTION

Coral reefs are biologically diverse habitats that provide important ecosystem services including coastal fisheries, and protection against storms, tsunamis and rising sea levels (Pratchett *et al.* 2008). Corals also play an important ecological function, providing biogenic structures for many species of fishes and other invertebrates (Jones *et al.* 2004). However, considerable evidence suggests that the abundance and physiological performance of reef building corals is declining in many areas (Gardner *et al.* 2003; Bellwood *et al.* 2006), potentially jeopardizing many of their ecosystem services.

Recent studies of coral dynamics have focused on a limited set of factors, including hurricanes (Woodley *et al.* 1981), competitors (e.g. algae: Carpenter & Edmunds 2006; Box & Mumby 2007), conspicuous predators (e.g. crown-of-thorns sea star, Done 1992;

fishes, Cole *et al.* 2008) and mutualists (Pratchett *et al.* 2000). Other studies have identified anthropogenic activities (e.g. nutrient enrichment, Bruno *et al.* 2003; sedimentation, McCulloch *et al.* 2003; and disease, Harvell *et al.* 2002; Bruno *et al.* 2003) as drivers of coral declines. These factors undoubtedly contribute to coral dynamics in many locations and times, but given the diversity of species and biological interactions that comprise coral reef ecosystems (and the relatively limited breadth of scientific study), it is likely that coral dynamics might be influenced by species interactions still unrecognized by scientists.

Although coral reefs are largely known for their more charismatic inhabitants, many small, relatively cryptic species (e.g. small invertebrates) are potentially important players but easily overlooked. For example, vermetid gastropods are sessile and feed via extruded mucus nets that often contact neighbouring substrates, including corals (Morton 1965; Hughes & Lewis 1974). The largest vermetid, *Dendropoma maximum* (see electronic supplementary material, appendix A), is common and widespread throughout the Indo-Pacific (Hadfield *et al.* 1972; Hughes & Lewis 1974; Zvuloni *et al.* 2008), and aspects of its feeding ecology have been examined by a number of workers (e.g. Smalley 1984; Kappner *et al.* 2000; Ribak *et al.* 2005; Gagern *et al.* 2008). In the Gulf of Aqaba (Red Sea), the presence of *D. maximum* was correlated with morphological anomalies and reduced size in a branching coral (Zvuloni *et al.* 2008). Here, we explore vermetid–coral interactions in more detail using a series of field observations combined with experiments designed to quantify the degree to which vermetids cause reductions in growth and survival of four coral species.

2. MATERIAL AND METHODS

(a) Field surveys

We surveyed 90 interspersed patch reefs in a shallow (2–3 m) lagoon of Moorea, French Polynesia (17.48°S and 149.81°W). Each reef was comprised entirely of a single massive *Porites lobata* coral colony (see electronic supplementary material, appendix B for discussion of coral taxonomy). We recorded reef morphology (binary response variable: either ‘flattened’ or ‘rugose’, see electronic supplementary material, appendix A, figure A1c) from a distance of approximately 5 m (where reef morphology was apparent but the presence of vermetids was not). We then surveyed each reef under closer inspection and recorded the presence or absence of vermetids. We evaluated the relationship between coral morphology and vermetid presence–absence using a χ^2 test.

We quantified covariation between vermetid densities and the proportion of the reef substrate that was dead (i.e. hard substrate other than live coral) in 103, 22.36 × 22.36 cm quadrats haphazardly placed on monotypic patches of four focal species (electronic supplementary material, appendix B) of common reef-building coral: *Porites lobata* ($n = 37$), *Pocillopora* ($n = 26$), *Porites rus* ($n = 20$) and *Montipora* ($n = 20$). We visually estimated the proportion of coral substrate that was dead, and counted the number of vermetids that were greater than or equal to 5 mm in aperture diameter (i.e. readily identifiable as *D. maximum*). We evaluated variation in vermetid densities among substrate types using ANOVA, and relationships between the proportion of dead substrate and vermetid density using least-squares linear regression.

(b) Field experiments

We conducted six field experiments to quantify the effects of vermetid gastropods on skeletal growth and survival of four focal coral species: *Porites lobata*, *P. rus*, *Pocillopora*, *Montipora* at a site in Maharepa lagoon, and on two of these species (*P. lobata* and *Pocillopora*) at another site (West Temae lagoon). Focal corals (juvenile *P. lobata*; fragments from larger colonies for other species) were attached to plastic bases (approx. 10 × 10 cm) using epoxy and weighed (Davies 1989).

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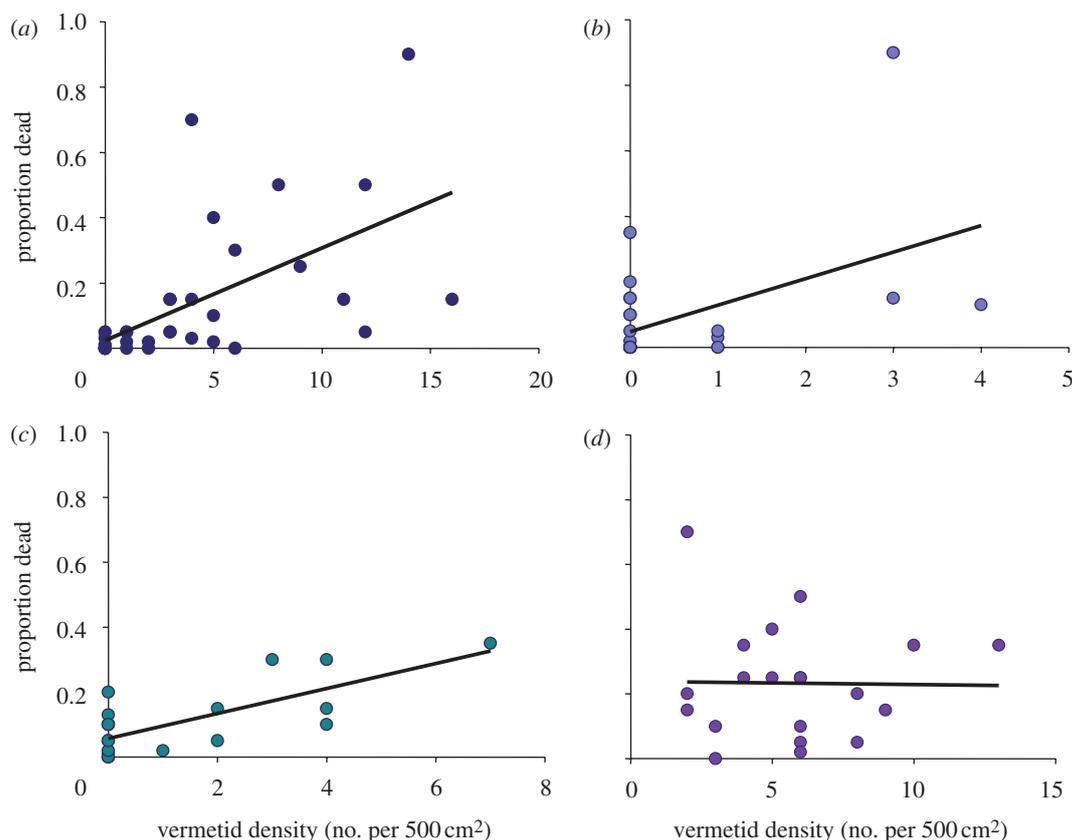


Figure 1. Relationships between the local density of *Dendropoma maximum* (number of snails ≥ 5 mm aperture diameter in a 500 cm^2 quadrat) and the proportion of that quadrat consisting of dead coral for monospecific sites consisting of (a) *Porites lobata* ($r = 0.59$, $p < 0.0001$, $n = 37$). (b) *Pocillopora* ($r = 0.48$, $p = 0.01$, $n = 26$). (c) *Porites rus* ($r = 0.73$, $p = 0.0002$, $n = 20$). (d) *Montipora* ($r = -0.01$, $p = 0.95$, $n = 20$).

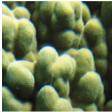
Our experiments were conducted on small (less than 5 m^2), shallow (approx. 2 m depth) patch reefs that (initially) had local populations of the vermetid gastropod, *D. maximum*. We randomly selected half of the 12 study reefs within each experiment ($n = 6$) and removed vermetids. The remaining reefs comprised a control group ($n = 6$) (vermetids were present at ambient densities). Focal corals were weighed in the laboratory, transplanted in triplicate to each reef and secured to galvanized staples (previously affixed to the reef) using plastic cable ties. All experiments were initiated between 2 June and 10 June 2006. Our observations after transplanting corals showed that most corals were directly contacted by mucus nets in the treatments, where vermetids were not removed, in a manner similar to what we have observed with naturally occurring corals.

Focal corals were collected after 47 days, returned to the laboratory and reweighed to assess growth (as change in skeletal mass: Davies 1989). Following weighing, all corals were immediately returned to their original location on experimental reefs. On 13 January 2007 (after 217–225 days), the proportion of coral surface area alive was estimated visually by a single observer in the field. The effects of vermetids on focal corals in each experiment were analysed using a nested-ANOVA (three corals/reef; six replicate reefs per treatment).

3. RESULTS

The presence of vermetids was strongly associated with growth anomalies of the reef-building coral, *P. lobata* (table 1). Large vermetids (i.e. individuals > 5 mm aperture diameter) occurred on all four focal substrates, although their densities varied ($F_{3,99} = 12.85$, $p < 0.0001$): vermetids were most common on *Montipora* (5.70 per 500 cm^2 ; s.d. 2.87) and *P. lobata* (3.81; s.d. 4.45) and least common on *P. rus* (1.35; s.d. 2.03) and *Pocillopora* (0.54; s.d. 1.10). The proportion of substrate that was dead was positively

Table 1. Surveys of 90 interspersed colonies of the coral *Porites lobata* reveal an association between the presence or absence of *D. maximum* and coral morphology. Presence of vermetid is associated with stunted and flattened coral growth forms and extensive dead patches on reefs ($\chi^2 = 65.0$, d.f. = 1, $p < 0.0001$). See also electronic supplementary material, appendix A.

reef morphology	with vermetids	without vermetids
 rugose	6	42
 flat	41	1

correlated with the local density of large vermetids for *P. lobata*, *Pocillopora* and *P. rus*, but not for *Montipora* (figure 1), suggesting either that vermetids harm coral or that vermetids recruit preferentially to degraded coral habitat.

Field experiments clearly demonstrated deleterious effects of vermetids on corals. Ambient densities of vermetids reduced coral skeletal growth of all four coral species (figure 2a). Vermetids reduced growth

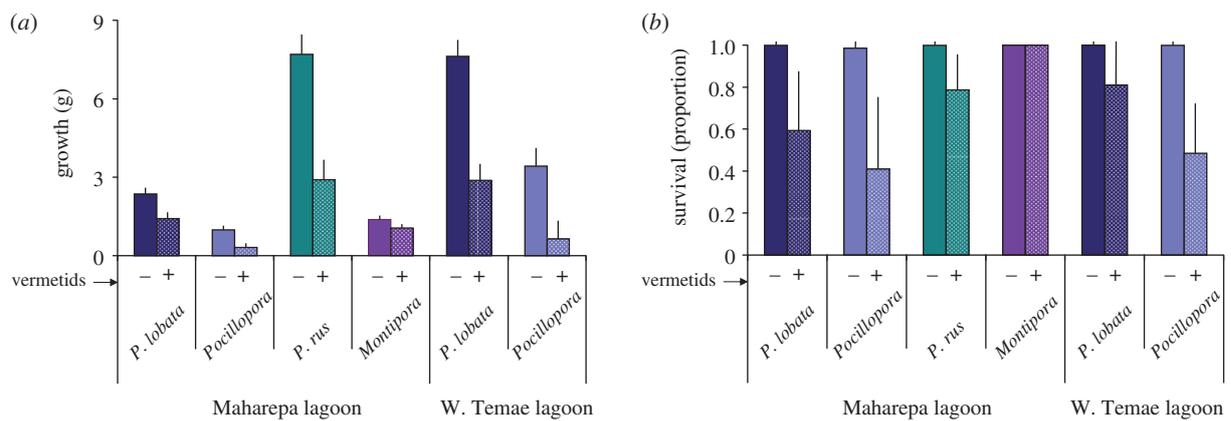


Figure 2. Effects of ambient versus reduced densities of vermetid gastropods (mean \pm 95% CI) on (a) coral growth; and (b) survival from field experiments conducted at two sites on Moorea. Stippled bars indicate vermetids present, solid bars indicate vermetids removed. Results of ANOVA—for growth (with initial mass (g)): *Porites lobata* ($F_{1,10} = 38.07$, $p < 0.0001$, (25.7)), *Pocillopora* ($F_{1,10} = 44.13$, $p < 0.0001$, (6.3)), *Porites rus* ($F_{1,10} = 97.87$, $p < 0.0001$, (7.4)), *Montipora* ($F_{1,10} = 12.07$, $p = 0.0060$, (3.7)), *Porites lobata* in Temae ($F_{1,10} = 141.90$, $p < 0.0001$, (25.7)), and *Pocillopora* in Temae ($F_{1,10} = 39.83$, $p < 0.0001$, (11.5)); for survival: *Porites lobata* ($F_{1,10} = 12.77$, $p = 0.0051$), *Pocillopora* ($F_{1,10} = 7.83$, $p = 0.0189$), *Porites rus* ($F_{1,10} = 14.80$, $p = 0.0032$), *Porites lobata* in Temae ($F_{1,10} = 8.37$, $p = 0.0160$) and *Pocillopora* in Temae ($F_{1,10} = 25.50$, $p < 0.0005$).

rates of *Pocillopora* by 68–81%, *P. rus* by 62 per cent, *P. lobata* by 40–62% and *Montipora* by 24 per cent. Vermetids also reduced survival of all species of coral except *Montipora* (which exhibited 100% colony survival: figure 2b).

Averaged across coral species and locations, vermetids reduced (i) coral skeletal growth by 56 per cent and (ii) colony survival for three of these four species by an average of 40 per cent (*Montipora* was unaffected). Coral species varied in their ambient growth rates and susceptibility to vermetid effects, suggesting that the relative abundances of corals may be appreciably altered by vermetid–coral interactions (see electronic supplementary material, appendix C for a simple extrapolation of our results).

4. DISCUSSION

Our field experiments demonstrate that vermetids can have deleterious effects on four species of coral. Ambient densities of *D. maximum* reduced coral growth by up to 82 per cent and survival by up to 52 per cent. Experimental results were concordant with field surveys, in which vermetid densities were positively correlated with dead coral for *P. lobata*, *P. rus* and *Pocillopora*, but not *Montipora*. Two other studies (one experiment in Guam: Colgan 1985; and one observational study in the Red Sea: Zvuloni *et al.* 2008) suggest the negative effects of vermetids on corals, which we observed in Moorea may also occur in other locations. Our research strengthens and extends the inferences drawn from these previous two studies (one based upon correlative evidence, the other published in symposium proceedings; both focused on a single coral species). Importantly, our field experiments demonstrate interspecific variation in the responses of corals to *D. maximum*, which collectively suggest that vermetids may alter the structure of coral communities (e.g. electronic supplementary material, appendix C).

Despite these demonstrably strong effects: (i) vermetids are not uniformly distributed across the reef environment; and (ii) considerable live coral persists around vermetids even in the shallow habitats where vermetids are common. The patchy distribution of vermetids indicates that corals may have spatial refuges from deleterious effects of *D. maximum*. The occurrence of live coral adjacent to *D. maximum* does not preclude the existence (or importance) of strong deleterious effects. We posit that this co-occurrence probably reflects productive microsites, where net coral growth remains positive despite vermetid-induced effects.

Although the mechanisms underlying strong vermetid–coral interactions remain unknown, we speculate that they probably involve vermetid mucus nets. Thus, deleterious effects on corals will depend on vermetid density, possibly generating strong spatio-temporal variation in responses reflecting local vermetid dynamics. Further, we hypothesize that vermetid recruitment dynamics (possibly facilitated by an initial disturbance causing partial death of a coral colony) may play an important role in vermetid–coral interactions. Anecdotal evidence also suggests that the density of *D. maximum* has increased recently in the Red Sea (Zvuloni *et al.* 2008) and Moorea (B. Salvat & Y. Chancerelle, personal communication), possibly in response to coastal eutrophication driven by human activities (Zvuloni *et al.* 2008), and/or a reduction in harvesting (*D. maximum* is a traditional food source in Polynesia: electronic supplementary material, appendix D).

Vermetid gastropods, though poorly studied, have the potential to greatly influence corals and possibly induce cascading effects on associated fish and invertebrate communities. Unfortunately, vermetids are a zoological ‘oddity’ and remain understudied. We therefore lack detailed information on their distribution, historical dynamics, evolution and ecological effects. In this respect, vermetids are representative of many coral reef organisms, and they underscore our

very limited understanding of the basic biology and natural history of most inhabitants of coral reefs, some of which will undoubtedly contribute to the trajectories of these important and diverse ecosystems.

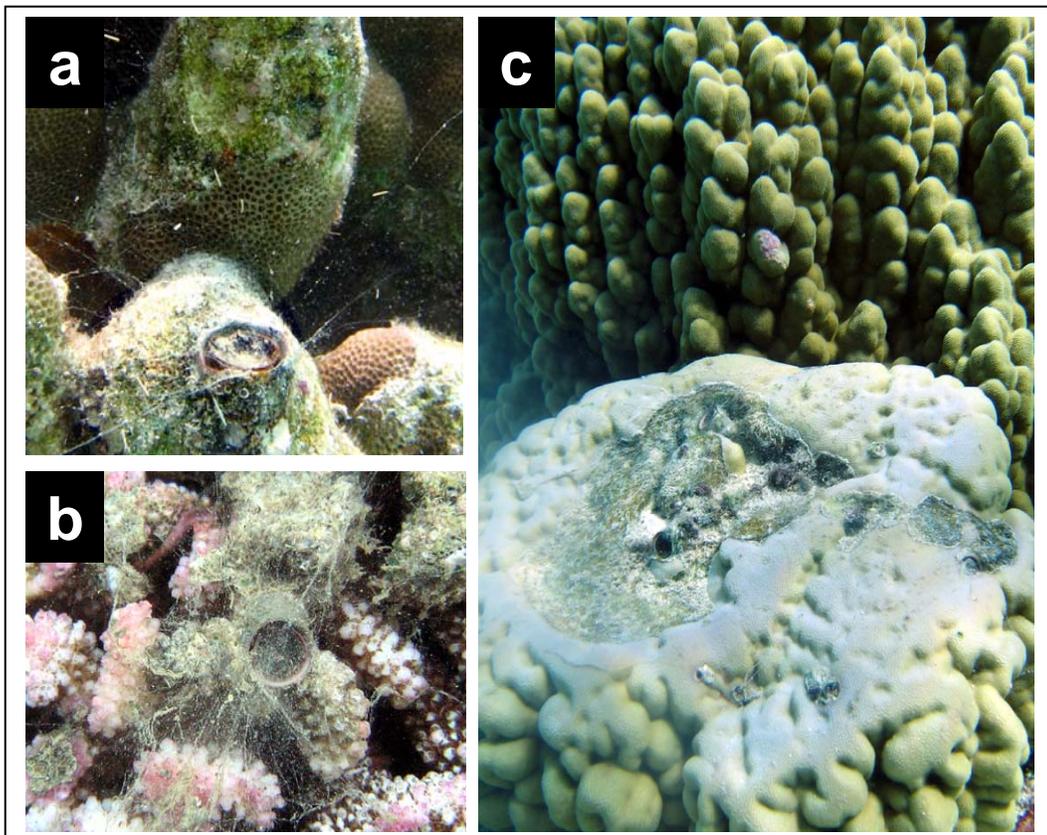
Funding was provided by grants from NSF (OCE-0242312) and ISAT Linkage Fund (RSNZ). We thank B. Salvat, Y. Chancerelle and CRIOBE for vermetid density data; P. Edmunds, M. Maheigan and N. Phillips for useful discussions; S. Boyer for field assistance. This is a contribution from UC Berkeley's Richard B. Gump South Pacific Research Station, Moorea, French Polynesia.

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Appendix A: The vermetid gastropod, *Dendropoma maximum*

Figure A1. The vermetid gastropod, *Dendropoma maximum*, with mucus feeding nets extended over a colony of the reef building coral (a) *Porites lobata*. and (b) *Pocillopora*. (c) Morphological variation in *P. lobata* correlated with absence (top reef) or presence (bottom reef) of vermetid gastropods (see Table 1).

Fig A1



Appendix B: Coral Taxonomy.

Coral taxonomy is challenging given tremendous variation in morphology and the lack of reliable field traits for many taxa. Coralite structure is often used as a diagnostic tool, but requires bleaching and microscopic examination. Using coralite structure, we identified the *Porites* reefs that we surveyed as *P. lobata*. For our field experiments, we did not examine corallite structure (because we did not want to sacrifice the corals). In a previous study in Moorea, but at a different site, Edmunds (2009) inspected 20 juvenile *Porites* colonies and based on corallite structure determined they were a mix of *P. lobata* and *P. lutea*.

However, in a detailed molecular phylogenetic analysis of *Porites*, Forsman et al (2009) showed that corals with the same gross morphology and coralite structure and identified as the same “species” could be deeply divergent. Similarly, they showed that different species might be more closely related than individuals from the same species: e.g., their “Clade I” included seven “species” (and three corallite morphologies) with little apparent phylogenetic structure to the classically defined groups. *P. lobata* samples were contained in this clade as well as a very divergent group (their Clade IV), the latter of which consisted of *P. lobata* and *P. lutea* from Samoa. Similar taxonomic challenges exist for *Montipora* and *Pocillopora* (e.g., Bergsma 2009), although *Porites rus* seems to be well resolved (Forsman et al. 2009).

Based on gross morphology, we tentatively identified the four focal species we used in the field experiments as *Porites lobata*, *P. rus*, *Pocillopora verrucosa*, and *Montipora floweri*. Although these identifications may be in error, and may consist of closely related species, our experiment should be robust to any variation within a taxonomic variation within a “species” because individuals were randomly assigned to treatment groups. Thus, taxonomic variation would add to the noise but not introduce bias. Because our results

were all strongly significant, any underlying variability was relatively minor (and did not affect our interpretations). To clearly distinguish “species” in the main text, but to avoid any undue assertion about species names, we refer to these four groups as *Porites lobata*, *P. rus*, *Pocillopora*, and *Montipora*, respectively.

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Appendix C: Projected dynamics

We used data from our field experiment to project changes in coral cover. Our approach was simplistic, but designed to allow us to extrapolate our short-term results to evaluate if vermetids might be able to produced long-term shifts in coral composition. Because corals are modular, clonal growth (especially for small corals, such as the ones we used) is often approximately geometric (e.g., Vago et al. 1997, Guzner et al. 2007), although more complex models growth models work better (e.g., Merks et al. 2003). Given the simplicity of our data, we used an exponential growth model to project changes in coral cover:

$$A_{t,\text{live}} = A_{0,\text{live}} e^{(bg-m)t}, \quad (\text{Eq. C.1})$$

where A was areal cover of coral, b was the allometric scaling between coral skeletal mass (S) and surface area (which we assumed to be $2/3$ based on the relative scaling of area and volume of a solid of fixed shape, and was required because g was estimated from changes in mass: i.e., volume), g was growth of coral skeletal mass (from Eq C.2), and m was estimated iteratively based upon observed growth (g) and the fraction of live coral cover, P , observed at the end of the experiment, (~223 days): see below. Because we were interested in relative changes (and because the eventual outcome of this simple model is not sensitive to initial conditions), we started with equal representation of each species and then projected the community dynamics of each coral species using Equation C.1 and expressing each species' live cover as a fraction of the total cover.

To accomplish this projection, we required estimates of g and m from our data. To estimate g , we used our growth data from the first 47 days of the field experiments. These data were based on the mass of a focal coral, as well as the attached base. In our main

paper (Figure 1) we therefore analyzed the effects of vermetids on growth as the difference in mass (to remove the effect of the base); this was the most defensible approach for that purpose. Here, we needed a different approach because we wanted to extrapolate through time and directly compare the different coral species. We had measured the mass of the base for a subset of the corals (but not all). We therefore first determined the mean mass of the coral (and bases) and then subtracted the mean base mass to get an estimate of the initial (and final) mean coral skeletal mass (S). We then estimated growth for each coral species over the 47 day growth period using these means (we therefore do not have estimates of variance in growth):

$$g = \ln\left(\frac{\bar{S}_{47}}{\bar{S}_0}\right) / 47 \quad (\text{Eq. C.2})$$

To estimate m , we used the estimates of g and our estimate of the proportion of the coral that was dead after ~220 days. We assumed that dead coral accumulated in proportion to live coral cover:

$$A_{\text{dead}} = \int mA_{t,\text{live}} dt = [e^{(bg-m)t} - 1][mA_{0,\text{live}}/(bg-m)] \quad (\text{Eq. C.3})$$

Furthermore, because $P = A_{t,\text{live}} / (A_{t,\text{live}} + A_{\text{dead}})$, we combined Eqs. C.1 and C.3, and rearranged, to obtain:

$$P = e^{t(bg-m)} / [e^{t(bg-m)} + (e^{(bg-m)t} - 1)m/(bg-m)] \quad (\text{Eq. C.4})$$

which we solved iteratively for m , given $b=2/3$, $t=217, 221, 223$ or 225 d (depending on the experiment), the value of g estimated from Eq. C.2, and the observed P .

Population projections based upon our experimental results suggested that reef systems containing vermetids may trend towards domination by *Montipora* (Fig C1b), which is less strongly affected by vermetids (though notably, also a comparatively slow-

growing coral). Systems without vermetids, in contrast, may tend towards domination by the more rapidly growing *Porites rus* (Fig C1b).

This model is admittedly simplistic, focusing only on growth and partial mortality and ignoring a variety of other important ecological processes (e.g., recruitment, competitive interactions, disturbances, etc). Nonetheless, it provides a quantitative synthesis of the data on growth and survival responses, allowing us to project what is already suggested from the core results: species are differentially susceptible to vermetids and that alone can lead to dramatic changes in species composition. If unchecked by other processes, a large change in vermetid density could shift coral community composition in as little as 5 years. The community implications are potentially important because *P. rus* (a species strongly affected by *D. maximum*) provides a complex habitat suitable for many fishes and invertebrates (Holbrook et al. 2002a,b), whereas *Montipora* (the species least affected), at least in Moorea, is a poor habitat for fishes (and grows slowly, thus further jeopardizing reef dynamics).

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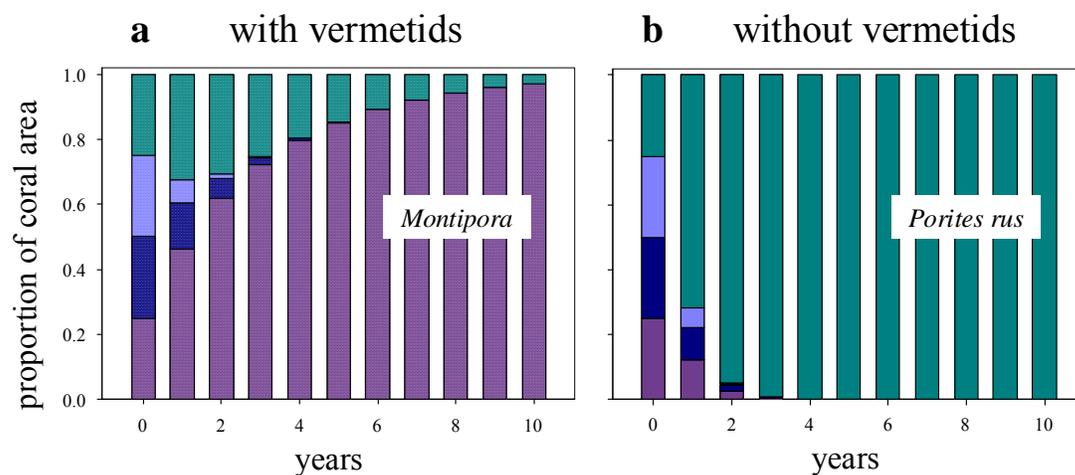
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Table C1. Parameters used to project coral composition (Figure B1) based on data from the Maharepa lagoon (based on data from Figure 2).

Species	g (per day): with, without vermetids	m (per day): with, without vermetids
<i>P. lobata</i>	0.00271, 0.00399	0.00266, 0.00007
<i>P. rus</i>	0.00437, 0.01205	0.00153, 0.00005
<i>Pocillopora</i>	0.00049, 0.00229	0.00307, 0.00035
<i>Montipora</i>	0.00354, 0.00468	0.00000, 0.00000

Figure C1. Projected proportion of the live coral landscape covered by each of four species of reef building coral **(a)** with vermetids present (stippled bars) and **(b)** with vermetids absent (solid bars). Projection is based upon an exponential growth model parameterized from field experiments (Table B1), assuming a uniform initial composition of the coral community, and ignoring other processes (e.g., competitive interactions and recruitment). ■ = *Porites lobata*, ■ = *Pocillopora*, ■ = *Porites rus*, ■ = *Montipora*.

Fig. C1



Appendix D: Harvesting of vermetid gastropods

Polynesians harvest larger vermetid gastropods (*Dendropoma maximum*) for consumption and local sale (Figure D1). Although there are no quantitative data available on harvesting rates or patterns, our discussions with local fishers suggest that harvesting rates can be sufficiently high to alter vermetid dynamics.

Figure D1. Vermetid gastropods (*Dendropoma maximum*) for sale at a fish market in Tahiti, French Polynesia. Tahiti is ~15 km from Moorea, where our studies occurred. Inset provides a close-up from another photo. Photos courtesy of Frank Murphy.

Fig D1

