Consistent deleterious effects of vermetid gastropods on coral performance

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ARTICLE INFO

ABSTRACT

The strength of species interactions is a key driver of ecological dynamics, yet relatively little is known about spatial, temporal, or among-individual variation in interspecific interactions. Here, we evaluate variability in the strength of interactions between a guild of sessile vermetid gastropods and a reef-building coral, *Pocillopora verrucosa*. Vermetid gastropods are sessile, tube-building snails that feed on drifting particulate matter via extruded mucus nets. Previous work indicates that vermetids can reduce growth and survival of neighboring coral colonies, though the generality of this result (e.g., among coral genotypes, and across environmental gradients) is unknown. Here, we manipulated the presence/absence of vermetids on 10 patch reefs within each of 6 field sites, and quantified the growth and survival of small transplanted corals (taken from three distinct colonies) over 155 days. Two-way ANOVA indicated that vermetids had deleterious effects on both coral growth and survival, and that these effects did not vary substantially across sites spanning an area of ~350 ha. Generalized linear mixed models were used to account for correlated responses of corals across environmental gradients, and these analyses indicated that the effects of vermetids were also consistent among coral colonies (i.e., putative genotypes that likely differed in phenotype, zooxanthellae/microbial composition, environmental history, etc.). Deleterious effects of vermetids on corals thus appear to be consistent in space and across coral colonies.

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1. Introduction

Interactions between species (e.g., predation, competition, mutualism) shape dynamics of populations and contribute to the structure and function of ecological communities (Elton, 1927; Paine, 1966; Wootton and Emmerson, 2005). Interaction strengths between species vary in both space and time (Freidenburg et al., 2007; McNeely and Power, 2007; Menge et al., 1994), and among individuals of differing genotype (Peacock and Herrick, 2000), physiological condition (Wood et al., 2010), and developmental history (Holmes and McCormick, 2009). Heterogeneity in responses of one species to another can affect the resilience of ecological communities (Navarrete and Berlow, 2006) and the responses of populations and communities to management (Shears et al., 2008) and environmental change (McNeely and Power, 2007; O'Connor, 2009).

Coral reefs are exceptionally diverse ecosystems that comprise a large number of species interactions (Knowlton, 2001; Pandolfi et al., 2003; Roberts et al., 2002). Within these systems, reef-building corals are of particular importance because they provide structural habitat and other resources for many species (Hughes et al., 2003; Jones et al., 2004). Many interactions affect the demographic performance of corals, notably, mutualisms between corals and their symbionts (e.g., zooxanthellae: Hughes et al., 2003; coral guard crabs:

Stewart et al., 2006; Stier et al., 2010), competition with other sessile organisms (Box and Mumby, 2007; Mumby et al., 2007), and predation (e.g., by crown-of-thorns starfish: Done, 1992). Here, we focus on a newly identified strong interaction between vermetid gastropods and reef-building corals (Shima et al., 2010; Stier et al., 2010).

Vermetid gastropods (Family Vermetidae) are common and abundant on many coral reefs (Hadfield et al., 1972; Hughes and Lewis, 1974; Zvuloni et al., 2008). Unlike most other gastropods, vermetids are sessile: e.g., the uncoiled shell of many vermetids often becomes partially or entirely overgrown and embedded within the coral skeletal matrix. Many vermetid species feed by extruding and retracting mucus nets to capture suspended particles from the water column (Hughes and Lewis, 1974; Morton, 1965). The largest species of vermetid gastropod, *Dendropoma maximum*, reduces skeletal growth of corals by up to 81% and survival by up to 52%, presumably by an undescribed mechanism involving the mucus nets (Shima et al., 2010). These large effects suggest that the interaction between vermetids and corals (regardless of underlying mechanisms) has the potential to reduce coral cover and alter coral reef community structure (Shima et al., 2010).

Here, we conduct a follow-up experiment to evaluate the generality of our previous findings. Specifically, we ask whether the strong deleterious effects of vermetids on corals vary spatially, and among individual coral colonies (i.e., that putatively vary in genotypes, symbiont clades, etc.; for convenience we use 'genotype' to refer to colony-related effects in our analyses, though we did not evaluate genetic

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heterogeneity of corals or symbionts). We address these questions using a spatially hierarchical field experiment that takes advantage of our ability to transplant fragments (i.e., clones) of distinct coral colonies, to evaluate the potential for genotype-environment interactions. We evaluate the effects of a guild of vermetids (including *D. maximum*) on the branching coral, *Pocillopora*, a genus that provides essential habitat for a wide range of fishes and invertebrates (Beukers and Jones, 1998; Bonin et al., 2009; Holbrook and Schmitt, 2002; Shima, 2001; Shima et al., 2008; Stewart et al., 2006).

2. Methods

2.1. Study sites

We quantified variation in the effects of vermetid gastropods on the growth and survival of the branching coral, *Pocillopora verrucosa*, on discrete patch reefs within each of 6 sites along the north shore of Moorea, French Polynesia (S17.48 W149.81). The local vermetid assemblage consists of 7 species (*Dendropoma platypus*, *D. gregaria*, *D. maximum*, *D. meroclista*, an undescribed *Dendroma*, *Petaloconchus keenae*, and *Serpulorbis variabilis*). *D. maximum* (the focus of our previous studies, Shima et al., 2010; Stier et al., 2010) is the largest species, occurs at densities up to 320 individuals per m², and is present on a wide range of reef substrates (Shima et al., 2010). Although *D. maximum* dominates the local vermetid biomass, other vermetid species can also occur in high densities. Here, we evaluate the effects of the collective vermetid assemblage on *P. verrucosa* performance. The mean ambient density of vermetids (collectively across all species, for sites used in this study) was 93 per m² (SD = 50, min = 8, max = 264; see also electronic Supplement 1).

We established six discrete sites within the shallow lagoon system (Fig. 1; see Shima et al., 2008 for a description). Sites were separated from one another by > 500 m, and some sites were located near natural and/or municipal discharges. We chose to evaluate vermetid–coral interactions across multiple sites because we expected local environmental conditions (e.g., temperature, light regimes, sedimentation) to also vary across these scales (we infer this abiotic variation from our personal observations of variation in sediment loads and algal blooms among sites). In addition, we have quantified variation in the

demographic rates of other species among these sites (e.g., Shima, 1999, 2001; Shima et al., 2008).

We selected 10 patch reefs haphazardly from within each of our 6 sites (n = 60 reefs in total), with the imposed constraint that all selected reefs contained established populations of vermetid gastropods. We quantified the size (maximum length, maximum perpendicular width, and maximum height) and water depth of each reef, and we visually estimated percent cover of dominant substrate types (after Shima et al., 2008). Selected reefs had a mean footprint area of 1.84 m² (SD 1.0), mean depth to reef top of 1.08 m (SD 0.32), mean depth to reef base of 1.77 m (SD 0.38), and a mix of benthic substrata (average percent cover, SD): *Porites lobata* (47%, 33), *P. rus* (7%, 19), *Montipora* sp. (2%, 7) and non-coral (e.g., bare, turf algae, or macroalgae: 42%, 28).

Within each site we randomly assigned half of the focal reefs to an experimental treatment where we removed vermetids with small wire hooks, leaving the shells intact. Removals targeted all vermetid species, and though we attempted to remove all vermetids from the reefs in this treatment, some individuals were inadvertently missed due to their cryptic nature and complex reef topography. The remaining reefs were unmanipulated and therefore contained vermetids at ambient densities.

Our experimental subjects came from three distinct colonies of *P. verrucosa*. Colonies were collected from a lagoon site near the reef crest (approximately 600 m west of MOE, see Fig. 1). Within this collection site, we selected colonies from separate patch reefs (separated by > 100 m), in an attempt to maximize probability of selecting differing genotypes while minimizing potentially confounding effects of differing collection sites. From each colony we broke off terminal portions of branches (each ~5 cm in length). Fragments from a given colony were assumed to share a common genotype, as well other sources of among-individual heterogeneity (e.g., clades of zooxanthallae, past environmental effects, etc.). We used these discrete colonies to evaluate potential variation in the response of corals to vermetids. We attached each fragment to a small (~10 × 10 cm) plastic base using A-788 splash zone epoxy (Z-spar), and estimated the initial skeletal mass of each focal coral and its base using a buoyant weight technique (Davies, 1989). We secured one fragment of each colony (i.e., a ramet from each genet) to each study reef by securing each base (and attached coral) via a cable tie to galvanized staples that had been
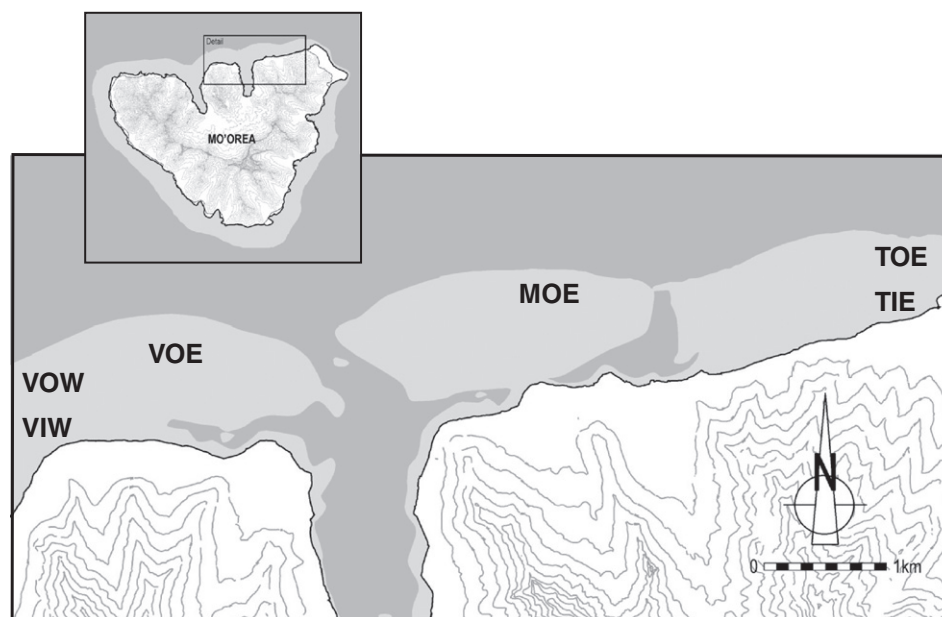

Fig. 1. Location of six sites along the north shore of Moorea (position shown in inset) where presence/absence of vermetid gastropods was manipulated on patch reefs. Land is shown in white with contours, shallow lagoon habitat is shown in light grey, and deeper water is shown in dark grey.

hammered into the reef in haphazard positions (Fig. 2). We assessed all coral fragments 8–9 days after transplantation and noted no evidence of short-term mortality (i.e., due to handling artifacts).

After 155 days, we recollected all corals and returned them to the laboratory sea water system, where we estimated their final skeletal mass (Davies, 1989) and the proportion of coral surface area that was alive (estimated visually by a single observer, without knowledge of reef/treatment origin). We estimated growth as the change in coral skeletal mass divided by 155 days.

2.2. Analyses

We evaluated variation in vermetid effects on corals (1) among sites and (2) among coral genotypes, in separate analyses.
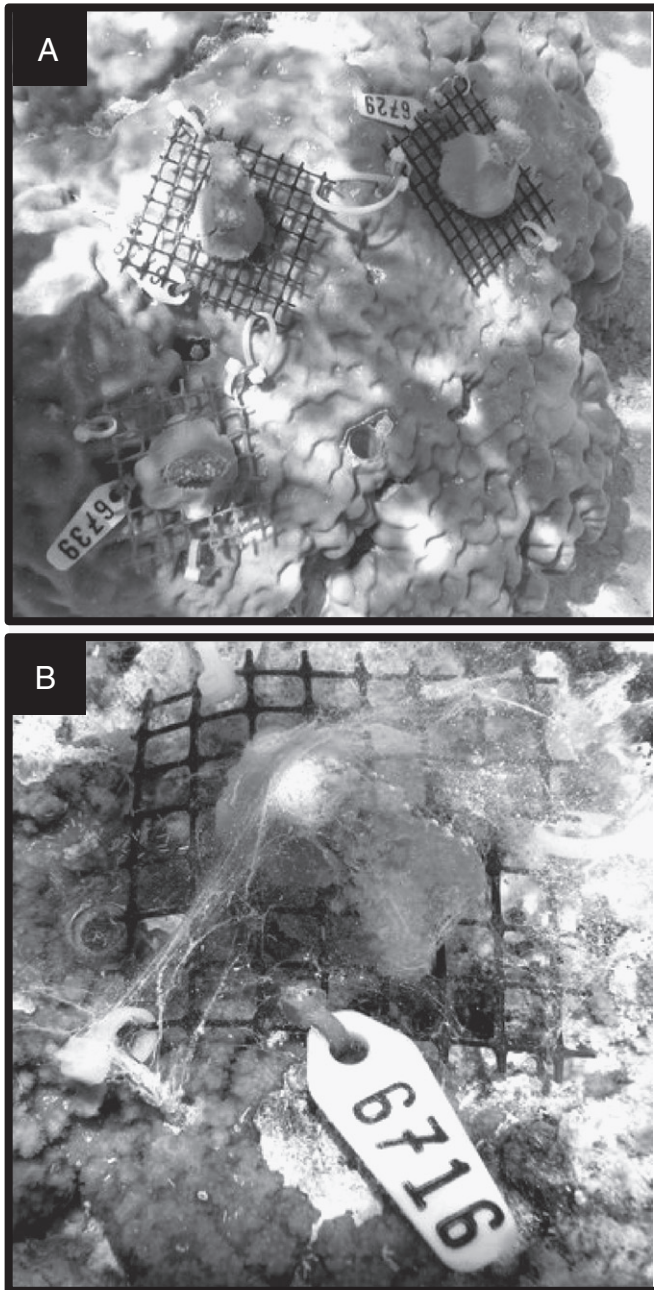
Fig. 2. Photograph of (A) three distinct coral clones (i.e., putative genotypes) transplanted to a single reef where vermetids have been experimentally removed, and (B) a single coral clone covered by the mucus nets of several vermetids (on a reef where vermetids were unmanipulated and present at ambient densities).

2.3. Variation in vermetid effects on coral growth and survival among sites

We evaluated variation in the growth and the proportion of coral surface area that was alive (after 155 days) of *P. verrucosa* in separate two-way ANOVAs (PROC GLM, SAS). These models evaluated variation in coral performance between experimental treatments (presence versus absence of vermetids, fixed effect), among sites (random effect), and their interaction (random effect). For these analyses, we first averaged responses across coral fragments (i.e., genets) within each reef, giving 5 replicate reefs per treatment for each site. We arcsin square-root transformed proportional survival to improve normality and homoscedasticity.

2.4. Variation in vermetid effects on coral growth and survival among genotypes

Reefs varied in extrinsic characteristics (e.g., size, depth, substrate types) that could potentially affect the responses of corals to vermetids. To incorporate this variability into our analyses of genotype effects, we paired coral fragments that were transplanted to reefs where vermetids were present in ambient densities, with coral fragments of identical genotype (i.e., clones) that were transplanted to nearby reefs within the same site, but where vermetids had been experimentally removed. We used a cluster analysis (PROC CLUSTER, Ward method, SAS) to select "reef pairs" (i.e., blocks, consisting of one reef from the treatment group and one reef from the control group at the same site, based upon similarity in reef size, depth, and percent cover of substrate types). These blocks were included as random effects in generalized linear mixed models.

We evaluated variation in the growth and the proportion of coral surface area that was alive (after 155 days) of *P. verrucosa* in separate generalized linear mixed models (PROC GLIMMIX, SAS). These models evaluated variation in coral performance as a function of (1) experimental treatment (presence versus absence of vermetids, fixed effect); (2) genotype (fixed effect); (3) the interaction between treatment and genotype (fixed effect); and (4) a set of random effects to account for correlated responses of corals deployed to similar environmental conditions (i.e., sites; clone pairs deployed to similar reef environments nested within sites; an interaction between treatment and clone pairs nested within sites). We analyzed variation in coral growth using a Normal distribution. However, we analyzed variation in coral "survival" in our generalized linear mixed model using a binomial distribution because 90% of all observations for 'proportion of coral surface alive' were either 0 or 1. Thus, we converted all observations to a binomial response (observations from 0 to 0.49 were re-coded as 0; observations from 0.5 to 1 were re-coded as 1).

3. Results

3.1. Variation in vermetid effects on coral growth and survival among sites

Growth rates of corals did not vary among sites ($F_{5,5} = 2.01$, $P = 0.23$), but varied between treatments ($F_{1,5} = 7.86$, $P < 0.038$), and vermetids had a strong deleterious effect on coral growth. The interaction between site and treatment was not significant ($F_{5,48} = 1.90$, $P = 0.11$), suggesting that the effect of vermetids on coral growth was not demonstrably different among sites (Fig. 3A), though the three eastern-most sites (MOE, TIE and TOE) show a (non-significant) trend for minimal effects of vermetids on coral growth.

Patterns in survival (the proportion of colonies alive after 155 days) were similar to those observed for growth. Coral survival did not vary among sites ($F_{5,5} = 2.80$, $P = 0.14$). Vermetids had deleterious effects on survival ($F_{1,5} = 28.64$, $P < 0.0031$, Fig. 3B), and this effect was consistent across sites (i.e., the interaction was non-significant: $F_{5,48} = 0.65$,
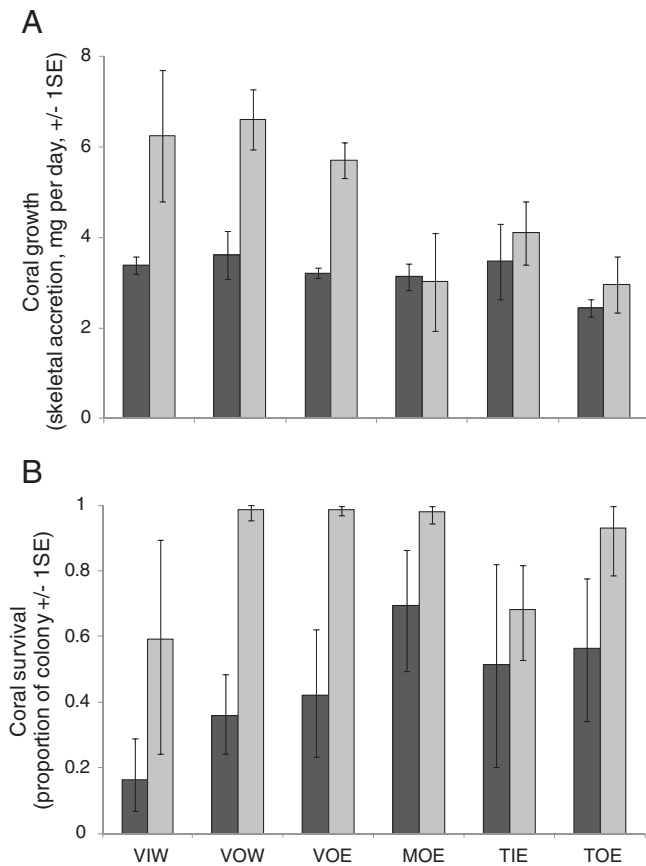
Fig. 3. Variation among six sites in (A) coral growth and (B) coral survival in response to experimental manipulations of vermetid gastropods. Light bars indicate coral performance on reefs where vermetids were removed; dark bars indicate performance on reefs where vermetids were present at ambient densities. Growth and survival were estimated from fragments of the branching coral, *Pocillopora verrucosa*, transplanted in triplicate to reefs, and responses of individual fragments were averaged to obtain a single value for each replicate reef ($n = 60$ reefs; 10 per site split evenly between experimental treatments). Error bars are $+/−$ 1SE, and back-transformed values are given for (B).

$P = 0.66$), although for eastern sites (MOE, TIE, and TOE), the effects of vermetids were comparatively weak.

3.2. Variation in vermetid effects on coral growth and survival among coral genotypes

Our analysis using a generalized linear mixed model confirmed that growth rates of corals varied between treatments ($F_{1,29} = 13.77$, $P = 0.0009$, Fig. 4A). Coral growth did not vary among coral genotypes ($F_{2,116} = 1.98$, $P = 0.14$). The interaction between genotype and treatment was not significant ($F_{2,116} = 0.06$, $P = 0.95$; see also electronic Supplement 2A), suggesting that the effect of vermetids on coral growth was not demonstrably different among genotypes. Variance components for random effects in our model were small (Fig. 4B), suggesting that coral growth did not vary markedly at the level of sites, clone pairs within sites, or the interaction between treatment and clone pairs nested within sites. Residuals were large (Fig. 4B), suggesting substantial among-individual variation in coral growth. Normalizing for variation in all other effects in our model, individual corals surrounded by vermetids (at ambient densities) grew, on average, 33% less than corals without vermetids.

A generalized linear mixed model indicated that survival of corals varied between treatments ($F_{1,29} = 11.71$, $P = 0.0019$, Fig. 4C) but not among coral genotypes ($F_{2,116} = 1.81$, $P = 0.17$). The interaction between genotype and treatment was not significant ($F_{2,116} = 0.17$, $P = 0.84$; see also electronic Supplement 2B). Variance components

for random effects in this model also were small (Fig. 4D), suggesting that coral survival did not vary markedly at the level of sites, clone pairs within sites, or the interaction between treatment and clone pairs nested within sites. Normalizing for variation in all other effects in our model, vermetids reduced the survival of coral colonies by 40%.

4. Discussion

Our results suggest that vermetid gastropods adversely affect the growth and survival of the reef-building coral, *Pocillopora verrucosa*. These effects were concordant with our earlier experiments (conducted in different years; Shima et al., 2010; Stier et al., 2010). Our analyses suggest that the effects of vermetids on corals were statistically indistinguishable among 6 sites that were distributed over an area of roughly 350 ha. However, we also note a non-significant trend for weaker effects of vermetids on coral performance at some sites (particularly, the three eastern-most sites: MOE, TOE and TIE), suggesting that the interaction strength of vermetids on corals may vary weakly in this system. Our inability to detect significant spatial variation in the effects of vermetids on corals may be attributable to limited statistical power (i.e., greater replication may have enabled us to detect spatial variation), although we note that our sampling effort for this experiment was informed by observed variation from a prior study (Shima et al., 2010). In addition, we repeated our GLM analyses without first averaging the responses of coral fragments within reefs (note this design is pseudoreplicated though it gives some indication of the effects of a tripling of experimental effort), and found no qualitative differences in our interpretations. We infer from these analyses that vermetids generally have negative effects on coral performance, and that any spatial variation in these effects appears to be weak (at best).

Our experimental design facilitated a more detailed evaluation of variation in the effects of vermetids on distinct coral colonies (which may reflect differences in genotype, phenotype, zooxanthellae/microbial composition, environmental history, etc.). The three chosen coral colonies are unlikely to fully reflect the full distribution of among-individual variability that may be present in our system. Indeed, work from other systems (Ridgway et al., 2001) suggests that as many as 1 in 3 colonies of *Pocillopora* in a South African population may reflect a repeat genet. However, a particular strength of our design is that we were able to evaluate variation among these three colonies across a range of environmental conditions (reefs of different size and composition, distributed across 6 sites over an area of ~350 ha). We found no evidence that effects of vermetids differed between the three coral colonies that we used in our study, and this suggests that there may be little among-individual variation in coral responses to vermetids.

The negative results (i.e., inability to detect spatial or among-individual variation in the effects of vermetids on corals) should be taken with some caution (because statistical power may be limited, and/or because we may not have sampled the full range of among-individual variation in the coral population). Given the seemingly weaker effects of vermetids on coral growth rates at the eastern-most sites in particular (Fig. 3A), readers may wish to consider the potential biological significance of this pattern irrespective of the criteria for statistical significance. We note, however, that presence/absence of vermetids had (by far and away) the largest effect on coral growth and survival. Evidence for any amelioration from spatial refuges and/or individual heterogeneity is non-significant and comparatively weak. However, high residual variation in coral growth (Fig. 4B) suggests that corals may vary in their performance (and possibly in their response to vermetids) at the scale of microsites (e.g., potentially arising from fine scale variation in vermetid density, size structure, species composition, and/or orientation with respect to flow patterns, etc.).

Our previous modeling of coral dynamics with and without vermetids (Shima et al., 2010) suggests that, in the absence of spatial
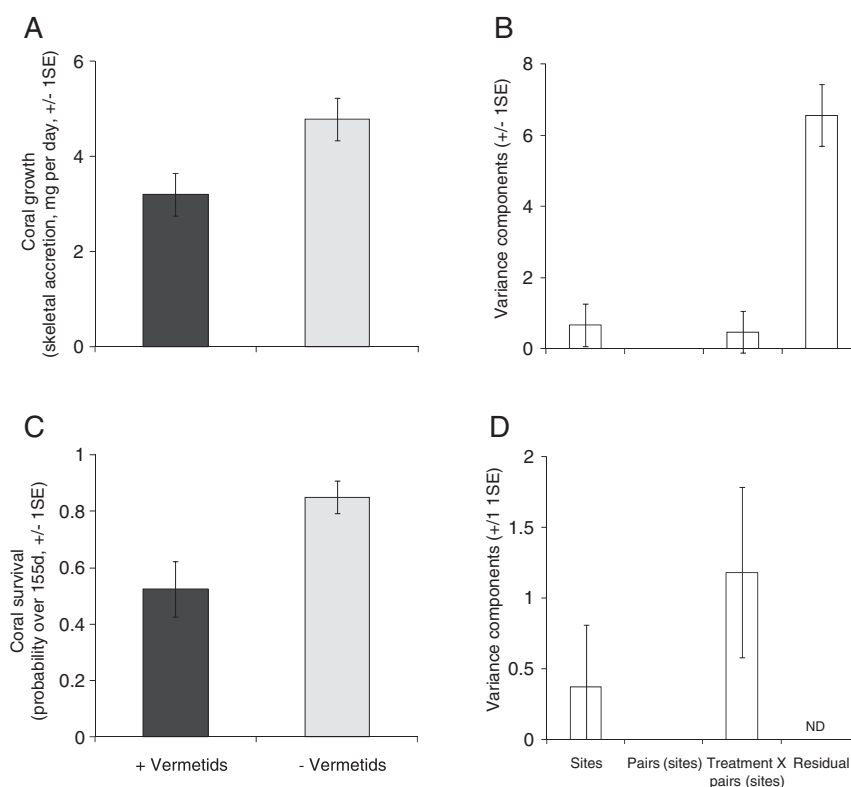
Fig. 4. Effects of vermetids on (A) coral growth and (C) coral survival. Light bars indicate coral performance on reefs where vermetids were removed; dark bars indicate performance on reefs where vermetids were present at ambient densities. Given are LS-means that normalized variation among coral genotypes (NS), the interaction between genotype and treatment (NS), and for the following random effects: Sites; paired reefs within sites; and the interaction between experimental treatment and paired reefs within sites. Co-variance parameters (i.e., variance components) across random effects are given for (B) coral growth and (D) coral survival.

refuges, vermetids could dramatically alter the cover and composition of coral assemblages on relatively short time-scales (5–10 year; Shima et al., 2010). Such changes may have profound implications for the fishes and invertebrates that rely on live coral (e.g., Holbrook et al., 2002).

We note that our experiments in this study were conducted on small corals (i.e., fragments). We know from our other experiments (Stier et al., 2010) that commensal crabs (*Trapezia*) can ameliorate the deleterious effects of vermetids on larger colonies of *Pocillopora*. Thus, the distribution and ontogenetic pattern of occupancy for *Trapezia* in *Pocillopora* will further influence expected coral dynamics, and may facilitate spatial refuges not observed for smaller/younger corals.

Data we have compiled from colleagues and the literature suggest that vermetids from tropical and temperate coastal waters have increased in density in recent years: e.g., *D. maximum* increased ~200× in the lagoons of Moorea from 1997 to 2008 (Y. Chancerelle and B. Salvat, unpub.), coincident with increased coastal development in Moorea. Zvuloni et al. (2008) also reported increased densities of *D. maximum* in the Red Sea over the past 10 years and attributed those increases to coastal eutrophication (leading to increased production of vermetid food resources). Using photos from permanent sites (taken and provided by Pete Edmunds of the Moorea Coral Reef LTER), we also have documented increased abundance of *D. maximum* from 2006 to 2009 (C. Osenberg and P. Edmunds, unpub.). The estimated population growth of *D. maximum* in Moorea was 0.49 year^{-1} (using the densities from 1997 to 2008) and 0.26 year^{-1} (using data from 2006 to 2009, C. Osenberg and P. Edmunds, unpub). These rapid growth rates, combined with the deleterious effects of vermetids, could easily drive dramatic changes in the reef ecosystems.

Overall, these results suggest that vermetids (1) play a key role in the dynamics and distribution of corals irrespective of local environments and/or coral colony identity; (2) contribute to declines in reef-building corals; (3) are increasing in density, possibly due to environmental changes caused by human activities in coastal waters; (4) will influence the dynamics and biodiversity of reef-associated taxa through effects on coral cover and composition. Despite these implications, vermetid–coral interactions remain underappreciated and poorly studied.

The strength of these deleterious interactions (quantified here across sites, and genotypes; and for multiple species of coral in Shima et al., 2010), coupled with the ecological importance of reef-building corals (which provide essential habitat for an unprecedented diversity of organisms), argues strongly for an urgent need to improve our understanding of the biology and ecological role of vermetid gastropods, and the mechanisms that underlie their interactions with corals.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2012.10.012.

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