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ORIGINAL PAPER

Variation in the growth and survival of the tropical vermetid gastropod *Ceraesignum maximum* is driven by size, habitat, and density

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Abstract The vermetid *Ceraesignum maximum* is a sessile tube-dwelling snail with a wide geographic distribution that can strongly reduce the growth and survival of corals, alter coral morphology, and shift coral species composition. Thus, this species has the potential to drive dramatic changes in coral reef ecosystems; yet, very little basic demographic information exists for *C. maximum*; nor do we know factors that potentially contribute to variation in vital rates. This study estimated individual growth (change in shell aperture diameter) and survival of focal (tagged) vermetids ($n = 297$) over 646 days, to test hypotheses that growth and/or survival rates were size-dependent, density-dependent, and/or habitat-dependent. This study was conducted on 80 haphazardly selected patch reefs, split evenly among eight discrete sites. The design also incorporated an experimental density reduction (e.g. on half the study reefs at each site divers reduced the densities of vermetids). Vermetid growth rates decreased with body size, and the slope of this relationship was steeper for reefs with experimentally reduced densities. Vermetid growth decreased weakly with local biomass of vermetids (i.e. estimated biomass within a 20 cm radius of focal individuals) but did not vary with local substrate composition. Vermetid survival increased with body size and local biomass; the relationship with biomass was steeper for reefs where vermetid densities had been experimentally reduced. Survival was also greater on living coral *Porites lobata* (where coral growth covered longitudinal extensions of vermetid shells) relative to dead coral substrate (where vermetid shells extensions remained exposed). These data suggest little scope for regulation of vermetid population growth via direct density dependence in demographic rates. However, given that vermetids can kill corals, and vermetid survival probabilities appear to depend upon coral cover, it is predicted that vermetids may experience cyclical dynamics that are coupled to the dynamics of living coral.

Introduction

Vermetids are unusual among gastropods; they are sessile and feed via extruded mucus nets that often contact neighbouring substrates, including corals (Fig. 1a; Morton 1965; Hughes and Lewis 1974; Kappner et al. 2000). The largest species of vermetid, *Ceraesignum maximum* (formerly *Dendropoma maximum*; see Golding et al. 2014 for recent taxonomic revision), is common and widespread throughout the Indo-Pacific (Hughes and Lewis 1974; Hadfield et al. 1972; Zvuloni et al. 2008). At first glance, vermetids appear to be minor players in the reef system. However, vermetids can cause growth anomalies in corals (Colgan 1985; Zvuloni et al. 2008; Shima et al. 2010, 2015), reduce coral growth by up to 80 %, and reduce coral survival by ~50 % (Shima et al. 2010, 2013; Stier et al. 2010). Due to differential effects on coral species (which may also be context-dependent, e.g. Lenihan et al. 2011), vermetids also could shift coral species composition (Shima et al. 2010). Collectively, the effects of vermetids are large, surprising, and have potentially important implications for the rest
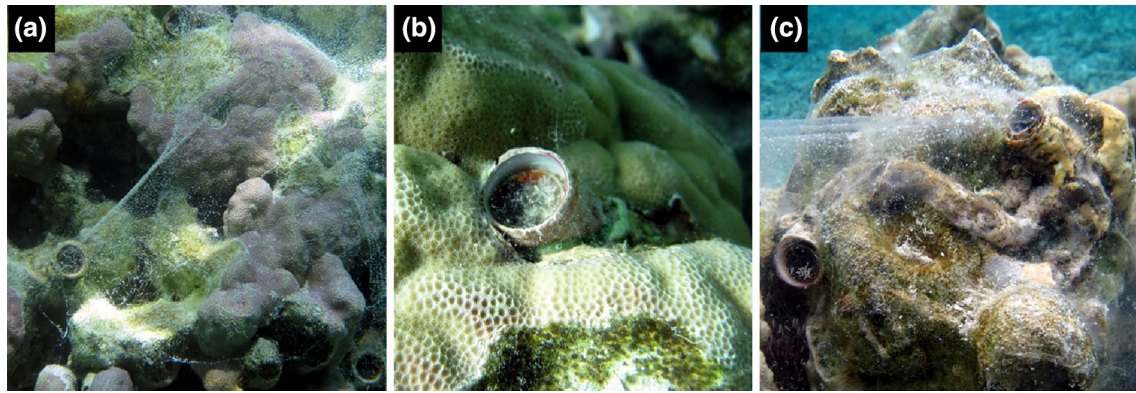
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Fig. 1 Vermetid gastropod, *Ceraesignum maximum.* **a** Extruded mucus nets in contact with live and dead coral (*P. lobata*) substrate. **b** Vermetid shell aperture exposed and recent longitudinal shell growth becoming covered by re-growth of coral. **c** Longitudinal shell growth along dead coral substrate remains uncovered and exposed

of the coral reef community. They also raise unanswered questions about the dynamics of vermetids and the factors that may limit and/or regulate vermetid populations.

Data we have compiled from colleagues and the literature suggest that vermetid density in Moorea, French Polynesia, has increased in the recent past. For example, based on surveys from the Tiahura transect in the lagoon of Moorea in 1997 and 2008 (Y. Chancerelle and B. Salvat, unpublished data), *C. maximum* had increased ~200×, corresponding to a population growth rate of 0.49 year^{-1}. Similarly, using photographs from permanent sites (taken and provided by P. Edmunds of the Moorea Coral Reef LTER), we estimated an annual increase in density of 0.26 year^{-1} (using data from 2006 to 2009: Osenberg et al., unpublished). Zvuloni et al. (2008) also reported increased densities of *C. maximum* in the Red Sea over the previous 10 years and attributed those increases to coastal eutrophication (leading to increased production of vermetid food resources). These rapid population growth rates, combined with the deleterious effects of vermetids, could drive dramatic changes in the reef ecosystems.

Though *C. maximum* is native to Moorea, its recent increases in density are more consistent with the dynamics of a recently established invasive species. Our previous work (Phillips et al. 2014) suggests that living coral tissue inhibits vermetid recruitment (live corals can kill and consume vermetid larvae), so high coral cover may provide initial 'resistance' to vermetid establishment, preventing population outbreaks from starting. Vermetids also increase coral mortality (e.g. Shima et al. 2010, 2013), so once established, the deleterious effects of vermetids on coral cover may open up additional space and facilitate further recruitment of vermetids.

Sources of variation in post-settlement growth and survival of vermetids (e.g. effects of local environment and/or density) are unclear. We therefore conducted a large-scale study to estimate growth and survival rates of tagged vermetids (*C. maximum*) as a function of individual size, local (neighbourhood) densities, reef-scale densities, and benthic substrate composition. We address fundamental hypotheses that body growth and/or survival rates of vermetids are (1) size-dependent, (2) density-dependent, and/or (3) substrate-dependent. We evaluate these patterns over a range of spatial scales to shed light on potential sources of variation in demographic rates that contribute to the population dynamics of this species.

Methods

We established eight discrete sites (separated by >500 m) along the north shore of Moorea, French Polynesia (S17.48 W149.81; Fig. 2). We haphazardly selected 10 small patch reefs within each site for further study. These reefs were originally established for another study (Shima et al. 2013) that evaluated the effects of vermetids on coral growth and survival. As part of that earlier experiment, we randomly assigned reefs to one of two treatments: we removed vermetids from half of the reefs at each site and left the remaining reefs with ambient densities of vermetids. The previous experimental manipulation of vermetids helped create a more extreme gradient in vermetid densities within each of our sites (from near 0 to ambient), which we used to our advantage in the present study.

In early October 2008, we selected and marked up to five focal *C. maximum* vermetids on each reef ($n = 297$ total) with numbered plastic tags affixed near vermetid apertures using A788 splash zone epoxy (Z-Spar). For the reefs where we had previously removed vermetids, focal animals were individuals that we failed to effectively remove as part of the previous manipulation, or else they were recent recruits. As a result, they tended to be slightly smaller than

Fig. 2 Location of eight study sites within lagoon system on the north shore of Moorea, the Society Islands archipelago (French Polynesia)
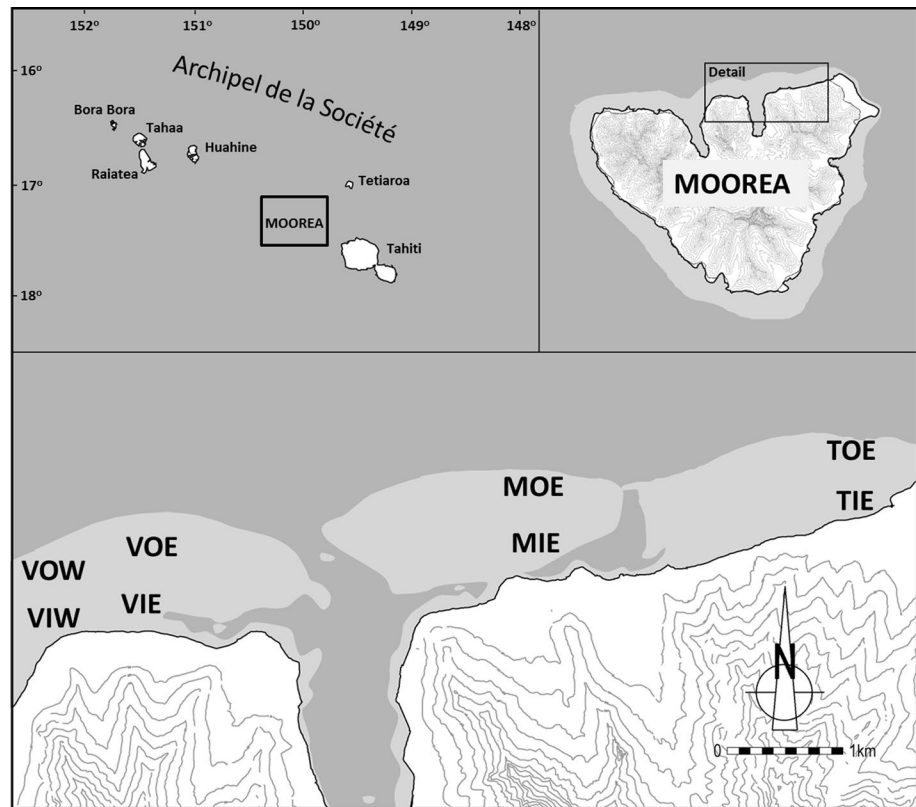
the snails on the control reefs. We measured the aperture size of focal vermetids with callipers (to nearest 0.1 mm) and characterized the surrounding 'substrate type' as either living *Porites lobata* coral, living *P. rus* coral, living *Montipora* spp. coral, algal turf, or dead coral substrate. We quantified all other vermetids within a 20 cm radius of focal animals and assigned each neighbouring vermetid to one of three size classes based upon aperture diameter (<5; 5–10; or >10 mm); we used size class medians and a known relationship between wet mass and aperture diameter (Phillips and Shima 2010) to estimate 'local vermetid biomass' ($g \cdot 1257$ cm^{-2}). Vermetid biomass and density were positively strongly correlated ($r = 0.79$, $p < 0.0001$) and because we expected that any possible intraspecific effects would scale with body size, we use biomass density (rather than density, per se) in all of our analyses.

In July 2010, after 646 days, we terminated the study because longitudinal growth of shells (>20 cm away from numbered tags in many cases) and tag fouling challenged our ability to continue to track individuals. We confirmed identities of all focal vermetids by retracing their shell extensions back to numbered tags, noted whether they were alive or dead, and re-measured their shell apertures.

We evaluated the hypotheses that growth and survival of *C. maximum* depended upon (1) body size, (2) local biomass of nearby vermetids (i.e. density dependence), (3) experimental removals of vermetids (density dependence

at a reef scale), and/or (4) substrate type using generalized linear mixed models (Proc Glimmix, SAS 9.3). Specifically, we evaluated sources of variation in growth (the difference between final and initial aperture size) as a function of (1) initial aperture size; (2) local vermetid biomass (an average from three census dates); (3) treatment (reefs with ambient densities of vermetids vs. reefs with density reductions); (4) substrate type; and (5) the interactions between vermetid size, local vermetid biomass, treatment, and substrate. We modelled 'site' and 'reef nested within site' as random effects. We evaluated a full model that included all possible interactions, sequentially removed nonsignificant interaction terms, and interpreted a final 'reduced' model that included random effects, all main effects (i.e. fixed factors), and any significant interaction terms (involving fixed factors). We evaluated sources of variation in survival (a binomial response: 1 = alive, or 0 = dead after 646 days) using an identical procedure, though with a binomial response distribution for generalized linear mixed models.

Results

Vermetid growth

Of the 297 focal vermetids tagged at the beginning of our study, we successfully relocated 256 tags after
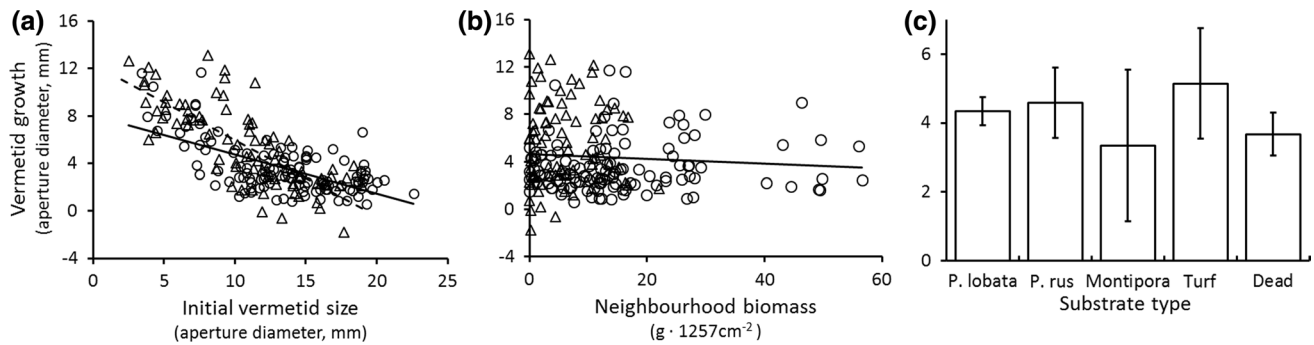
Fig. 3 Variation in growth (estimated as the difference between final and initial shell aperture diameter) of tagged individuals of the vermetid gastropod, *Ceraesignum maximum*, over 646 days. **a** Effects of initial vermetid size and treatment (density reductions given by *triangles and dashed line*; ambient densities given by *circles and solid line*) on growth. **b** Effect of local vermetid biomass on growth. *Fitted lines* in (**a**) and (**b**) are linear regressions on raw data (shown for presentation purposes) and do not account for fixed and random effects in our formal analysis (a linear mixed model). **c** Least-squared mean estimates ($\pm 95\ \%$ CI) of vermetid growth on different substrate types (living corals *P. lobata*, *P. rus*, *Montipora* spp., algal turf, and dead coral substrate)

646 days. Of the relocated vermetids, 205 were alive, and three of these had damaged or deformed shell apertures (these were excluded from estimates of growth); the other 51 were dead. Three vermetids had marginally smaller apertures at the end of the study (giving 'negative' estimates of growth), but because their shells did not appear visibly damaged or deformed, they were retained in our analysis. Therefore, we had estimates of aperture growth from 202 individuals. Over the 646-day study period, focal vermetids increased in aperture diameter by an average of 4.4 mm (SD = 2.9) and, based upon a previously established biomass–aperture relationship (Phillips and Shima 2010), increased in mass by 6.9-fold.

The reduced model accounting for variation in growth included fixed effects of size, local biomass, substrate, treatment, and the interaction between size and treatment. Vermetid growth declined with initial aperture size ($F_{1,125} = 210.33$; parameter estimate = -0.65, SE = 0.05; $p < 0.0001$), but the effect of initial aperture size depended upon treatment (interaction: $F_{1,125} = 17.64$; parameter estimate for control relative to removal = 0.29, SE = 0.07; $p < 0.0001$; Fig. 3a). Vermetid growth also declined, albeit weakly, with local vermetid biomass ($F_{1,125} = 4.26$; parameter estimate = -0.03, SE = 0.016; $p = 0.04$; Fig. 3b). The main effect of treatment was significant ($F_{1,125} = 15.35$; parameter estimate for control relative to removal = -3.53, SE = 0.90; $p < 0.0001$), though it depended on vermetid size (see above); small vermetids grew more on reefs where overall densities of vermetids were reduced, while large vermetids grew at similar rates in the two treatments (Fig. 3a). Vermetid growth did not vary significantly with substrate type ($F_{4,125} = 1.49$, $p = 0.21$; Fig. 3c).
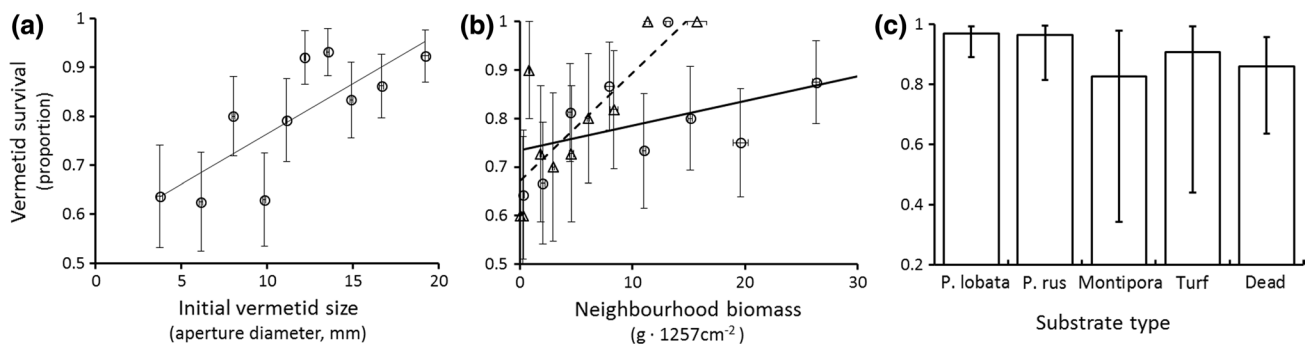
Vermetid survival

Collectively, focal vermetids had a 0.80 probability of survival over 646 days (205 individuals of 256 relocated individuals were alive at the end of the study). The reduced model included fixed effects of size, substrate, treatment, local biomass, and the interaction between treatment and local biomass. Survival increased with initial aperture size ($F_{1,172} = 14.94$: parameter estimate = 0.20, SE = 0.05; $p = 0.0002$; Fig. 4a). Survival also increased with local vermetid biomass ($F_{1,172} = 13.1$; parameter estimate = 0.29, SE = 0.09; $p = 0.0004$), though the relationship with biomass was steeper where vermetid densities had been experimentally reduced (biomass × treatment: $F_{1,172} = 4.85$ parameter estimate for control relative to removal = -0.2, SE = 0.09; $p = 0.03$; Fig. 4b). Vermetid survival also varied as a function of substrate type ($F_{4,172} = 2.61$, $p = 0.04$; Fig. 4c), being greatest on living *P. lobata* (mean probability = 0.97; 95 % CI 0.89–0.99), followed by living *P. rus* (0.96; 0.81–0.99), and algal turf (0.91; 0.44–0.99). Survival was lowest on dead coral substrate (0.86; 0.63–0.95) and living *Montipora* spp. (0.83; 0.34–0.98). Post hoc Tukey's tests conducted for all pairwise comparisons indicate that survival was significantly different only between living *P. lobata* and dead coral substrate ($p = 0.004$). To more clearly envision this difference, we expressed these results for survival over 646 days in terms of longevity (calculated as $-646/(365 \cdot \ln(S))$, where S is the estimated proportion surviving). The expected longevity for snails on living *P. lobata* versus dead coral was 58.1 versus 11.7 years, a 5-fold difference.

Discussion

Our data provide the first estimates of vital rates for *C. maximum*, and suggest that growth and survival varied with

Fig. 4 Variation in survival of the vermetid gastropod, *Ceraesignum maximum*, over 646 days. **a** Proportional survival of vermetids across 10 'bins' of initial vermetid size. **b** Proportional survival of vermetids across 10 'bins' of local vermetid biomass for each treatment (density reductions given by *triangles and dashed line*; ambient densities given by *circles and solid line*). *Fitted lines* in (**a**) and (**b**) are linear regressions on bin means (shown for presentation purposes), and error bars are ±1 standard error (most error bars in the *x*-direction are smaller than the symbol size) and do not account for fixed and random effects in our formal analysis (a linear mixed model conducted with a binomial response distribution). **c** Least-squared mean estimates (±95 % CI) of vermetid survival on different substrate types (living corals *P. lobata*, *P. rus*, *Montipora* spp., algal turf, and dead coral substrate)

respect to body size and local vermetid biomass. Smaller individuals grew more than larger individuals (and this difference was accentuated where we reduced vermetid densities at a reef scale). Previous work suggests *C. maximum* may be a protandrous hermaphrodite (Phillips and Shima 2010), and the energetic costs of reproduction would undoubtedly increase following a transition from male to female. In addition, Phillips and Shima (2010) found that reproductive output of females increased with size (Phillips and Shima 2010). The reduced growth rates of larger vermetids (Fig. 3a) is consistent with a shift in energy allocation from growth to reproduction (e.g. Stearns 1992).

Our data also suggest that smaller vermetids grew more on reefs with reduced conspecific densities (Fig. 3a, interaction between vermetid size and density manipulation), and irrespective of size, individual growth rates decreased marginally as a function of local vermetid biomass (Fig. 3b). Collectively, these results suggest weak density dependence in growth rates, consistent with interference competition involving neighbouring mucus nets (Smalley 1984; Gagern et al. 2008).

Contrary to what we found for growth, survival of *C. maximum* decreased with size and increased with local vermetid biomass. Size-dependent mortality (e.g. Fig. 4a) is common among marine invertebrates and is often attributed to the attainment of a size refuge from predators or physical stress (Paine 1976; Nakaoka 1996; Katsanevakis 2007). However, other mechanisms could also account for this pattern. For example, Rossetto et al. (2012) documented similar patterns of growth and mortality for abalone and suggested that smaller, faster-growing individuals had less well-developed immune systems and were therefore more vulnerable to disease and physiological stress.

Survival increased with local vermetid biomass (and this effect was most pronounced where we reduced vermetid densities at a reef scale, Fig. 4b), suggesting that survivorship is facilitated by living in larger groups. This contradicted our expectations and much of the evidence from other marine invertebrates (e.g. Jenkins et al. 2008; Puckett and Eggleston 2012; Tezuka et al. 2012), where per capita mortality rates commonly increase with density. However, positive (inverse) density-dependent survival is known to occur (e.g. Bertness and Grozholz 1985; Bertness 1989; Bruno et al. 2003; Gascoigne et al. 2005; Miller et al. 2007), and we hypothesize that the mucus nets normally used by vermetids for feeding may also deter some types of predators when net production is sufficiently high (i.e. when the local biomass of vermetids is high). The significant interaction between neighbourhood biomass and density manipulation is difficult to explain. We suspect this also may be a statistical artefact (due to a small number of observations with high leverage, or a limited range of 'neighbourhood biomass' for the 'vermetid removal' treatment), and/or potentially, a nonlinear relationship between 'neighbourhood density' and survival.

Ceraesignum maximum growth was not affected by the substratum on which it was living. Because *C. maximum* uses mucus nets to capture phytoplankton, zooplankton, and detritus (Kappner et al. 2000), this may indicate that the substratum underneath the net does not affect food amount (or quality) or feeding success (or efficiency). Nevertheless, substrate type had significant effects on vermetid survival. We hypothesized that vermetids may be more vulnerable to potential predators (e.g. pufferfish, triggerfish, parrotfish, octopus, muricid gastropods: Brown et al. 2014) when their shells are exposed (i.e. not concealed or covered by coral; *c.f.* Fig. 1b, c). Our results partially support

that hypothesis demonstrating that survival was significantly greater on some types of living coral substrata (e.g. *P. lobata*) than on dead coral substrata. Rare instances of shell damage consistent with some forms of predation (e.g. triggerfish) were only ever observed on exposed vermetid shells (e.g. Fig. 1c). However, further experimental manipulations would be required to formally test this hypothesis. Similarly, the potential species-specific effects hinted at in our results might warrant further investigation. Although both species of *Porites* supported relatively high survival and growth of *C. maximum*, vermetid performance on the other species of live coral examined, *Montipora*, tended to be lower (although not significantly) and more highly variable. *C. maximum* in turn affects these coral species differentially, having strong negative effects on *Porites*, but negligible effects on *Montipora* (Shima et al. 2010). Thus, the strength of coupling of dynamics between vermetids and different species of coral will likely be variable and the outcomes complex.

Our work suggests that per capita survival of vermetids (1) is greater for larger animals and (2) increases with their density. Given sufficient recruitment, both of these demographic traits will (in spite of the weak density-dependent body growth that we also documented) lead to unregulated (and accelerating) population growth (assuming density-dependent effects on other unmeasured demographic rates, e.g. reproduction or recruitment, do not alter these patterns). However, vermetids can also kill corals and reduce their growth (Colgan 1985; Zvuloni et al. 2008; Shima et al. 2010, 2013, 2015; Stier et al. 2010), and here, we show that survivorship of vermetids is significantly reduced on dead coral substrate. Furthermore, we observed many of our tagged vermetids grew considerably in shell length (≥20 cm over the course of our study), almost suggesting a 'search path'. We speculate vermetids may continually degrade local neighbourhoods, and their linear growth may enable them to move to new microsites with higher cover of living coral. Although we found limited evidence that direct density dependence regulates populations of *C. maximum*, these vermetid populations could be regulated indirectly, through feedbacks involving their deleterious effects on coral cover. If true, then we would expect that the vermetid gastropod, *C. maximum*, may experience cyclical dynamics that are coupled to the dynamics of living coral.

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