

Research



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Community ecology

When environmental factors become stressors: interactive effects of vermetid gastropods and sedimentation on corals

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Environmental stressors often interact, but most studies of multiple stressors have focused on combinations of abiotic stressors. Here we examined the potential interaction between a biotic stressor, the vermetid snail *Ceraesignum maximum*, and an abiotic stressor, high sedimentation, on the growth of reef-building corals. In a field experiment, we subjected juvenile massive *Porites* corals to four treatments: (i) neither stressor, (ii) sedimentation, (iii) vermetids or (iv) both stressors. Unexpectedly, we found no effect of either stressor in isolation, but a significant decrease in coral growth in the presence of both stressors. Additionally, seven times more sediment remained on corals in the presence (versus absence) of vermetids, likely owing to adhesion of sediments to corals via vermetid mucus. Thus, vermetid snails and high sedimentation can interact to drive deleterious effects on reef-building corals. More generally, our study illustrates that environmental factors can combine to have negative interactive effects even when individual effects are not detectable. Such 'ecological surprises' may be easily overlooked, leading to environmental degradation that cannot be anticipated through the study of isolated factors.

1. Introduction

Environmental stressors, factors that can cause a deleterious response in an organism, population or ecosystem [1], occur simultaneously, yet most ecological studies examine effects in isolation [2–4]. Thus, cumulative impacts of multiple stressors are often assessed by summing individual effects; however, if combined effects of stressors are non-additive, then their actual effects may be greater (if stressors act synergistically) or lesser (if stressors act antagonistically) than expected [4,5]. Indeed, meta-analyses suggest that multiple stressor effects are usually non-additive, with synergisms and antagonisms approximately equally common ([2,3], but see [6]). However, only 14% of the 314 studies reviewed in these meta-analyses [2,3] featured a biotic stressor, leaving interactions between abiotic and biotic stressors poorly understood. This dearth of studies of abiotic and biotic stressors may give a false view of the effects of non-additivity, especially if the biotic stressor is directly affected by the abiotic stressor.

Coral reefs are affected by many stressors that, alone or in combination, can threaten reef resilience [1]. Here we focus on two stressors: vermetid gastropods and high sedimentation. The vermetid *Ceraesignum maximum* (formerly *Dendropoma maximum* [7]) is a common sessile gastropod inhabiting coral reefs throughout the Indo-Pacific [8,9]. *C. maximum* feed by secreting mucus strands that coalesce into nets that can cover the surfaces of corals [8]. Exposure of corals to vermetids induces anomalies in coral morphology [9,10] and reduces coral growth and survival [10–13]. The mechanisms by which vermetids harm coral are unknown, but likely involve allelopathic chemicals or effects of mucus nets on water flow, gas exchange, coral mucus production or microbial communities (see electronic supplementary material, appendix). It is unclear how the

effects of vermetids may be modified by other common stressors, such as sedimentation, which also can contribute to deterioration of reef-forming corals [14].

We hypothesized two alternative ways in which vermetids and sediments could interactively affect corals: (i) a synergistic ‘adhesion effect’, in which vermetid mucus combines with sediments to better stick to coral surfaces [8] or (ii) an antagonistic ‘conveyance effect’, by which vermetid nets remove sediment from coral surfaces (thus benefiting the coral [15]). We therefore tested the nature and strength of the interactive effect of vermetids and sedimentation on coral growth.

2. Material and methods

In June–August 2012, we conducted a field experiment on the north shore of Mo’orea, French Polynesia. We crossed the presence of *C. maximum* with sedimentation, yielding four treatments, and we measured the growth of massive *Porites* (a species complex of functionally similar reef-building corals (electronic supplementary material, appendix)).

We selected 36, approximately 1 m diameter, mostly dead colonies of massive *Porites* as deployment sites for our experimental corals. Because differences in water flow could affect vermetid net casting and sediment removal rates, we quantified relative flow among sites using clod cards [16]. The flat top of each site contained 5 ± 1 (mean \pm s.d.) vermetids in a 400 cm² area, which is within the mucus net casting range of adult *C. maximum*.

We randomly assigned each site to one of four experimental treatments. We removed all vermetids from sites assigned to the ‘–vermetid’ treatments. We then collected 36 juvenile *Porites* colonies from a nearby location, to serve as our experimental corals. Each coral was attached to a small plastic base using marine epoxy and buoyantly weighed [17]. We then grouped the corals into nine blocks, based on minor differences in morphology, and randomly assigned them to sites. We attached the plastic bases of the corals to sites using u-nails. To assess the efficacy of our treatments, we quantified how often corals were fully covered by vermetid mucus.

For the ‘+sedimentation’ treatments, 11 g (dry mass) of sediments from the adjacent seafloor were applied to corals every 1–2 days. This yielded an average sediment deposition rate of 54.2 ± 5.8 (mean \pm 95% CI) mg (dry mass) cm⁻² d⁻¹, which is within the range of that observed in Mo’orea (electronic supplementary material, appendix). Fourteen corals (seven blocks) in the ‘+sedimentation’ treatment were videotaped to quantify sediment removal rates, estimated (using IMAGEJ software) as $[(C_0 - C_6)/C_0]$, where C_0 and C_6 are the coral surface areas covered by sediment at the start (0 h) versus end (6 h) of the trial.

After 54 days, we retrieved, reweighed and measured the surface areas of corals [18] to calculate coral growth (per-area change in coral skeletal mass). We used a linear mixed-effects model (vermetids and sedimentation were fixed effects; block was a random effect) to analyse coral growth rate, excluding one statistical outlier in the ‘+sedimentation’ treatment that did not qualitatively affect our results. Coral growth rates met assumptions of normality and homoscedasticity, as revealed by residual plots. We used a paired *t*-test to analyse sediment removal rates by corals (paired by morphology) in the presence versus absence of vermetids.

Additional methodological details can be found in the electronic supplementary material, appendix.

3. Results

Water flow did not significantly differ among treatments (ANOVA, $F_{3,34} = 2.02$, $p = 0.14$) and our surveys demonstrated

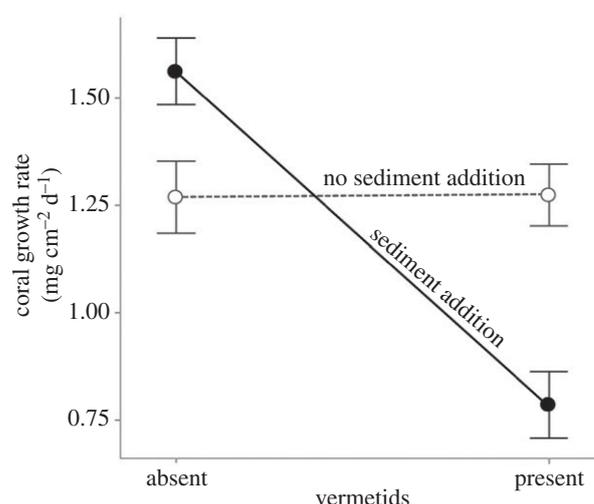


Figure 1. Effects of vermetid gastropods and added sediment on coral skeletal growth during a 54 day field experiment (mean \pm 95% CIs). There was a significant interaction between vermetids and sedimentation ($F_{1,23} = 6.62$, $p = 0.017$), but no significant main effect of vermetids ($F_{1,23} = 0.0005$, $p = 0.98$) or sedimentation ($F_{1,23} = 1.74$, $p = 0.20$): growth = $\beta_{\text{block}} + \beta_S \times S + \beta_V \times V + \beta_{SV} \times S \times V$, where $S = (0,1)$ and $V = (0,1)$ indicates the presence (1) or absence (0) of the factor, and $S \times V = 0$ for all treatments except for the one with both sediments and vermetids (in which case $S \times V = 1$). Fitted fixed effects (\pm s.e.) were: $\beta_S = 0.29$ (0.22), $\beta_V = 0.0047$ (0.21), $\beta_{S \times V} = -0.77$ (0.30).

the effectiveness of the vermetid treatment: ‘+vermetid’ and ‘–vermetid’ corals were covered by mucus nets 97.8% ($\pm 4.1\%$) and 0.001% ($\pm 0.008\%$) of the time (mean \pm s.d.), respectively.

Skeletal growth did not vary among blocks ($p > 0.90$), nor was it significantly affected by either putative stressor alone, but growth was affected by the interaction between vermetids and sedimentation ($F_{1,23} = 6.62$, $p = 0.017$; figure 1). Because growth was more greatly reduced in the presence of both factors than predicted by their individual effects, the stressors acted synergistically [5], supporting hypothesis (i) and refuting hypothesis (ii). As expected under hypothesis (i), corals removed on average 66% (95% CI: 54–78%) less sediment when vermetids were present compared with when they were absent ($p < 0.0001$; figure 2).

4. Discussion

Our study revealed that a biotic stressor and an abiotic stressor, both at levels that were not demonstrably harmful in isolation, became harmful to juvenile corals when combined. The negative effect of vermetids and sediments on coral growth was likely driven by an ‘adhesion’ mechanism (hypothesis (i)), in which vermetid mucus combined with sediments to form a more stable conglomerate (figure 2).

Surprisingly, and in contrast to previous studies [10–13], we found no deleterious effect of vermetids in the absence of sediment addition, possibly because the relationship between vermetids and coral growth might vary spatially or temporally, owing to variation in vermetid density, water flow, nutrients, sedimentation, or the local coral microbiome [13]. Alternatively, our study may have used corals that were better able to withstand effects of vermetids, possibly because the high density of vermetids [10] could have selected for juveniles

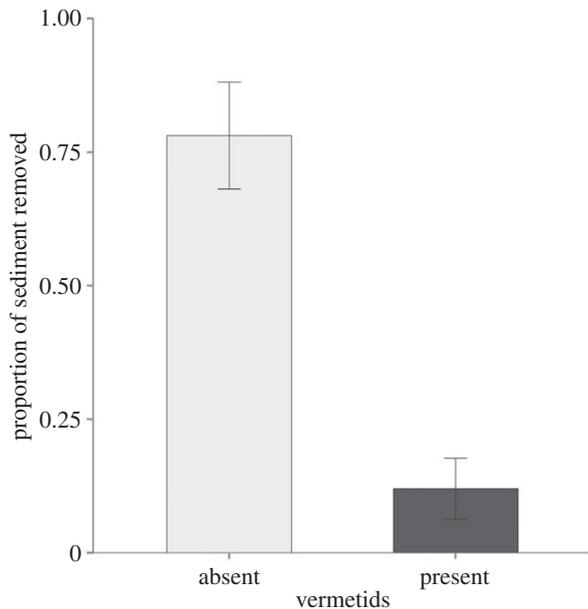


Figure 2. The proportion of coral tissue cleared of sediments 6 h after sediment application (means \pm 95% CI, $N = 7$, paired t -test: $p < 0.001$).

resistant to vermetids or because phenotypic plasticity (in corals or their microbiomes) could have made corals less sensitive (electronic supplementary material, appendix).

It also was unexpected that sedimentation alone did not have detrimental effects on corals, as demonstrated in previous studies [14]. However, findings from natural sedimentation gradients show that corals can resist harmful effects of sedimentation [19]. The convex morphology of our corals may have facilitated this resistance by reducing the retention of sediments—an advantage that was lost in the presence of the adhesive vermetid net (figure 2). Corals may have also fed on organic matter in the fine sediments [20], masking the expected deleterious effects of sediments (electronic supplementary material, appendix).

The absence of main effects of the two stressors could suggest an alternative view to our perspective. Instead of a synergy between stressors, the interactive effect of vermetids and sediments could be due to context-dependency, e.g. vermetids never have a direct effect on corals—they simply modify the

strength of effects of sediments. While plausible, this explanation is inconsistent with past work identifying vermetids and sediments as stressors to corals ([10,13,14]; electronic supplementary material, appendix). Because context-dependency arises when the effect of one factor depends on the level of another, the contrast between context-dependency and interactive stressors disappears if both factors are known to be deleterious at some level.

No matter the term used, it is essential that we understand interactions among environmental factors to facilitate better ecosystem management and conservation [4]. Yet studies testing interactive effects of biotic and abiotic factors (or stressors) remain rare. Rarer still (for logistical reasons) are studies that examine possible interactions between apparently neutral factors (but see [21]). Yet, as we come to appreciate the possibly strong synergisms among otherwise weak stressors [5], it becomes imperative that we have such knowledge. Context-dependent and non-additive effects pose a serious challenge to ecology [22,23], and interactions among stressors may represent a large source of error in projections of ecological change. This error may be even more profound when we consider that environmental factors may only act as stressors when combined.

Ethics. This study was conducted under a research protocol approved by the French Polynesian government and facilitated by the Richard B. Gump South Pacific Research Station.

Data accessibility. Data from this study are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.p59n8> [24]. An appendix with additional background information, methodological details and discussion of our findings has been uploaded as electronic supplementary material.

Authors' contributions. J.A.Z., M.A.G. and C.W.O. designed the study and wrote and revised the manuscript. J.A.Z. and M.A.G. collected and analysed the data. All authors approved the final manuscript and agreed to be accountable for all aspects of the study.

Competing interests. We have no competing interests.

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