

# Hidden predators on coral reefs: muricid consumption of vermetids

A. L. Brown<sup>1,2,\*</sup>, T. K. Frazer<sup>2,3</sup>, G. Li<sup>4</sup>, J. R. Hilsenroth<sup>2</sup>, J. S. Shima<sup>5</sup>,  
C. W. Osenberg<sup>1</sup>

<sup>1</sup>Odum School of Ecology, University of Georgia, Athens, GA 30602, USA

<sup>2</sup>School of Natural Resource and Environment, University of Florida, Gainesville, FL 32611, USA

<sup>3</sup>School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program, University of Florida, Gainesville, FL 32611, USA

<sup>4</sup>UC Berkeley Richard B. Gump Marine Station, BP 244, Maharepa 98728, Mo'orea, French Polynesia

<sup>5</sup>School of Biological Sciences, Victoria University of Wellington, Wellington 6140, New Zealand

**ABSTRACT:** Predators, through their effects on prey densities, sizes, and behaviors, can shape ecological communities. Thus, quantitative assessments of predator–prey relationships are key to understanding these effects. Here, we documented the patterns and processes underlying the effects of 2 predatory muricid gastropods, *Mancinella armigera* and *Menathais tuberosa*, on the sessile vermetid gastropod *Ceraesignum maximum*. We used a combination of field surveys and manipulative lab and field experiments to quantify muricid abundances, predator feeding rates, and effects of predator density on vermetid mortality. The 2 predators exhibited spatial segregation, with *M. armigera* being more common close to the reef crest and *M. tuberosa* increasing in density away from and shoreward of the reef crest. We demonstrated that recently killed vermetids were more common in the vicinity of *M. armigera*. Laboratory assays revealed that *M. armigera* killed 0.55 *C. maximum* predator<sup>-1</sup> d<sup>-1</sup>, a rate that was ~60% greater than for *M. tuberosa*. Although the 2 predators were spatially segregated in the field, they did not demonstrate interference competition or intraguild predation in the lab. Consumption rates of *C. maximum* by *M. armigera* in the field were approximately equal to those quantified in the lab, and although consumption rates decreased over time, predator density had no effect on predator consumption rate. In addition, we observed no evidence of size selectivity by predators. This study is the first to quantitatively examine predator–prey interactions involving *C. maximum*, and our findings suggests that muricids can limit vermetid populations where both are present.

**KEY WORDS:** Predation · *Ceraesignum maximum* · Multiple predator effects · Coral reefs

—Resale or republication not permitted without written consent of the publisher—

## 1. INTRODUCTION

Predators alter prey behavior (Werner & Peacor 2003), densities (Preisser et al. 2005), and size distributions (Brooks 1968), and in so doing, have a profound influence on community dynamics, energy flow, and material transport. Predator density (Johnson 2006) and identity (Sih et al. 1998) are particu-

larly important in determining the magnitude of effects of predators on prey populations (Soluk & Collins 1988, Abrams 1993, Griffin et al. 2008). Additionally, interactions among predators due to intraspecific density dependence, interspecific interference, or intraguild predation (Soluk & Collins 1988, Arditi & Ginzburg 1989, Vance-Chalcraft et al. 2007) can modulate predator effects. For exam-

\*Corresponding author: anyabrown@ufl.edu

ple, combinations of predators can lead to multiple predator effects (MPEs) in which effects of 2 or more predator species combine non-additively to either increase or reduce predation risk (Sih et al. 1998, McCoy et al. 2012). Additionally, effects on prey may have important implications for other species in the community that are affected directly or indirectly by the prey (e.g. via trophic cascades; Terborgh & Estes 2010). A first step in understanding the role of predators in a community is a quantitative description of the relationships between predators, prey, and their habitat.

While we have a detailed understanding of consumer–resource interactions in some systems (e.g. planktivore–zooplankton in lakes; Brooks & Dodson 1965, Mittelbach et al. 1995, Maszczyk & Gliwicz 2014), other systems remain relatively understudied. This is particularly true for species-rich tropical systems, such as coral reefs. Studies of predators on coral reefs often focus on species that directly consume coral or impose indirect effects on coral via herbivory. For example, crown-of-thorns sea stars selectively consume branching corals, leading to dramatic changes in coral cover and community composition following sea star outbreaks (Kayal et al. 2012). Herbivorous fish often limit the abundance of algae and thus affect coral dynamics; i.e. the removal of herbivores increases algae, which can then lead to declines in coral cover via competition (Hughes 1994, Lirman 2001, Bellwood et al. 2004, Burkepile & Hay 2006). Thus, the persistence of coral colonies and their associated communities will often depend on the effects of consumers (e.g. predators), although many predator–prey interactions involving prey that affect corals are currently unknown.

Vermetid snails reduce coral growth, survival, and photophysiology (Shima et al. 2010, 2013, 2015). Thus, understanding how predators affect vermetid populations can have important implications for understanding indirect responses of coral communities to changes in food-web structure on coral reefs. We recently published the first observation that the predatory muricid snail, *Mancinella* (formerly *Thais*) *armigera* consumes *Ceraesignum maximum* (Brown et al. 2014), although the details of this interaction remain unknown. *M. armigera*, found throughout the South Pacific, is a predatory gastropod in the family Muricidae (Taylor 1978). Other muricid gastropods, such as *Coraliophila* and *Drupella*, are more widely studied as they consume corals and affect coral growth and distribution (Hamman 2017). *M. armigera* often co-occurs with other muricids (e.g. *Menathais tuber-*

*osa*), but little is known about its fine-scale distributional patterns or interactions with other species, including other muricids (e.g. via competition or intra-guild predation). Additionally, there are no quantitative data detailing muricid–vermetid interactions (e.g. feeding rates or size preferences). Prior observations suggest that *M. armigera* consumes vermetids (Brown et al. 2014), and due to their somewhat similar size and ecology, we hypothesized that *M. tuberosa* might also be a predator of vermetids. Furthermore, given the slightly larger size of *M. armigera*, we also hypothesized that *M. armigera* is a predator of *M. tuberosa*, and that this predation (or threat of predation) could drive spatial patterns of the muricids and influence the mortality of vermetids.

Here, we report on studies conducted in Mo'orea, French Polynesia, to quantify the interactions among muricids and the vermetid snail, *C. maximum*. We used field surveys to determine the habitat distribution of the muricids and their relationship to patterns of vermetid mortality by examining (1) the density of *M. armigera* and *M. tuberosa* on reefs; (2) the degree of spatial segregation between *M. armigera* and *M. tuberosa*; and (3) patterns of snail mortality in the local vicinity of *M. armigera*. In the laboratory, we investigated the potential for MPEs between *M. armigera* and *M. tuberosa* using an experiment designed to evaluate intraspecific and interspecific interactions. We used a manipulative field experiment to assess the effect of *M. armigera* density on vermetid survival. In both the laboratory and field experiments, we also quantified patterns of size-selective mortality of vermetids.

## 2. MATERIALS AND METHODS

### 2.1. Study site

The field surveys and experiment were conducted in the shallow back reef along the north shore of Mo'orea, French Polynesia (17.48° S, 149.82° W). Laboratory studies were conducted at the UC Berkeley Richard B. Gump Laboratory. At the time of the studies, *Ceraesignum maximum* (hereafter, 'vermetid') was common in the backreef, attaining densities as high as 32 vermetids m<sup>-2</sup> (Shima et al. 2010). The back reef is also inhabited by several muricid species, of which *Mancinella armigera* and *Menathais tuberosa* are the largest and most conspicuous (89.28 ± 8.17, 66.76 ± 0.91 cm, respectively; Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m615/p121\\_supp.pdf](http://www.int-res.com/articles/suppl/m615/p121_supp.pdf)).

## 2.2. Field surveys

To determine the densities and habitat distributions of *M. armigera* and *M. tuberosa*, we conducted surveys from 20–24 June 2014. Starting at the reef crest, we laid out seven 50 m long reference lines perpendicular to the reef crest. Each reference line was at least 37 m from the next nearest reference line. Transects were located in areas that were a combination of hard reef substrate and sand. At 10 m intervals along each reference line, a 30 m transect tape was laid out parallel to the reef crest (i.e. perpendicular to the reference line). We used the belt transect method and searched for both species of muricids within 1 m of the 30 m transect tape. The densities (muricids m<sup>-2</sup>) of *M. armigera* and *M. tuberosa* were calculated separately at each 10 m interval. We compared densities of *M. armigera* and *M. tuberosa* across distance using a mixed effects model with each reference line comprising a block (and modeled with a random intercept), and analyzed the data with ANOVA using the Satterthwaite approximation for degrees of freedom (Kuznetsova et al. 2016). These, as well as all other analyses were conducted in R (R Core Team 2016). Residuals were visually assessed to ensure distributions were approximately normally distributed around zero.

Additionally, whenever we encountered at least one *M. armigera*, we placed a 1 × 1 m<sup>2</sup> quadrat (n = 37) on the bottom substrate (centered on the muricid), counted all of the *C. maximum* shells in the quadrat, and categorized each shell as alive (with the snail intact) or recently killed (i.e. a bright, white empty tube; see Brown et al. 2016). Tubes with interiors that were fouled with algae or invertebrates were not recorded. Control quadrats were positioned ~3 m away from the focal *M. armigera* and inspected to ensure they did not contain another muricid. We similarly counted all live and recently killed vermetids in the control quadrats (n = 32 paired quadrats). We hypothesized that recently killed vermetids were attributed to the focal muricid, as would be expected if muricids did not move great distances (as suggested by our field experiment; see Section 3.3), and therefore used a paired *t*-test to compare the number of recently killed vermetids in quadrats with vs. without muricids (R Core Team 2016). Similarly, we tested if the total number of vermetids (alive and recently killed) differed among plots with vs. without a muricid to determine if muricids were more likely to be found among denser concentrations of vermetids.

## 2.3. Lab experiment: consumption rates of multiple predators

To determine the feeding rates of *M. armigera* and *M. tuberosa*, and to assess if intraguild interactions (and MPEs) affected feeding rates and habitat distributions, we conducted a lab experiment in 5 large (~1000 l, ~135 cm diameter, 85 cm deep) outdoor mesocosms with constant seawater inflow, at the Richard B. Gump Marine Station, Mo'orea, French Polynesia. In each mesocosm, we placed 5 pieces of coral rubble collected from the field that had vermetids attached to them. Live and dead vermetids were counted on each piece of rubble (mean ± SD: 60.67 ± 6.17 live vermetids tank<sup>-1</sup>), and their aperture diameters were recorded. We then randomly assigned 1 of 5 treatments to each of the 5 mesocosms: (1) 10 *M. armigera* (10 Ma), (2) 10 *M. tuberosa* (10 Mt), (3) 10 *M. armigera* and 10 *M. tuberosa* combined (10 Ma + 10 Mt), (4) 5 *M. armigera* and 5 *M. tuberosa* combined (5 Ma + 5 Mt), and (5) a control with no muricids (control). This design combines a substitutive design (in which the total density of muricids is fixed) and an additive design (in which adding another species leads to an increase in the total number of predators). Although the additive design uses densities that exceed ambient (see Section 3.1), we used these densities to facilitate our tests of multiple predator effects. MPE studies typically use additive designs, but these studies confound the effects of intra- and interspecific MPEs. This limitation can be overcome by combining additive (treatments 1, 2, 3, and 5) and substitutive (treatments 1, 2, 4, and 5) designs (Griffen 2006). Muricids were maintained in feeding tanks with vermetids and then starved overnight before the start of the trial.

Individual trials were carried out for 6 d. On each day, the cumulative number of newly killed vermetids was counted (as determined by the abundance of new empty white tubes). We ran 3 sets of trials (i.e. blocks): early October 2014, late October 2014, and late January 2015. We observed no mortality in the 0-predator treatment and therefore interpret all mortality to be due to consumption by muricids. To determine the shape of the relationship between the cumulative number of vermetids that were consumed and time, we compared models fit with a random effect of block and fixed effects of day and treatment, where day was modeled with a linear or quadratic term. We compared the linear and quadratic models using Akaike's information criterion (AIC).

We also compared the total mortality of vermetids (i.e. on Day 6) across the 5 treatments using a linear

mixed effects model with a random effect of block using the 'lme4' package (Bates et al. 2015) in R v.3.3.2, with 4 orthogonal contrasts: (1) the effect of muricids (i.e. all treatments with vermetids vs. control: treatments 1, 2, 3, and 4 vs. treatment 5); (2) the effect of composition, holding total density fixed (i.e. 10 Ma and 10 Mt vs. 5 Ma + 5 Mt: treatments 1 and 2 vs. treatment 4); (3) the effect of total density (i.e. treatments with 10 snails vs. the treatment with 20 snails: treatments 1, 2, and 4 vs. treatment 3); and (4) the effect of species (i.e. 10 Ma vs. 10 Mt: treatment 1 vs. treatment 2).

To calculate per capita feeding rates in each treatment, we divided the total number of vermetids killed by length of the experiment (6 d) for each treatment and by the number of muricids. We compared the feeding rates in treatments 1–4 using a linear mixed effects model, with a random effect for experimental block ( $n = 3$ ), followed by a Tukey's HSD multiple comparison test.

To specify the null expectation for the expected vermetid mortality in the presence of 2 predator species, we generated a prediction based upon the responses observed in the 2 single-predator treatments with 10 muricids (i.e. 10 Ma in treatment 1 and 10 Mt in treatment 2). We assumed that predators were handling-time limited (i.e. that feeding rates did not depend on prey density), as justified by the observed linear relationship between cumulative number of prey killed and time (see Section 3.2). We therefore predicted the number of vermetids killed in the other treatments as:  $F_a N_a T + F_t N_t T$ , where  $F_i$  is the average feeding rate per predator of species  $i$  (in treatment 1 or 2),  $N$  is the density of predator species  $i$  (in the treatment of interest),  $T$  is the duration of a trial ( $T = 6$  d), and  $i = a$  indicates *M. armigera* while  $i = t$  indicates *M. tuberosa*. Note that this formulation differs from some other studies (e.g. Vonesh & Osenberg 2003) which assume that predators are primarily search-time limited (see McCoy et al. 2012).

#### 2.4. Field experiment

To assess how the density of *M. armigera* influenced vermetid mortality under field conditions, we set up an experiment on the north shore of Mo'orea, French Polynesia (17° 28.349' S, 149° 47.026' W). In July 2014, we selected 16 reefs that ranged in size from 10–23 m<sup>2</sup> (area estimated as the surface area of a cylinder excluding its base). All dead vermetid shells on the reefs were notched (using a hammer and chisel) so that we could distinguish them from

live snails that subsequently died during the experiment. We removed all muricids from the reefs, randomly assigned reefs to 1 of 4 muricid treatments, and then placed 0, 3, 6, or 12 *M. armigera* on each reef. On Days 3, 10, 12, and 24 we counted the number of vermetids on each reef that had recently died (i.e. their shells were bright white and not notched). We notched all recently killed vermetid shells. At each census, we also recorded the number of muricids (i.e. *M. armigera*) on each reef. If reefs deviated from their initial assigned treatment densities of muricids, we removed or added muricids; we restocked to experimental densities on 4 occasions over the course of the experiment (Fig. S2: i.e. on 11 July, 15 July, 23 July, and 25 July 2014). In October 2014 (Day 60 of the experiment), we counted and measured the aperture diameter of all vermetid shells greater than 7 mm and classified vermetids as alive or dead and notched or unnotched.

We calculated the cumulative mortality of vermetids by summing the number of unnotched, dead vermetids (i.e. those that died since the last census) over the course of the experiment, and obtained the initial number alive by summing the final number alive and the cumulative number that died over the experiment. We analyzed the cumulative number of vermetids killed (i.e. on Day 60) using a generalized linear model with a negative binomial distribution (from the MASS package; Venables & Ripley 2002) with the fixed effect: average number of muricids.

For each interval, we also estimated the predation rate of muricids on vermetids (vermetids consumed muricid<sup>-1</sup> d<sup>-1</sup>) on reef  $x$  as:

$$P_x = [N_{x,i}(1 - C) - N_{x,f}] / [(M_{x,i} + M_{x,f}) / 2] T \quad (1)$$

where  $N_{x,i}$  and  $N_{x,f}$  are the number of live vermetids at the start and end of the interval for reef  $x$ ,  $M_{x,i}$  and  $M_{x,f}$  are the number of muricids at the beginning and end of the interval for reef  $x$ ,  $T$  is the duration of the interval (in days), and  $C$  is the loss rate from the 4 reefs in the control treatment: i.e.  $\sum_1^4 (N_{x,f} - N_{x,i}) / \sum_1^4 (N_{x,i})$  over the same interval. During the last time interval (Days 24 to 60) only 3 of the control reefs were included because the fourth reef included one *M. armigera*.

We analyzed the predation rate by *M. armigera* using a mixed effects model in which reef identity was a random effect (random intercept) and fixed effects were the average number of muricids on each reef, the number of days after the experiment was initiated (0, 3, 12, 24, 60 d), and the initial abundance of vermetids on each reef. These data were analyzed in R (R Core Team 2016) with the 'lme4' and 'lmerTest' pack-

ages (Bates et al. 2015, Kuznetsova et al. 2016). Data were checked for temporal autocorrelation by applying a correlation matrix including a variable for autocorrelation in the mixed effects model (ACF, in the 'nlme' package; Pinheiro et al. 2017).

## 2.5. Size selection

We used the laboratory and field data to quantify the size-selection of muricids feeding on vermetids. For the lab study, we assessed size-selective predation at the end of our study. We divided living and recently consumed vermetids into size bins based upon aperture diameter: >7–9, >9–10, >11–12, and >13–15 mm. Vermetids >15 or <7 mm were not sufficiently abundant to analyze. For the field experiment, we assessed size-selective predation using data collected between Days 24 and 60, using the same ranges of aperture diameter to construct size bins (and for field-based observations we had sufficient numbers to evaluate an additional size class comprised of individuals with aperture diameters >15 mm). For each replicate in each experiment, we calculated selectivity using the Manly-Chesson Index ( $\alpha$ ) that accounted for depletion (Manly et al. 1972, Chesson 1983):

$$\alpha_i = \frac{\ln[(n_i - r_i) / n_i]}{\sum_{j=1}^m \ln[(n_j - r_j) / n_j]} \quad (2)$$

where  $r_i$  is the number of vermetids in size class  $i$  that were eaten during the foraging period (i.e. from Day

0–6 in the lab study and Day 24–60 in the field study),  $n_i$  is the number of vermetids in size class  $i$  that were alive at the start of the foraging period (i.e. on Day 0 in the lab, or Day 24 in the field), and  $m$  is the number of size classes (4 or 5). The standardization in the denominator of Eq. (1) assures that elements in a given preference vector sum to 1.0. Alpha ranges from 0–1, with  $\alpha < 1 / m$  indicating avoidance and  $\alpha > 1 / m$  indicating preference (Chesson 1983). Selectivity vectors were compared using a linear mixed effects model with reef (for the field experiment) or temporal block (for the lab experiment) as the random effect, and size class of vermetids and treatment (density of muricids or density and identity of muricid) as fixed effects using the 'lme4' and 'lmerTest' packages (Bates et al. 2015, Kuznetsova et al. 2016) in R v.3.3.2.

## 3. RESULTS

### 3.1. Field surveys

The density of *Mancinella armigera* was greatest in transects close to the reef crest (10 m), decreased shoreward, and was entirely absent in transects 50 m from the reef crest (Fig. 1). *Menathais tuberosa* showed the opposite pattern with the greatest density further from the reef crest (i.e. at the 40 and 50 m sites). The opposing habitat use patterns resulted in a significant interaction between distance and muricid species ( $F_{1,60} = 9.30$ ,  $p = 0.003$ ) (Table 1).

Where we found a *M. armigera*, we were more likely to find recently killed vermetids in close proximity (within ~0.5 m) compared to nearby plots that did not contain *M. armigera*. Frequencies of recently killed vermetids were 8 times greater in plots with *M. armigera* (mean  $\pm$  SE:  $0.72 \pm 0.19$  recently killed vermetids when muricids were present vs.  $0.09 \pm 0.07$  recently killed vermetids when muricids were absent;  $t_{1,31} = -3.13$ ,  $p = 0.004$ ). We found no significant difference in the overall density of vermetids in quadrats with muricids ( $7.13 \pm 1.65$  vermetids quadrat<sup>-1</sup>) vs. without muricids ( $6.88 \pm 1.46$ ;  $t_{1,31} = -0.156$ ,  $p = 0.87$ ).

### 3.2. Lab experiment: consumption rates of multiple predators

The field data suggest that *M. armigera* consumes vermetids, and due to their somewhat similar size and ecology, we hypothesized that *M. tuberosa* might also be a predator of vermetids. Furthermore,

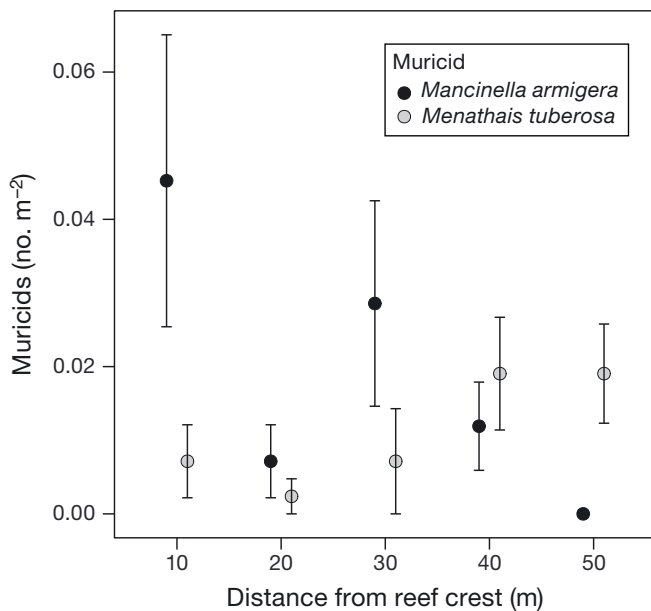


Fig. 1. Mean ( $\pm$ SE) muricid density in band transects 10 m shoreward of the reef crest



given the negative spatial correlation between the abundances of the 2 muricids, and the slightly larger size of *M. armigera*, we also hypothesized that *M. armigera* is a predator of *M. tuberosa*, and that this predation (or threat of predation) could be responsible for the spatial patterns we observed. Thus, we tested the relative predation rates of the 2 muricids on vermetids, and we assessed whether the presence of both predators resulted in risk reduction for vermetids (as is expected in many systems with intra-guild predators; Polis et al. 1989).

No vermetids died in the control treatment, suggesting that handling artefacts were minimal and that there were no cryptic sources of mortality in the mesocosms. Thus, we attributed all mortality to pre-

dition by muricids. During the 6 d predation trials, vermetid densities declined up to 62%. Despite this strong reduction in the number of living vermetids, the cumulative number of killed vermetids was approximately linear over the 6 d (AIC linear = 565.5; quadratic model = 573.0; Fig. 2), suggesting that predator feeding rates were independent of prey density and thus that feeding rates were primarily limited by handling time, not search time. The treatment with 10 *M. armigera* yielded a per predator feeding rate ( $0.55 \pm 0.14$ ) that was 60% greater than the feeding rate in the treatment with 10 *M. tuberosa* ( $0.31 \pm 0.07$ ; ANOVA:  $F_{3,6} = 5.64$ ,  $p = 0.035$ ; Fig. 3), suggesting that *M. armigera* is a more effective predator of vermetids. To evaluate synergistic effects, we compared the total consumption of vermetids in the presence of 5 *M. armigera* and 5 *M. tuberosa* to that expected based upon the mono-specific treatments—the observed consumption rate was very close to the expected consumption (Fig. 2;  $24 \pm 9.01$  vermetids vs. 25.8) and was not significantly different from the single-species treatments (treatments 1 and 2: 10 Ma and 10 Mt, vs. treatment 4: 5 Ma + 5 Mt;  $t_{1,8} = -0.43$ ,  $p = 0.68$ ; Table S1). Importantly, none of the *M. tuberosa* died during this experiment, suggesting that it is not a preferred prey item of *M. armigera*.

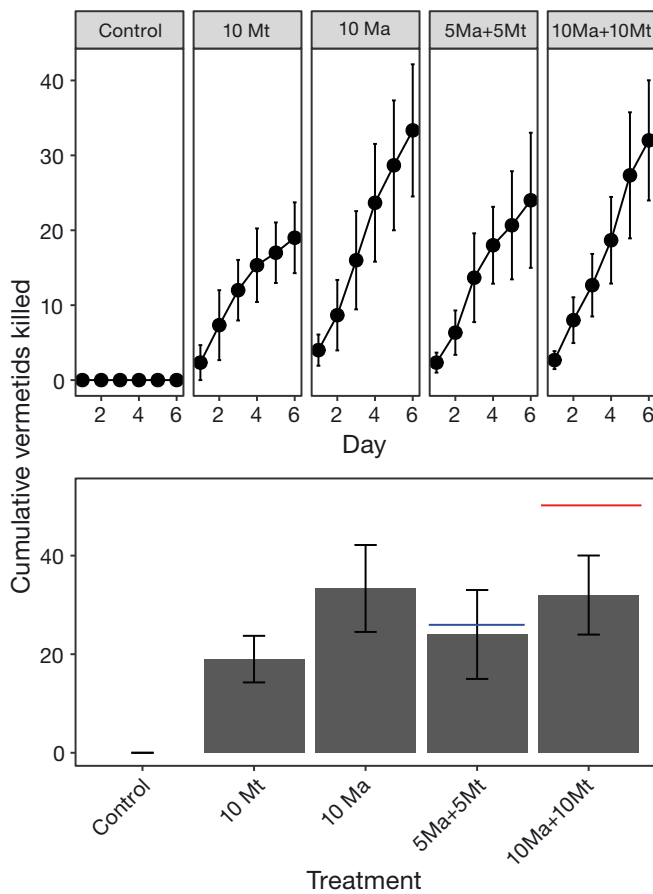


Fig. 2. Consumption of the vermetid gastropod *Ceraesignum maximum* by 2 species of predatory muricid: *Mancinella armigera* (Ma) and *Menathais tuberosa* (Mt). Top panel: cumulative mean ( $\pm$ SE) number of vermetids killed across 6 d in each of the 5 treatments, averaged across blocks. Bottom panel: total number of vermetids killed over 6 d in each treatment (mean  $\pm$  SE,  $n = 3$ ). Blue and red lines: the expected number of vermetids consumed in the 2-species treatments based on the consumption rates in the single-species (10 Ma and 10 Mt) treatments

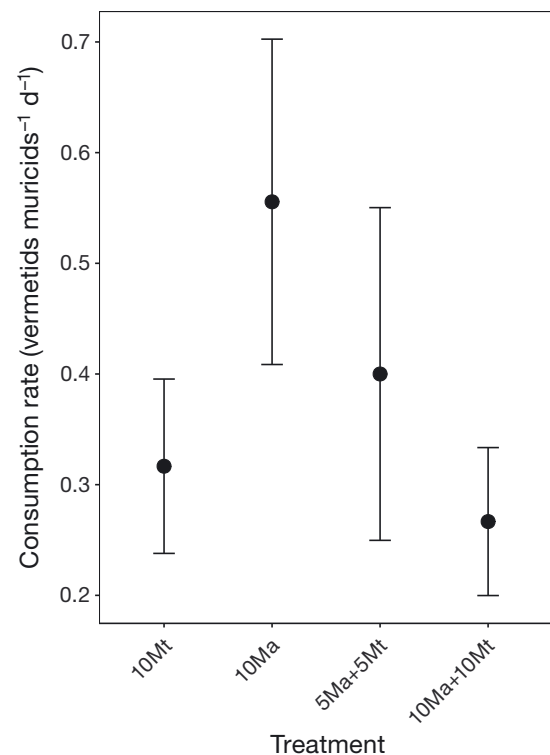


Fig. 3. Mean ( $\pm$ SE;  $n = 3$ ) per capita consumption rate of vermetids in each treatment with muricids after 6 d. Abbreviations as in Fig. 2

Table 1. Results of a 2-way mixed effects model comparing distance  $\times$  muricid species, with transects treated as a random effect and the distance effect fit using a linear relationship. The intercept value was 3.38, which is the predicted value for the density of *Mancinella armigera* (Ma) at distance of 0 m from the reef crest. Thus, the distance estimate in the table applies to Ma, while the interaction indicates how this estimated slope is modified for *Menathais tuberosa* (Mt) (i.e. it shifts from negative,  $-0.07$  for Ma, to positive,  $0.034$  for Mt). ANOVA results were calculated with Satterthwaite approximation for df

	Slope estimates (mean $\pm$ SE)	SS	MS	Numer- ator df	Denomi- nator df	F-value	p-value
Distance (D)	$-0.07 \pm 0.02$	7.30	7.30	1	60.1	2.69	0.11
Muricid (M)	$-3.47 \pm 0.89$	41.5	41.5	1	57.9	15.2	$2.51 \times 10^{-4}$
D $\times$ M	$0.09 \pm 0.03$	32.8	32.8	1	57.9	12.1	$9.84 \times 10^{-4}$

Based upon these data, we reject the hypothesis of risk reduction and intraguild predation when overall density is held constant.

In contrast to the results observed in the substitutive portion of the experiment, the cumulative loss of vermetids in the presence of 10 *M. armigera* and 10 *M. tuberosa* (10 Ma + 10 Mt) was only slightly greater than in the monospecific treatments (i.e. 10 Ma or 10 Mt), despite the presence of twice as many predators (Fig. 2; orthogonal contrast:  $t_{1,8} = 1.38$ ,  $p = 0.2$ , Table S1). The observed consumption rate ( $32 \pm 8.02$  snails) was appreciably lower than the expected loss of 51.6 vermetids if predator effects were additive (which we obtained by adding the observed losses in the treatments with 10 *M. armigera* and 10 *M. tuberosa*). Thus, we conclude that there was risk reduction, but it only manifested at the highest predator density.

### 3.3. Field experiment

The treatments were effective at maintaining a gradient of densities of *M. armigera* (Fig. S2), although there was some loss (and some gain) of predators on all reefs, indicating some degree of muricid movement. Deviations from treatment levels were most apparent on Day 60 (when predators had not been restocked for over 1 mo; Fig. S2). We also observed loss of vermetids on the 0-muricid treatment reefs, potentially indicating other sources of mortality.

Vermetid mortality increased approximately linearly with muricid density, but decreased over time (except in the control treatment). We observed the highest abundance of dead vermetids where muricid densities were greatest: e.g.  $\sim 100$  vermetids died over the 60 d on reefs with 12 muricids, while  $< 10$  died on the control reefs (Fig. 4; significant difference be-

tween treatments on Day 60, deviance<sub>1,14</sub> = 41.51,  $p < 0.001$ ). Similarly, the loss rate ( $d^{-1}$ ) during each sampling period increased approximately linearly with muricid density (Fig. S3), but the slope of this relationship decreased over time (muricid density  $\times$  time:  $F_{1,47.39} = 6.670$ ,  $p = 0.0123$ ; Fig. S3). The highest loss rates occurred after the first 3 d, especially on the reefs stocked with 12 muricids ( $5.1$  vermetids  $d^{-1}$ ). As a result, there was a consistent per predator

rate of consumption across predator density treatments (ranging between  $0.44$ – $0.47$  vermetids muricid $^{-1}$   $d^{-1}$ ;  $F_{1,55} = 0.02$ ,  $p = 0.89$ ; Fig. 5) and this consumption rate decreased over time ( $F_{1,55} = 6.9$ ,  $p = 0.01$ ). We found no lag effects (AIC comparing models with and without lag were 27.93 and 25.97, respectively).

### 3.4. Size selection

We did not observe any strong variation in size selection in the lab or field experiment (Fig. 6). In the lab experiment, muricids preferentially consumed

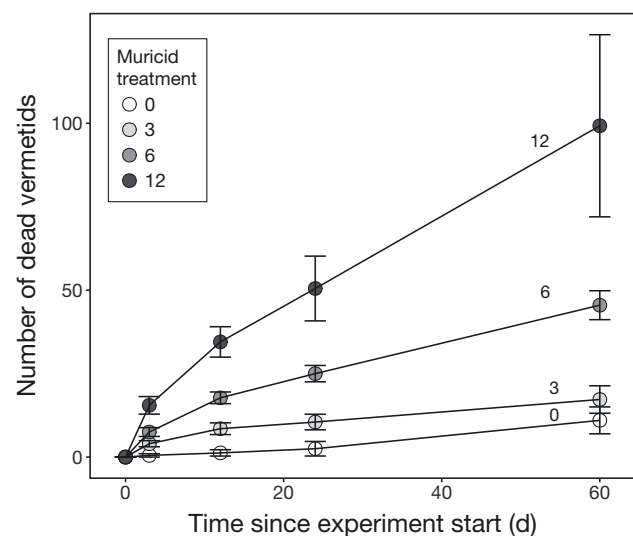


Fig. 4. Mean ( $\pm$ SE;  $n = 4$ ) cumulative loss of vermetids over 60 d for each predator density treatment in the field experiment. Muricid densities of 0, 3, 6, and 12 reef $^{-1}$  are represented by white, light gray, gray, and dark gray shades, respectively. Cumulative mortality is the total number of vermetids killed since the start of the experiment through Days 3, 12, 24, and 60

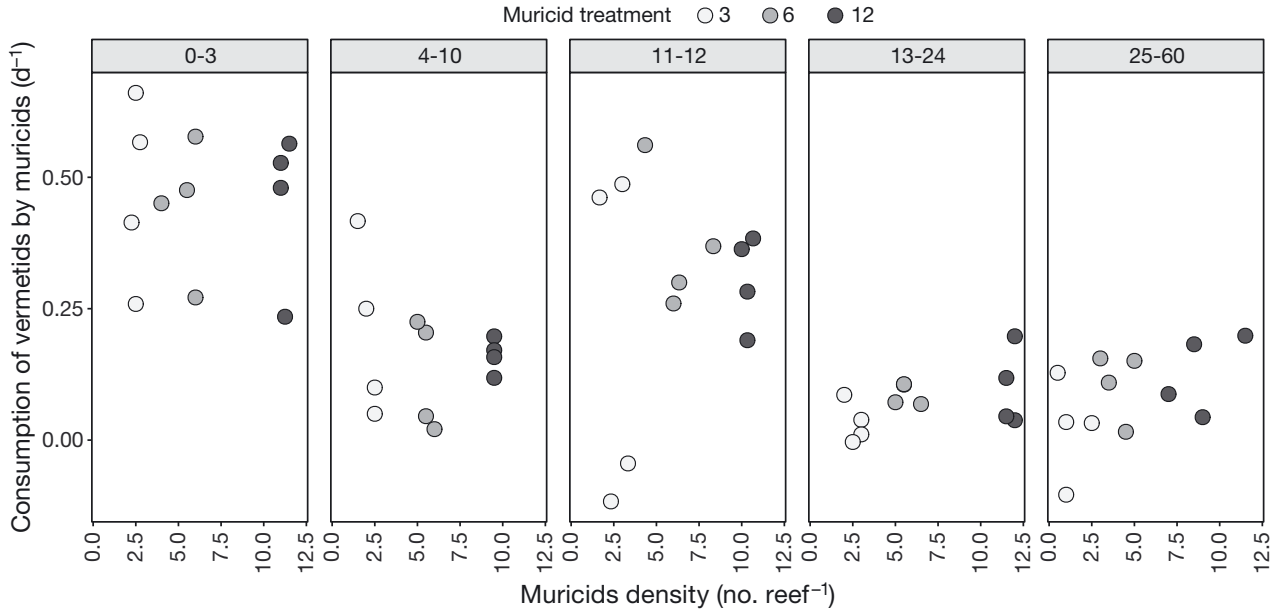
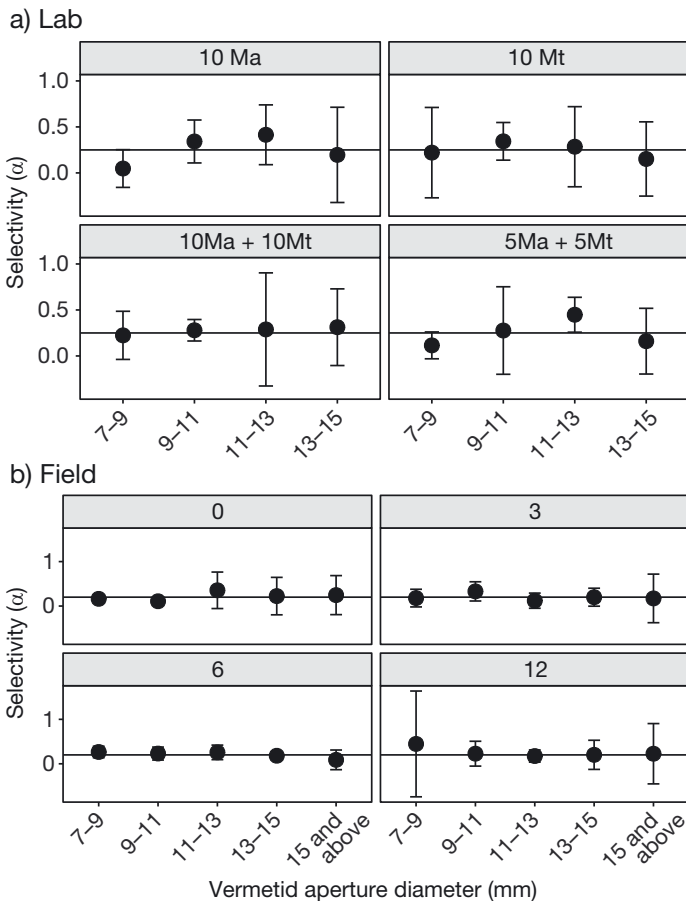


Fig. 5. Per muricid consumption rate of vermetids (based on Eq. 1) in the field experiment. Gray shaded circles represent muricid treatments (densities: 3, 6, and 12 reef<sup>-1</sup>); the y-axis gives the average number of muricids observed during the time interval, and the headers of each panel provide the period, in days, over which consumption was estimated. Negative consumption rates indicate that the loss of vermetids in a treatment was less than the loss of vermetids in the control (see Eq. 1). There was no significant difference in the per muricid consumption rate across treatments or as a function of muricid numbers; however, consumption rate decreased over time



vermetids of intermediate size relative to the smallest and largest size classes (significant effect of size class,  $F_{3,31} = 5.14$ ,  $p = 0.005$ ); i.e. selectivity was highest for the 11–13 mm size classes (mean  $\pm$  SE:  $0.35 \pm 0.04$ ). Generally, selectivity was higher for the 9–11 mm ( $0.31 \pm 0.03$ ) and 11–13 mm size classes (above the random expectation of 0.25), whereas selectivity for the smallest size class (7–9 mm,  $0.15 \pm 0.03$ ) and largest size class (13–15 mm,  $0.19 \pm 0.04$ ) were below the null expectation of 0.25. This pattern of size-selectivity, however, did not vary across the muricid treatments ( $F_{3,31} = 0.09$ ,  $p = 0.96$ ), suggesting that prey choice did not vary with muricid density or

Fig. 6. Mean  $\pm$  95% confidence interval selectivities (alpha values) based on Manly selection criterion for (a) the lab and (b) the field experiments. Each panel represents a treatment within each experiment. For the lab experiment, data are based on prey losses from Days 0–6, and treatments are as described in Fig. 2. For the field experiment, data are based upon losses of vermetids from Days 24–60. All aperture diameters are represented by 2 mm size classes, except for largest size class in the field experiment. Horizontal lines give the expectation if muricids feed indiscriminately; values above the line indicate preference, whereas values below the line indicate avoidance. Confidence intervals that overlap the horizontal line indicate no preference. This null expectation is based on the reciprocal of the number of prey categories



predator species composition, nor was there a significant interaction (size class  $\times$  muricid treatment:  $F_{9,31} = 0.95$ ,  $p = 0.50$ ). In the field experiment, selectivity was fairly uniform, ranging from 0.18–0.24, and did not vary among treatments ( $F_{3,53} = 0.21$ ,  $p = 0.89$ ) or size classes ( $F_{4,53} = 0.33$ ,  $p = 0.85$ ). See Fig. S4 in the Supplement for numbers of vermetids alive and dead in each size class.

#### 4. DISCUSSION

This is the first study to investigate the predator–prey relationship between muricids and vermetids. We demonstrated that both *Mancinella armigera* and *Menathais tuberosa* consume vermetids, although *M. armigera* appears to be a more voracious predator. Furthermore, the combined effects of these 2 species are approximately additive, except under very high predator densities. Additionally, increased conspecific predator density in the field did not affect the per-predator feeding rate. The lab experiment suggested that muricids may preferentially consume vermetids of intermediate size; however, in the field, muricids were non-selective.

*M. tuberosa* and *M. armigera* exhibited spatial segregation in the field; however, our results provide no evidence that their habitat partitioning results from either intraguild predation or interspecific competition. When *M. tuberosa* and *M. armigera* were combined for a total density of 10 snails in the lab experiment, we did not observe any evidence of interference competition: muricids did not consume each other or alter their feeding rates nor did we observe a decline in feeding rates (substitutive design). However, at a density of 20 snails (10 of each species, additive design), the observed feeding rate was considerably less than expected based upon the conspecific trials. We suspect that this reduction in feeding rate may have been due to an increase in competition. One effect that may manifest at this high density could be a reduction in the feeding rate of *M. tuberosa*. Indeed, consumption in the 10 Ma + 10 Mt treatment matched the consumption rate in the 10 Ma treatment, suggesting that the smaller muricid (i.e. *M. tuberosa*) may have stopped feeding in the presence of the other predator. These multiple predator effects, in this case risk reduction, only arose at very high densities; i.e. when muricid densities exceeded  $\sim 1$  snail  $m^{-2}$ , which is much greater than the average we observed in the field.

In contrast, the highest density of predators in the field experiment did not reduce the per-predator

feeding rate. This difference with the laboratory results (where we observed a decline in feeding at the highest predator density), is likely a consequence of the higher density used in the lab experiment: i.e. 20 muricids per small rubble pile with  $\sim 60$  vermetids vs. 12 muricids on a small reef with over 100 vermetids. Both of the highest densities used in the experiments exceeded the density observed in the field survey. As a result, we conclude that predator interference is unlikely under all but the most extreme conditions.

The field experiment also showed that feeding rates declined over time. This may have been the result of prey depletion, although such an interpretation is unlikely because (1) the lab studies incurred strong reductions in density but very little reduction in feeding rates (i.e. the cumulative number of vermetids killed increased linearly with time; Fig. 2); and (2) the field data showed no effect of muricid density on feeding rates despite much higher prey depletion in the high density treatment (Fig. 5). The lack of a response to prey depletion suggests that exploitative competition for vermetids is not strong, although these muricids could compete for other types of prey (Taylor 1978). It is likely that other factors, not competition or intraguild predation, control the distributions of these 2 predators, especially at the muricid densities we observed in the field. We therefore suggest that other factors likely caused the temporal decline in feeding rates, possibly due to changes in water temperature (Fig. S5), current velocity, inaccessibility of prey or the availability of an alternate prey during the 2 mo duration of the field experiment.

Vermetids (notably *Ceraesignum maximum*) have deleterious effects on corals, reducing their growth, survival, and photophysiology (Shima et al. 2010, 2013, 2015, but see Zill et al. 2017). As a result, it is likely that the removal of *C. maximum* by these predators could lead to an indirect beneficial effect on corals. Additionally, as both muricids and *C. maximum* are found mainly in high-flow, shallow portions of the reef near the reef crest, their spatial association potentially increases the intensity of their interaction. To provide a rough estimate of the possible role of muricids on the population dynamics of *C. maximum* (and thus their potential to have positive indirect effects on corals), we used the available data to estimate field feeding rates. Our field experiment suggests that the mortality of vermetids in the absence of muricids is relatively low (Fig. 5), suggesting that muricids are a major cause of vermetid mortality. Using the average (3 muricids per 60  $m^2$ , or 0.05  $m^{-2}$ )

and the maximum (9 muricids per 60 m<sup>2</sup>, or 0.15 m<sup>-2</sup>) density of the 2 species of muricids that we observed on our transects, and the average feeding rate estimated in our lab experiment (~0.5 vermetids muricid<sup>-1</sup> d<sup>-1</sup>), the muricid assemblage would be predicted to kill an average of 9 vermetids m<sup>-2</sup> yr<sup>-1</sup> (max. of 27 vermetids m<sup>-2</sup> yr<sup>-1</sup>). As these estimates are based on transects that were approximately 50% sand, and vermetids are only found on hard substrate, it is possible that average and maximum consumption of vermetids could double (18 or 54 vermetids m<sup>-2</sup> yr<sup>-1</sup>). In Mo'orea, French Polynesia, *C. maximum* were found in densities up to 32 m<sup>-2</sup> of hard reef substrate (Shima et al. 2010). Thus, these muricids could potentially remove one-third of the population of *C. maximum* in a single year, and in some locations could potentially remove the entire local population. Because muricids have an approximately constant consumption rate, these predators might be even more effective at controlling vermetids when densities of vermetids are low. Recently, *C. maximum* experienced a massive die off in Mo'orea (and surrounding islands; Brown et al. 2016). Although muricids did not cause this population crash, it is possible that they could greatly limit the recovery of the vermetid population.

*Acknowledgements.* We thank the staff at the UC Berkeley Richard B. Gump Research station and the Odum School Writing Club (R.S., L.H., C.P., A.M., and A.S.). This research was funded by the NSF (grant OCE-1130359).

#### LITERATURE CITED

- Abrams PA (1993) Why predation rate should not be proportional to predator density. *Ecology* 74:726–733
- Arditi R, Ginzburg LR (1989) Coupling in predator-prey dynamics: ratio-dependence. *J Theor Biol* 139:311–26
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67: 1–48
- Bellwood DR, Hughes T, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Brooks LJ (1968) The effects of prey size selection by lake planktivores. *Syst Biol* 17:273–291
- Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. *Science* 150:28–35
- Brown AL, Zill J, Frazer TK, Osenberg CW (2014) Death and life: muricid snails consume the vermetid gastropod, *Dendropoma maximum*, and use empty shells for reproduction. *Coral Reefs* 33:497
- Brown AL, Frazer TK, Shima JS, Osenberg CW (2016) Mass mortality of the vermetid gastropod *Ceraesignum maximum*. *Coral Reefs* 35:1027–1032
- Burkepile D, Hay M (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* 87:3128–3139
- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64: 1297–1304
- Griffen BD (2006) Detecting emergent effects of multiple predator species. *Oecologia* 148:702–709
- Griffen JN, De La Haye KL, Hawkins SJ, Thompson RC, Jenkins SR (2008) Predator diversity and ecosystem functioning: density modifies the effect of resource partitioning. *Ecology* 89:298–305
- Hamman EA (2017) Multi-scale spatial patterning of corals and their symbionts. PhD dissertation, University of Georgia, Athens, GA
- Hughes T (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551
- Johnson DW (2006) Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. *Ecology* 87:1179–1188
- Kayal M, Vercelloni J, Lison de Loma T, Bosserelle P and others (2012) Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLOS ONE* 7:e47363
- Kuznetsova A, Brockhoff PB, Christensen RHB (2016) lmerTest: tests in linear mixed effects models. R package version 2.0-33. <https://CRAN.R-project.org/package=lmerTest>
- Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19:392–399
- Manly BFJ, Miller P, Cook LM (1972) Analysis of a selective predation experiment. *Am Nat* 106:719–736
- Maszczyk P, Gliwicz ZM (2014) Selectivity by planktivorous fish at different prey densities, heterogeneities, and spatial scales. *Limnol Oceanogr* 59:68–78
- McCoy MW, Stier AC, Osenberg CW (2012) Emergent effects of multiple predators on prey survival: the importance of depletion and the functional response. *Ecol Lett* 15:1449–1456
- Mittelbach GG, Turner AM, Hall DJ, Rettig JE, Osenberg CW (1995) Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. *Ecology* 76:2347–2360
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) nlme: linear and nonlinear mixed effects models. R package version 3.1-131. <https://CRAN.R-project.org/package=nlme.2017>
- Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Shima J, Osenberg C, Stier A (2010) The vermetid gastropod *Dendropoma maximum* reduces coral growth and survival. *Biol Lett* 6:815–818
- Shima JS, Phillips NE, Osenberg CW (2013) Consistent deleterious effects of vermetid gastropods on coral performance. *J Exp Mar Biol Ecol* 439:1–6
- Shima JS, McNaughtan D, Strong AT (2015) Vermetid gastropods mediate within colony variation in coral growth

- to reduce rugosity. *Mar Biol* 162:1523–1530
- ✦ Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355
- ✦ Soluk DA, Collins NC (1988) Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. *Oikos* 52:94–100
- ✦ Taylor JD (1978) Habitats and diet of predatory gastropods at Addu Atoll, Maldives. *J Exp Mar Biol Ecol* 31:83–103
- Terborgh J, Estes J (2010) *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington, DC
- ✦ Vance-Chalcraft HD, Rosenheim JA, Vonesh JR, Osenberg CW, Sih A (2007) The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology* 88:2689–2696.
- Venables WN, Ripley BD (2002) *Modern applied statistics with S*. Springer-Verlag, New York, NY
- ✦ Vonesh JR, Osenberg CW (2003) Multi predator effects across life history stages: non additivity of egg and larval stage predation in an African treefrog. *Ecol Lett* 6: 503–508
- ✦ Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100
- ✦ Zill JA, Gil MA, Osenberg CW (2017) When environmental factors become stressors: interactive effects of vermetid gastropods and sedimentation on corals. *Biol Lett* 13: 20160957

*Editorial responsibility: Romuald Lipcius,  
Gloucester Point, Virginia, USA*

*Submitted: October 12, 2018; Accepted: March 4, 2019  
Proofs received from author(s): April 15, 2019*