Title: Overlooked coral predators suppress foundation species as reefs degrade

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Abstract:

Loss of larger consumers from stressed ecosystems can lead to trophic release of mid-level consumers that then impact foundation species, suppressing ecosystem function and resilience. For example, in coral reef ecosystems, outbreaks of coral predators like crown-of-thorns sea stars have been associated with fishing pressure and can dramatically impact the composition and persistence of corals. However, the ecological impacts, and consequences for management, of smaller, less obvious corallivores remain inadequately understood. We investigated whether reef state (coral vs. seaweed domination) influenced densities and size frequencies of the corallivorous gastropod *Coralliophila violacea* on its common host, the coral *Porites cylindrica*, within three pairs of small Marine Protected Areas (MPAs) and adjacent fished areas in Fiji. *C. violacea* densities were 5-35 times greater, and their size frequencies more broadly distributed, within seaweed-dominated fished areas than adjacent MPAs dominated by corals. Tethering snails (4-9 mm in shell height) in-place on their coral hosts indicated that suppression of snails in MPAs was due to predation, apparently by fishes. When tethered on the benthos (where they rarely occur), rather than on their host, mortality of larger snails (15-25 mm in shell height) was high in all areas, primarily due to hermit crabs killing them and occupying their shells. Because *C. violacea* is a sessile gastropod that feeds affixed to the base of corals and produces minimal visible damage, it has been considered a “prudent feeder” that minimally impacts its host coral. We assessed this over a 24-day feeding period in the field. Feeding by individual *C. violacea* reduced *P. cylindrica* growth by ~18-43% depending on snail size. Our findings highlight the considerable, but underappreciated, negative impacts of this common corallivore on degraded reefs. As reefs degrade and corals are lost, remaining corals (often species of *Porites*) may gain the full attention of elevated densities of coral consumers. This will

further damage the remaining foundation species, suppressing the resilience of corals and enhancing the resilience of degraded, seaweed-dominated reefs.

Keywords: coral reefs, *Coralliophila*, feedback mechanisms, mesopredator, predation,

Introduction

As ecosystems degrade and lose species, they can also lose critical ecosystem functions that enhance the speed of decline and suppress the possibility of recovery (Naeem et al. 2012, Oliver et al. 2015). This may be especially true following loss of larger consumers, which are commonly critical for controlling damaging competitors, predators, or parasitoids of foundation species and for critical aspects of biogeochemical cycling (Estes et al. 2011, Rasher et al. 2013, Roman et al. 2014). As an example, coral reefs worldwide face numerous natural and human stressors that lead to sustained coral loss, community shifts from corals to seaweeds, and reduced ecosystem resilience (Bellwood et al. 2004, Hughes et al. 2010). Among these stressors, coral predators (corallivores) are increasingly recognized for their direct (e.g. consumption, disease vectoring) and cascading effects on corals and on reef community dynamics (Rotjan and Lewis 2008, De'ath et al. 2012). Predation also acts synergistically with other stressors (e.g. storms, heat stress) to exacerbate harmful effects on foundation species (Anderegg et al. 2015, Bright et al. 2015, Shaver et al. in press). Additionally, disturbance of reef trophic structure (e.g., overfishing) may also allow corallivores to escape top-down control and enhance predation pressure on the lesser numbers of remaining corals, decreasing resilience, hastening declines, preventing recovery, and facilitating phase-shifts to algal-dominated reefs (Knowlton et al. 1990,

Rotjan et al. 2006, Wolf and Nugues 2013). That said, the role and impact of many corallivores on healthy vs. degraded reefs remain poorly understood and a challenge for effective coral reef management (Mumby 2009).

Negative effects of predation often become obvious when corallivores are overabundant, such as during population ‘outbreaks’ of crown-of-thorns sea stars (*Acanthaster* spp.; Kayal et al. 2012, Pratchett et al. 2014) and *Drupella* spp. snails (Shafir et al. 2008). Both experimental and correlative studies suggest that predation can regulate corallivore densities, but that this top-down forcing may be lost or suppressed if consumers are overfished (McClanahan 1989, Dulvy et al. 2004, Burkepile and Hay 2007, Sweatman 2008). Implementing no-take Marine Protected Areas (MPAs) is one strategy expected to lessen corallivore outbreaks (Graham et al. 2011), but most MPAs are small (Costello and Ballantine 2015) and the reserve size necessary to foster top-down control remains uncertain (Sale et al. 2005, Claudet et al. 2008, D'Agata et al. 2016, Clements and Hay 2017). Furthermore, whether similar outcomes extend to other, less well-known, corallivores deserve further investigation.

In this study, we used a combination of observational and manipulative experiments to investigate the impacts of reef protection status on: 1) *Coralliophila violacea* population densities in small MPAs and adjacent fished areas in Fiji, 2) predation on *C. violacea*, and 3) effects of *C. violacea* feeding on the common host coral *Porites cylindrica*. *C. violacea* is one of the few corallivores known to feed almost exclusively on *Porites* spp., and *Porites* spp. are among those corals that exhibit lower sensitivity to a number of stressors (e.g., climate-induced bleaching, macroalgal allelopathy, crown-of-thorns predation) commonly contributing to coral decline (Aronson et al. 2005, Pratchett 2007, Carpenter et al. 2008, Rasher et al. 2011, Bonaldo and Hay 2014). Species of *Porites*, and especially *P. cylindrica*, often represent one of the few

remaining corals on severely damaged reefs (McClanahan and Mutere 1994, Green et al. 2008, Adjeroud et al. 2009) and as such may be especially important to maintain if total reef loss is to be prevented. Because *C. violacea* feed by inserting their proboscis into the coral's coelenteron and consuming resources that the coral translocates to recover from this damage (Oren et al. 1998), the snail's feeding produces only small and localized tissue damage. This absence of visual damage could result in *C. violacea* being underappreciated as a significant corallivore on coral reefs.

Here, we quantified: 1) whether *C. violacea* densities and size frequencies on *P. cylindrica* differed between three small MPAs vs. their adjacent fished areas, 2) whether rates of predation on *C. violacea* differed between MPAs and fished areas, and thus might explain density differences and population size structure differences between areas, 3) the effects of *C. violacea* feeding on growth and survivorship of *P. cylindrica*, and 4) how the impact of snail feeding varied with snail size.

Methods

***C. violacea* densities and size frequency distributions within paired Marine Protected Areas (MPAs) vs. fished areas**

Surveys assessing *C. violacea* densities on colonies of *P. cylindrica* were conducted during June 2015 within three, small, no-take MPAs and three adjacent fished reefs near Votua, Vatu-o-lalai, and Namada villages along the Coral Coast of Viti Levu, Fiji (Fig. 1). The MPAs are ~0.78, 0.45, and 0.48 km² in total area, respectively. Paired areas where we assessed densities are separated by ~300 m (at Votua and Vatu-o-lalai) to 1700 m (at Namada) and are embedded within an 11 km stretch of shallow (0-3 m deep at low tide) fringing back reef lagoon with similar physical regimes (e.g. depth, current strength). Established during 2002 (Vatu-o-lalai, Namada) to 2003 (Votua), the MPAs exhibit relatively high coral cover (~38-56%) and low

macroalgal cover (~1-3%) on hard substrates. In surrounding fished areas, coral cover is low (4-16%) and macroalgal cover is high (~49-91%; Rasher et al. 2013). Likewise, MPAs exhibit greater biomass and diversity of fishes (Clements et al. 2012, Rasher et al. 2013, Bonaldo et al. 2017), including durophagous fishes that have been associated with decreased abundance of *C. violacea* (e.g. balistids, McClanahan 1994). Cover of *Porites* spp. at Votua is ~4% in both the MPA and fished site; at Vatu-o-lalai and Namada, cover is higher in the MPA sites (~3% vs. 1% and ~6% vs. 4%, respectively) (Bonaldo and Hay 2014).

Differences in *C. violacea* density between the MPA and fished area at Votua Reef were quantified using 30 X 2 m transects ($n = 9$ transects area⁻¹) that were non-overlapping and distributed haphazardly within the center of the of the shallow back-reef lagoon of each area. Within each transect, we located all *P. cylindrica* colonies that exceeded 25 cm in at least one horizontal dimension. Colonies were searched for *C. violacea* for ≤ 6 minutes (duration depending on colony size) and all snails were collected using needle-nose pliers and pooled for that site. Size of each snail was assessed as shell height (tip of the apex to the edge of the bottom lip) to the nearest 0.5 mm using a vernier caliper. To estimate *C. violacea* density per 2-dimensional area of coral, the upper surface of each coral colony was photographed, and surface area quantified via ImageJ.

Due to logistical constraints and the high abundance of *C. violacea* on colonies of *P. cylindrica* at Votua reef (1503 snails collected and measured), subsequent assessments of *C. violacea* density at Vatu-o-lalai and Namada reefs consisted of haphazardly surveying 20 *P. cylindrica* colonies near the center of each area, collecting snails and measuring shell height as described previously. Differences in *C. violacea* density between the MPA and fished area at each reef site were compared separately with a Fisher-Pitman permutation test (10000

permutations) in the R (v. 3.3.2) package “coin” (v. 1.2-2).

Differences in *C. violacea* size-frequency distributions between paired areas were assessed using Kolmogorov-Smirnov tests and represented with probability density histograms. Mean shell height of *C. violacea* were compared between paired MPAs and fished areas with a Fisher-Pitman permutation test (10000 permutations) in the R (v. 3.3.2) package “coin” (v. 1.2-2).

Tethering experiments to assess predation

To investigate whether differences in *C. violacea* densities and size distributions between MPAs and fished areas might be explained by differential rates of predation, we conducted a series of tethering experiments within the MPA and fished area at Votua Reef using *C. violacea* collected during density surveys. After drying and sanding a small patch on the surface of each shell, a ~6 cm length of monofilament line (0.14 mm, 6.9 kg test) was attached to each shell via super glue. Tethers were secured to the reef bottom using a U nail, with 20 snails at each of 10 locations separated by ~7-10 m within a network of interconnected pools near the center of the MPA or the center of the fished area. At each of our 10 locations, snails were divided into a group of 5 smaller (4-14.5 mm) and 5 larger (15-25 mm shell height) individuals that were caged using 1-cm² grid metal screening (control) and a separate 5 smaller and 5 larger individuals that were left uncaged (treatment) ($n = 5 \text{ snails height}^{-1} \text{ treatment}^{-1} \text{ station}^{-1} \text{ area}^{-1}$, for a total of 200 snails in the MPA and 200 in the fished area). *C. violacea* mortality was then monitored over 48 hrs. Data on percent mortality at 48 hrs were analyzed with ANOVA using a permutation approach (5000 permutations) in the R (v. 3.3.2) package lmPerm (v. 2.1.0) with snail location (MPA vs. fished), size (4-14.5 mm or 15-25 mm), and treatment (caged vs. uncaged) as fixed factors. Due to extensive hermit crab (*Calcinus* & *Dardanus* spp.) induced mortality on larger

snails (15-25mm) (Appendix 1: Fig. S1), separate permutational ANOVA analyses were conducted to compare total mortality among treatments, as well as mortality due to hermit crabs (as evidenced by them occupying the shells) and mortality due to putative fish predators (i.e. snail shell partially or fully absent from the tether).

To simulate more ecologically relevant predation scenarios and possibly reduce mortality due to hermit crabs, we subsequently conducted a tethering experiment where three *C. violacea*, 4-9 mm in shell height, were tethered to small colonies of *P. cylindrica* that had been previously implanted within the cut-off necks of inverted plastic bottles using epoxy (Fig. 2). Snails were first attached to monofilament in the same manner as described above. The monofilament was then attached to a cable tie, which was secured to the cut-off bottleneck containing an individual coral (3 snails coral⁻¹). Each bottle portion and respective coral was then screwed into an inverted bottle cap embedded within the substrate near-shore in Votua Reef's MPA and surrounded by 1-cm² grid metal screening. Corals and tethered snails were held within cages ~48 hrs to allow snails to attach to the corals, after which each coral was then deployed into a bottle cap embedded within the substrate of either the MPA or fished areas at each of the 10 stations used in the prior tethering experiment. At each station, this included an uncaged *P. cylindrica* and a caged control surrounded by 1-cm² grid metal screening ($n = 10$ corals treatment⁻¹ area⁻¹). *C. violacea* mortality was then monitored over 72 hrs. No snail mortality occurred in the cage controls, so these were excluded from subsequent analyses. Percent mortality data of uncaged snails from the MPA and fished area were compared with a Fisher-Pitman permutation test (10000 permutations) in the R (v. 3.3.2) package "coin" (v. 1.2-2).

Influence of *C. violacea* feeding on coral growth and survivorship

To investigate the effect of *C. violacea* feeding on the growth and survivorship of *P. cylindrica*, and how this varies with *C. violacea* size, we manipulated *C. violacea* feeding on replicate *P. cylindrica* branches outplanted in the field. In May 2016, four branches (6-8 cm in length; 18.1-55.3 g wet mass) were collected from 15 *P. cylindrica* colonies at Namuka Reef along the Coral Coast of Viti Levu, Fiji (18° 8'5.70"S, 177°23'14.94"E). Individual branches were embedded within the cut-off necks of inverted plastic bottles using epoxy (Emerkit) and their upturned bottle caps were affixed to the substratum with a nail. This procedure allowed us to easily detach and reattach corals for periodic weighing with minimal disturbance (see Clements and Hay 2015, Clements et al. 2018 for methods). Following a ~1-month period of acclimation and recovery from fragmentation, corals originating from each colony were weighed in the field (see below) and then exposed to one of four treatments of *C. violacea* predation for 24 days: either (1) no snail (control), (2) one snail ~8 mm in height, (3) one snail ~15 mm in height, or (4) one snail ~22 mm in height. Height of each snail was measured to the nearest 0.5 mm using a vernier caliper, and range in shell height within a group was ± 0.5 mm. Initial mass of coral branches did not differ among treatments (ANOVA: $F_{3,57} = 0.634$, $p = 0.596$; mean mass of 33.3-37.7g). To ensure snails remained on their respective corals, we dried and sanded a small portion of each snail's shell, superglued a cable tie to the shell surface, and attached the tie around the base of each snail's *P. cylindrica* branch (Appendix 1: Fig. S2). Because these snails feed by staying in place at the base of a coral branch and consuming resources that the coral mobilizes to recover from feeding damage (Oren et al. 1998), this procedure mimicked natural feeding location and behavior seen in the field. After 24 days, corals were detached from the substratum and re-weighed in the field using an electronic scale (OHAUS Scout Pro) enclosed within a plastic container that was mounted to a tripod holding it above the water surface (as had

been done for the initial weighing). Twenty-four to 48 hrs before the weighing session, each coral's bottle-top/epoxy base was lightly brushed with a toothbrush to remove fouling organisms. Before weighing, each coral was gently shaken 30 times to remove excess water, and then weighed, immediately placed back into the water, and reattached to the substrate. Following weighing session, corals were separated from their epoxy base and each coral and base were weighed separately. Differences in mass change among corals exposed to different treatments (control, or one snail ~8 mm, ~15 mm, or ~22 mm in height) were assessed using ANCOVA with initial coral branch mass as a covariate, followed by a Tukey's post-hoc test, in JMP (v. 13.0.0).

Results

C. violacea densities on *P. cylindrica* colonies were ~4-35 times greater within fished areas (~8-12 individuals 1000 cm²) versus MPAs (~0.3-3 individuals 1000 cm²) ($p < 0.001$, Fig. 1), with snails from MPAs being significantly larger ($p \leq 0.013$) and exhibiting different size-frequency distributions ($p \leq 0.032$) than snails from paired fished areas (Fig. 3, Appendix 2: Table S1). Smaller size classes of snails were relatively less abundant in the MPAs versus fished areas.

After 48 hrs tethered on the benthos, snails of 15-25 mm in height suffered significantly greater mortality (72-94%) than snails 4-14.5 mm in height (8-28%) ($p < 0.001$, Fig. 4a), regardless of location (MPA or fished area; $p = 0.282$) or caging status (caged or uncaged; $p = 0.114$). The high frequency (60-94%) with which hermit crabs occupied the tethered shells indicated that 15-25 mm snails suffered greater hermit crab-induced mortality, regardless of location ($p = 0.051$) or caging status ($p = 0.081$), than 4-14 mm snails ($p < 0.001$, Fig. 4b). Placing hermit crabs and larger snails together in the lab also demonstrated that crabs were

actively killing larger gastropods and moving into their shells – usually within 6-8 hrs of initial contact (C. Clements, personal observation). Caging did significantly affect the probability of snails being completely missing from their tether ($p < 0.001$) – presumably due to fish predation, as we never noted larger, predatory crabs at these sites and never noted evidence of shells being drilled by predatory gastropods. Additionally, for snails in cages, differences in mortality due to snail size ($p = 0.482$) and location ($p = 0.130$) were not significant (Fig. 4c). When tethered in their normal feeding position on *P. cylindrica* corals (instead of on the substrate) for 72h in the field, small (4-9 mm in height) *C. violacea* experienced ~220% greater mortality (i.e. removal from tether) in the MPA than the fished area ($p = 0.039$, Fig. 5), presumably due to predation by fishes as evidenced by shell crushing and fragments remaining near the tethering site (Appendix 1: Fig. S4).

C. violacea feeding significantly reduced *P. cylindrica* growth (ANCOVA: $F_{4,56} = 25.6637$, $p < 0.001$), with magnitude of suppression being a function of snail size (Fig. 6). Twenty-two mm *C. violacea* reduced growth by 43%, 15 mm snails by 25%, and 8 mm snails by 18%. No corals died during the 24-day experiment.

Discussion

Ecosystem demise involves suppression or loss of both critical species and ecosystem function (Isbell et al. 2011, Valiente-Banuet et al. 2015). This can be especially consequential when foundation species, like corals, are suppressed. Recovery of foundation species is essential for resilience of the affected ecosystem, but as species diversity decreases, critical interactions that facilitate recovery of foundation species may be lost (Angelini et al. 2011, Valiente-Banuet et al. 2015). Communities may then enter a destructive death-spiral causing even greater loss of structure, function, and resilience (Mumby and Steneck 2008).

As corals decline and coral stressors increase (Hoegh-Guldberg et al. 2007, Carpenter et al. 2008, Hughes et al. 2017), predation on the lower number of surviving corals may become especially important (Knowlton et al. 1990). This becomes critical if basic trophic interactions that keep predators in check under normal conditions erode and predators of foundation species proliferate. Under these circumstances, even low metabolic rate, “prudent predators,” like snails (Oren et al. 1998) may strongly impact the persistence, recovery, and management of remaining corals (Burkepile and Hay 2007, Rotjan and Lewis 2008, Cole et al. 2011, Cole and Pratchett 2011). We found that densities of corallivorous gastropods increased dramatically in fished relative to protected areas and that predation by *C. violacea* reduced growth of *P. cylindrica* by 18-43% (depending on snail size). This could strongly impact corals in degraded areas given that snail densities were up to 35-fold higher in the low coral cover fished areas than in the high coral cover MPAs. The coral we assessed is common on both degraded and protected reefs in Fiji and elsewhere (McClanahan and Mutere 1994, Bonaldo and Hay 2014) and is commonly one of the last abundant survivors on stressed reefs due to its reduced sensitivity to numerous stressors associated with coral decline (Pratchett 2010, Rasher et al. 2011, Bonaldo and Hay 2014).

In addition to density differences, size distributions of *C. violacea* differed in MPAs vs. fished areas and snail mortality during tethering experiments suggested that MPAs were fostering trophic interactions that suppressed *C. violacea* densities. A comparison of size distributions within MPAs and fished areas (Fig. 2) suggests that younger age/size cohorts are persisting in the fished areas but being suppressed within the MPAs. That said, *C. violacea* densities in all size classes were much greater in fished areas than in MPAs. Densities of snails <10mm, 10-20mm, and >20mm were 12-281x, 2-19x, and 4-23x greater, respectively, within fished areas than paired MPAs (Appendix 2: Table S1).

C. violacea is said to use a ‘prudent’ mode of feeding, inserting its proboscis into the coral polyp’s coelenteron and feeding as the coral translocates resources to replace those being consumed (Oren et al. 1998). Visually, this produces only minor and localized tissue damage. This may have contributed to this consumer being overlooked as an ecologically important coral predator. However, their feeding can considerably suppress coral growth (Fig. 6), is associated with secondary colonization by competitors and pathogens such as algae and fungi (Raymundo et al. 2016), and may also weaken corals when exposed to other stressors such as ocean warming, which increases coral mortality more for corals hosting snail consumers than for those without (Shaver et al. in press).

C. violacea feeding did not affect mortality over the course of our study, but feeding by a single individual reduced *P. cylindrica* growth ~18-43%, depending on snail size. In our field surveys, we observed *P. cylindrica* colonies with *C. violacea* densities of up to 68 snails per 1000 cm², with one 1.2 m² colony hosting >200 snails (see Appendix 1: Fig. S3). Such densities may reduce colony growth substantially and impose growth-related opportunity costs that undermine coral fitness and resilience (e.g. increased mortality risk, and decreased fecundity and competitive ability; Hall and Hughes 1996, Zilberberg and Edmunds 2001, Edmunds and Gates 2004), especially for corals dealing with other stressors common to degraded reefs (e.g. macroalgal competition [McCook et al. 2001, Clements et al. 2017], disease [Raymundo et al. 2009, Nicolet et al. 2013, Katz et al. 2014], and physical stresses [Shaver et al. in press]).

C. violacea densities were significantly lower on *P. cylindrica* colonies within the MPAs compared to adjacent fished areas. Previous studies along the coast of Kenya also documented reduced densities of corallivorous gastropods, particularly *C. violacea*, in protected versus fished areas (McClanahan 1989, 2002). However, unlike the Kenyan MPAs that are tens to hundreds of

square kilometers in size, the Fijian MPAs that we surveyed are small community-managed initiatives ranging from 0.45-0.78 km² in total area. Our findings add to a growing body of evidence highlighting the utility of small MPAs (Russ and Alcala 1996, Halpern 2003, Clements et al. 2012, Rasher et al. 2013, Bonaldo et al. 2017, Espectato et al. 2017), the primary approach for management of reefs across the Pacific (Jupiter et al. 2014).

Based on correlative evidence, McClanahan (1994) hypothesized that predatory fishes, particularly labrids and balistids, were suppressing *C. violacea* in Kenyan MPAs compared to fished areas. Height-frequency distributions of *C. violacea* collected during our surveys, coupled with tethering experiments, also suggest that fish predators are suppressing *C. violacea* densities in the small MPAs we studied in Fiji. Our tethering experiment conducted with snails located in their normal feeding positions on corals indicated that predator suppression may occur primarily due to fish predation on *C. violacea*. When we tethered snails to *P. cylindrica* (their normal place of occurrence) in Votua's MPA and fished area, loss of uncaged snails over 72h was 220% greater in the MPA than the fished area (Fig. 5). We did not identify the predators, but shell remnants within < 30 cm of the tethering locations suggested predation by shell crushing fishes (e.g. balistids, labrids, tetradontids, etc.) (Appendix 1: Fig. S4). Predators of both invertebrates and fishes are more abundant in the MPAs versus the fished areas of our study reefs (Clements et al. 2012, Bonaldo et al. 2017).

Approximately 17-53% of small snails in the fished area and MPA, respectively, experienced predation from fishes when situated in their natural position on their host. When tethered on open benthic substrate, hermit crabs, instead of fishes, killed 60-94% of snails in the 15-25 mm size class, as evidenced by hermit crabs occupying the undamaged shell, often with remnants of tissue and the operculum of *C. violacea* laying nearby (see Appendix 1: Fig. S1).

For smaller snails (4-14.5 mm) whose shells would have been too small for most of the hermit crabs, hermit-crab induced mortality was low ($\leq 20\%$). Caging did not exclude mortality due to hermit crabs (Fig. 4c). Thus, differences in overall mortality were statistically indistinguishable between caged vs. uncaged snails, as well as between the MPA vs. fished area (Fig. 4a). Caging completely excluded predation events where snails were removed from their tether (i.e. fish predation; Fig. 4c). The high predation by hermit crabs that could enter our cages likely obscured our ability to assess between-site and between size class mortality via fish predation in this assay.

Although recent laboratory experiments have questioned whether hermit crabs can remove live snails from their shells (Laidre 2011), we commonly observed hermit crabs killing live snails and occupying their shells during our 48h duration field assay. Additionally, when we placed snails and hermit crabs together in the lab, hermit crabs commonly killed snails and occupied their shells within only a few hrs (C. Clements personal observation). This crab-induced snail mortality does not appear to be an anomaly of our study site; similar anecdotal cases have been reported in the literature (Brichtwell 1951, Randall 1964, Rutherford 1977, Iversen et al. 1986) and may be expected due to strong competition for limited shell resources (Kellogg 1976, Bertness 1981). The sessile feeding behavior of *C. violacea* (Oren et al. 1998) may occur in part due to the selective advantage of staying in place on one host and avoiding the need to move among hosts, during which time the snails seem especially susceptible to consumers (Fig. 4). This risk may be common; gastropods in other systems also are safer on, than when moving between, hosts (Schmitt et al. 1983).

Impacts of corallivores that were once considered negligible are increasingly being reconsidered (Cole et al. 2011) as reefs degrade and managers try to build resilience among remaining corals in the face of a global change (Hughes et al. 2010). Here we identify an

unappreciated feedback that may suppress coral resilience and enhance the resilience of degraded reef states due to elevated predation on remaining corals once reefs begin to degrade. However, our findings suggest that even small MPAs may be useful tools for suppressing numbers of harmful mesoconsumers like *C. violacea*. Their densities were 4-35x greater on fished reefs where corals were few and seaweeds common vs. adjacent MPAs where corals were common and seaweeds were rare (Rasher et al. 2013). In these degraded, seaweed-dominated areas, corals are suppressed by both the greater densities of consumers, and the greater densities of competing seaweeds (Clements et al. 2018). Despite being largely overlooked as a significant coral predator, *C. violacea* feeding considerably suppresses coral growth. The combination of low density of host corals and high density of mesoconsumers suggests a worrisome synergy of negative feedbacks that will further suppress remaining corals and enhance coral to seaweed transitions on overharvested reefs.

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Figure Legends

Fig. 1: (*Top panel*) Village and MPA locations along the coast of Viti Levu, Fiji. Dark gray sections represent the MPAs at each village site; ★ indicate approximate location where density/size assessments and assays were conducted. (*Bottom panel*) Violin plots depicting mean $\pm$ SE *C. violacea* densities (black dots and error bars) on *P. cylindrica* colonies within MPAs and adjacent fished areas at each village site. Numbers below individual violin plots indicate number of *P. cylindrica* colonies surveyed. Data for each pairwise comparison were analyzed with Fisher-Pitman permutation tests (10000 permutations).

Fig. 2: Manipulations used in tethering experiment to assess the impact of predation on *C. violacea* within the MPA and fished area at Votua Reef. White arrows point to tethered *C. violacea* actively feeding on *P. cylindrica*.

Fig. 3: Size-frequency distributions of *C. violacea* within MPAs and fished areas at Votua, Vatu-o-lalai, and Namada Reefs. Large dashed black lines denote mean *C. violacea* shell height (mm) for each area. Small dashed lines denote upper and lower quartiles. Number of *C. violacea* assessed are indicated in the upper right corner of each histogram. *P*-values above the top figures show contrasts of *C. violacea* size-frequency distributions (Kolmogorov-Smirnov tests [K-S]), and mean shell height (Fisher-Pitman permutation tests [F-P]) between paired MPA and fished areas. Number of snails assessed in each area are given in the upper right of each panel.

Fig. 4: Percent mortality (a), and the % due to hermit-crabs (b) versus other agents of mortality (c) (mean $\pm$ SE) of caged (black bars) and uncaged (gray bars) larger (left-side graphs) and smaller (right-side graphs) *C. violacea* during a 48 hr tethering experiment on the benthos within Votua reef's MPA and fished area. Five snails of each size class (4-14.5 mm or 15-25 mm) were tethered, both caged and not caged, at each of 10 locations within each habitat type (n = 10; 200 total snails per area). Data were analyzed with ANOVA using a permutation approach (5000 iterations). *P*-values for fixed terms from these analyses are presented in the upper right of each figure. A = area (MPA or fished area); T = treatment (uncaged or caged); S = shell height (4-14.5 mm or 15-25mm).

Fig. 5: Mortality (% mean $\pm$ SE) over 72h of uncaged *C. violacea* (4-9 mm shell height) when tethered on *P. cylindrica* branches within Votua Reef's MPA and fished area. Three snails with shell heights 4-9 mm were tethered to each coral ($n = 10$ corals area⁻¹). Data were analyzed with a Fisher-Pitman permutation test (10000 permutations).

Fig. 6: Change in mass (mean $\pm$ SE) of *P. cylindrica* exposed to feeding by different-sized *C. violacea* for 24 days. Results are least-square means from ANCOVA. P-value and letters above the bars represent significant groupings from a one factor ANOVA followed by Tukey's post-hoc test.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

740

741 **Fig. S1: (a&b)** Paguroid hermit crabs inhabiting shells of previously living *C. violacea* that were
742 tethered to the benthos at Votua Reef ~24 hrs earlier. **(C)** Remnants of tissue and the operculum
743 of *C. violacea* at the tethering location.

744

745 **Fig. S2:** Experimental set-up assessing the effects of *C. violacea* feeding on *P. cylindrica* growth
746 and survivorship.

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748 **Fig. S3:** Examples of *C. violacea* densities on *P. cylindrica* colonies in the field. Red arrows are
749 pointing to *C. violacea* actively feeding on *P. cylindrica*.

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751 **Fig. S4:** Remnants of a *C. violacea* shell (held by gloved fingers) previously tethered to *P.*
752 *cylindrica* within Votua Reef's MPA.

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Fig. S1

Fig. S2

Fig. S3

Fig. S4

Appendix S2

Table S1: *C. violacea* densities of different shell height (<10, 10-20, or >20mm) on *P. cylindrica* colonies when snail counts and coral 2-dimensional surface area were pooled by area (MPA or fished area) at each village site.

Village	Area	Shell height (mm)	Density (per 1000 cm ²)
Namada	MPA	<10	0.350
Namada	Fished area	<10	4.246
Namada	MPA	10-20	1.815
Namada	Fished area	10-20	7.068
Namada	MPA	>20	0.573
Namada	Fished area	>20	1.327
Vatu-o-lalai	MPA	<10	0.095
Vatu-o-lalai	Fished area	<10	3.640
Vatu-o-lalai	MPA	10-20	0.445
Vatu-o-lalai	Fished area	10-20	5.078
Vatu-o-lalai	MPA	>20	0.064
Vatu-o-lalai	Fished area	>20	1.201
Votua	MPA	<10	0.006
Votua	Fished area	<10	1.779
Votua	MPA	10-20	0.253
Votua	Fished area	10-20	5.798
Votua	MPA	>20	0.057
Votua	Fished area	>20	0.898