

Predation by feeding aggregations of *Drupella* spp. inhibits the recovery of reefs damaged by a mass bleaching event

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Abstract High densities of two corallivorous gastropods, *Drupella cornus* and *D. rugosa*, may delay the recovery of coral reefs impacted by mass bleaching events by aggregating on the remaining corals. Following severe bleaching in April/May 2016 that resulted in the loss of up to 80% of the living coral cover from reefs in South Malé, Maldives, aggregations of up to 250 *Drupella* per coral were recorded on surviving colonies. The distribution of snails was not random; larger aggregations were seen on reefs with fewer remaining live corals and also on the largest corals. Branching, digitate and tabular corals, especially species of *Acropora* and *Pocillopora*, sustained the highest mortality from the bleaching. Remaining colonies of these taxa exhibited the highest occurrence of snails and the most extensive snail predation, although less-preferred taxa such as *Montipora*, *Porites*, *Astreopora*, *Cyphastrea* and *Pachyseris* were also targeted. *Drupella* also concentrated on broken *Acropora* branches and overturned colonies; on some reefs, these were the only surviving acroporids, and many of them did not bleach. Continued predation pressure from *Drupella* may eliminate formerly dominant corals, including genets that are resistant to higher sea water temperatures.

Keywords *Drupella* · Corallivore · Coral predation · Bleaching

Introduction

Drupella gastropods are obligate corallivores that occur throughout the Indo-Pacific and Red Sea. These gastropods are generally found at low densities, although populations have increased exponentially on reefs in Japan, Eniwetak Atoll, Western Australia and other locations (Moyer et al. 1982; Boucher 1986; Turner 1994). Because these muricid gastropods feed primarily on fast-growing corals with high rates of recruitment, such as *Acropora*, *Pocillopora* and *Montipora*, their impacts are generally minimal. During outbreaks, however, *Drupella* have been responsible for large declines in live coral cover and shifts in species composition (Ayling and Ayling 1992; Turner 1994; Cumming 1999, 2009). They have also been found to redistribute among other coral taxa when their prey of choice declines in abundance (Morton et al. 2002).

Causes of rapid population explosions of *Drupella* are complex and incompletely understood. Progressive increases in population densities of *Drupella* have been reported from sites with chronic overfishing of balistids, labrids and other invertebrate predators (McClanahan 1994). Outbreaks have also been attributed to changes in environmental conditions that promote high recruitment, such as increasing eutrophication of coastal waters and elevated sea water temperatures (Turner 1994). Unusually large aggregations of snails have also been observed following catastrophic abiotic disturbances that have caused large reductions in prey species. For instance, the Caribbean corallivore, *Coralliophila abbreviata*, presently referred to as *C. galea* (Dillwyn, 1823) (Potkamp et al.

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2017), was reported to aggregate on remaining *Acropora cervicornis* (staghorn coral) colonies and broken branches following a hurricane (Knowlton et al. 1990).

Feeding preferences by *Drupella* are reported to change in response to the relative abundance of each coral taxon (Morton and Blackmore 2009). Some corallivores display plasticity with respect to their coral prey, feeding on other species when their preferred corals decline in abundance, while others compensate for reductions in prey abundance by increasing their numbers on individual coral colonies (Fujioka and Yamazato 1983; Shafir et al. 2008; Schoepf et al. 2010; Baums et al. 2003; Hoeksema et al. 2013). In a study from Florida, *C. galea* aggregations doubled in size on infested coral colonies in response to a decrease in coral cover rather than switching to another host (Baums et al. 2003). In contrast, *Drupella* populations in Thailand exhibited a dietary shift from *Acropora* and *Pocillopora* to fungiid corals following severe coral bleaching (Hoeksema et al. 2013).

Local and global stressors can cause large reductions in living coral and simultaneously impact surviving corals through breakage, tissue lesions, and disease, making them more susceptible to predation (Wolf and Nugues 2013; Bright et al. 2015; Scott et al. 2017). During April/May 2016, a catastrophic bleaching event occurred in the Maldives that resulted in the loss of 80–95% of the branching, tabular and digitate acroporids, and 30–50% of other corals (Perry and Morgan 2017). In addition to mass bleaching events, these reefs are negatively affected by the rapid growth of tourism and associated coastal development, land reclamation, sand extraction and pollution (Jaleel 2013; Nepote et al. 2016; Pisapia et al. 2016), and a recent outbreak of *Acanthaster* spp. (crown-of-thorns starfish; Saponari et al. 2015). *Drupella cornus* and *D. rugosa* were previously identified on three species of *Acropora*, and less frequently on *Echinopora*, *Pocillopora* and *Porites* in the southern Maldives (Taylor 1978), yet links between abiotic and biotic disturbances and outbreaks of corallivorous gastropods in the Maldives have not been reported. In South Malé (central Maldives), acroporids were also the most common host prey to *Drupella* prior to the bleaching event, although snails were relatively inconspicuous. As one component of a study to evaluate the patterns of reef recovery following catastrophic losses due to bleaching, we evaluate the changes in the distribution, feeding preferences and impact of *Drupella* spp.

Materials and methods

Changes in the cover, abundance and size of corals, and the associated population structure of corallivorous gastropods in the genus *Drupella* were assessed on an outer fore reef

(Marina; 3°58'30"N, 73°30'29"E) and a channel reef (Veli; 3°57'52"N, 73°30'14"E) on South Malé Atoll, Maldives, in April 2016 (prior to the initial onset of coral bleaching) and in October/November 2016 (post bleaching). Pre- and post-bleaching coral cover was estimated using point intercept surveys in two depth categories (three 10-m transects per depth on each reef for each time point, $n = 100$ points per transect). Belt transects (1 × 10 m length; $n = 20$) conducted at the seaward edge of the reef flat (5–7 m depth) and along the reef slope (8–12 m depth) were used to estimate the density and size structure of corals and the abundance of *Drupella*. Within each transect, all corals were identified to genus and growth form, and their maximum diameter was measured to the nearest centimeter. Each coral was carefully searched for signs of *Drupella* predation, and the total number of corallivorous gastropods on each coral was counted.

To evaluate size structure of *Drupella* and the density of snails, all snails identified within eight 2 × 30 m belt transects at the upper edge of the reef slope (four per reef; 6–8 m depth; $n = 2708$ snails) were collected. Every coral within this belt, 5 cm or larger in diameter, was recorded to genus and measured (maximum diameter). The snails from each coral were counted and placed into separate numbered bags to characterize the size structure of snails in each aggregate and the differences between coral genera. Snail length was determined by measuring the long axis of each shell (from the shell apex to the tip of the siphonal canal) with calipers to the nearest 0.1 cm. The specimens collected resembled *D. cornus* (Roding, 1798) and *D. rugosa* (Born, 1778) based on shell morphology and body color (Johnson and Cumming 1995). However, their shells were often encrusted with calcareous red algae, sponges and other epifauna, making field identification difficult. To avoid misidentification, species were pooled as *Drupella* spp. for transect surveys.

Two-way analyses of variance (ANOVAs) were performed on the datasets to test the null hypothesis that there was no difference in coral cover, density and size (diameter) between the two time periods and among reefs for all coral genera (pooled) and for five groups (*Acropora*, *Pocillopora*, *Porites*, *Montipora* and other genera) using transects as the independent replicate. Coral size measurements were log transformed to meet the assumptions of normality and homoscedasticity.

Drupella occurrence, host species preferences and size structure were examined using data from all belt transects from October 2016, for all genera of corals (pooled) and the five groups of corals (*Acropora*, *Pocillopora*, *Porites*, *Montipora* and other genera). The total number of corals, as well as the number of corals in each of the five groups, occupied and unoccupied by *D. cornus* on the two reefs were compared with Chi-square goodness-of-fit tests.

Differences in the abundance of snails on various prey were examined using a nested ANOVA with log-transformed abundance data and transect and site included as random factors. Generalized linear mixed-effects models (GLMM) with Poisson error distribution were calculated to investigate whether the number of snails occurring on each coral was related to the size (diameter) of the coral. Transect and site were included as random factors. The analyses were performed for each of the five genera separately (*Acropora*, *Pocillopora*, *Porites*, *Montipora* and other genera) and for all individuals pooled. To evaluate population structure of *Drupella* among different hosts, data were pooled into three size groups: recruits (<1 cm), juveniles (1–2 cm) and adults (>2 cm) according to Turner (1994). Variations in the abundance of juvenile and adult snails among genera of corals were analyzed using a multivariate analysis of variance (MANOVA). Snail recruits were omitted from this test because recruits were rare on these reefs. Snail abundance was log transformed to satisfy the assumptions of the statistical test. Pillai's trace statistic was used to determine the significance of the MANOVA, following Olsen (1976).

Results

Prior to the onset of the coral bleaching event in April 2016, both reefs had relatively high cover of coral (range 36–76%; Fig. 1a) and low prevalence of *Drupella* spp. gastropods. Coral communities consisted of dense assemblages of branching and tabular acroporids, *Pocillopora*, and *Porites*, and lower numbers of 15 other genera. *Drupella* were identified on two genera of corals, *Acropora* and *Pocillopora*, at mean prevalence of 0.37% within transects at Marina and Veli reefs; gastropods were absent from all other taxa. Aggregates of up to 18 snails (4.6 ± 5.2 , mean \pm SE) occurred on individual corals. *Pocillopora* had larger aggregates, even though colonies of *Pocillopora* were smaller in size (18 ± 6.5 cm vs. 23 ± 14.7 cm), but snails were generally smaller in size (12 mm vs. 23 mm on *Acropora*). Damage caused by the snails appeared to be minimal; infested colonies had small white lesions at the bases of branches and on the perimeter of encrusting colonies affecting <5% of the tissue area.

Living coral cover declined to <15% by October 2016 (Fig. 1a), mainly due to a decline in the *Acropora* and *Pocillopora* (Table 1). Coral losses due to bleaching were associated with a reduction in the density of colonies of all species (Fig. 1b), although declines were greatest among *Acropora* and *Pocillopora* (Table 2). Remaining colonies of *Acropora* were also smaller in size in October, while other genera did not show significant rates of change in diameter (Table 3). Many of the surviving acroporids

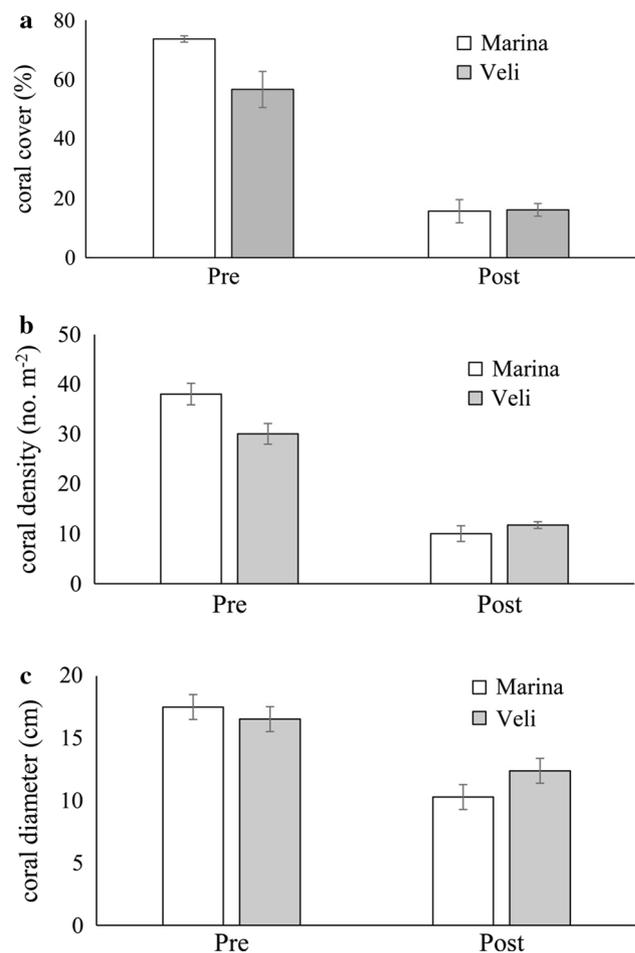


Fig. 1 Coral community on Marina and Veli reefs prior to the bleaching event in April 2016 and post bleaching in October 2016 showing **a** mean coral cover (percent \pm SE), **b** coral density (number of corals m^{-2} \pm SE), and **c** coral diameter (cm \pm SE)

consisted of detached and broken branches that had accumulated on the reef slope and under dead corals. Coral species assemblages in October 2016 also shifted from *Acropora*-dominated to a community composed primarily of small colonies of *Porites*, *Goniastrea* and *Pocillopora*.

While very little bleaching was noted in October, many of the surviving corals had conspicuous patches of white, recently denuded skeleton, and most had aggregates of *Drupella* at the margin of these lesions (Fig. 2). Of the 1525 corals sampled within 20 transects in October 2016, 189 (12.4%) were occupied by *Drupella*, with snails occurring on 12 scleractinian genera. While there was no evidence that the occurrence of *Drupella* among reefs was heterogeneous ($\chi^2 = 2.578$, $df = 1$, $p = 0.1$), *Drupella* spp. were not randomly distributed among the different coral genera ($\chi^2 = 52.559$, $df = 9$, $p < 0.001$). More than 54% of the *Drupella* were found on *Pocillopora* (12% of the coral sampled), 21% on *Porites* (54% of the corals sampled), 13% on *Acropora* (4.7% of the corals sampled),

Table 1 Two-way analysis of variance (ANOVA) assessing the impact of site and time (month) on the rate of change in coral cover of different coral genera

Source of variation	<i>Acropora</i>		<i>Pocillopora</i>		<i>Porites</i>		<i>Montipora</i>		Other	
	<i>F</i> (<i>df</i>)	<i>P</i>								
Site	5.100 (1)	*	23.59 (1)	***	0.808 (1)	0.378	0.022 (1)	0.882	0.011 (1)	0.916
Month	92.156 (1)	***	44.55 (1)	***	0.991 (1)	0.330	6.853 (1)	*	4.113 (1)	0.055
Site × month	7.817 (1)	*	10.570 (1)	**	0.247 (1)	0.624	1.632 (1)	0.215	2.755 (1)	0.111

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 2 Two-way analysis of variance (ANOVA) assessing the impact of site and time (month) on the rate of change in coral density of different coral genera

Source of variation	<i>Acropora</i>		<i>Pocillopora</i>		<i>Porites</i>		<i>Montipora</i>		Other	
	<i>F</i> (<i>df</i>)	<i>P</i>								
Site	0.550 (1)	0.468	0.941 (1)	0.345	1.443	0.246	2.227 (1)	0.153	2.280 (1)	0.148
Month	31.073 (1)	***	12.659 (1)	**	5.201 (1)	*	5.698 (1)	*	7.347 (1)	*
Site × month	0.307 (1)	0.586	0.025 (1)	0.878	4.469 (1)	*	0.123 (1)	0.730	1.564 (1)	0.227

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 3 Two-way analysis of variance (ANOVA) assessing the impact of site and time (month) on the rate of change in coral size of different coral genera

Source of variation	<i>Acropora</i>		<i>Pocillopora</i>		<i>Porites</i>		<i>Montipora</i>		Other	
	<i>F</i> (<i>df</i>)	<i>P</i>								
Site	2.313 (1)	0.146	9.193 (1)	**	1.729 (1)	0.205	1.258 (1)	0.277	4.514 (1)	*
Month	18.032 (1)	***	0.519 (1)	0.480	3.280 (1)	0.087	3.231 (1)	0.089	2.817 (1)	0.111
Site × month	9.409 (1)	**	3.196 (1)	0.091	0.914 (1)	0.352	1.502 (1)	0.236	0.412 (1)	0.529

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

8% on *Montipora* (2.8% of the corals sampled) and 4% were on other genera, including *Astreopora*, *Cyphastrea*, *Echinopora*, *Favites*, *Galaxea*, *Hydnophora*, *Pachyseris* and *Pavona* (24% of the corals sampled; Fig. 3).

The size of aggregates on individual corals ranged from 2 to 250, with 16.3 ± 13.3 *Drupella* per coral. The density of snails ranged from 3.1 ± 1.5 individuals m^{-2} at Marina to 3.8 ± 1.3 individuals m^{-2} at Veli. The mean number of individuals per occupied coral was 17.9 ± 1.76 for all individuals. Mean group size was not significantly different among genera (nested ANOVA, $F = 0.866$, $df = 4$, $p = 0.487$), possibly due to the large variation in aggregate size on conspecifics (range 2–86; Fig. 4). However, snails were almost twice as abundant on corals that were 30 cm diameter or larger (22.9 ± 3.96) than on corals that were 5–29 cm diameter (14.1 ± 1.97). This was reflected in the GLMM which identified a significant positive association between the number of *Drupella* and diameter of corals for all genera pooled ($z = 24.3$, $p < 0.001$) and for

Acropora ($z = 11.79$, $p < 0.001$), *Pocillopora* ($z = 13.26$, $p < 0.001$), *Porites* ($z = 11.5$, $p < 0.001$) and *Montipora* ($z = 3.0$, $p < 0.01$), but not for other genera ($z = 0.24$, $p = 0.81$; Fig. 5).

Drupella ranged in size from 6 to 43 mm, with 59% of all individuals classified as adults with a shell length of 3 cm or larger, and 40% juveniles (1–2.9 cm); recruits <1 cm in length were uncommon (0.99%). Most corals (97.8%) were occupied by at least one adult, while 63.5% of the corals contained mixed assemblages of adults and juveniles. Although there were more adult *Drupella* (58.8%) in the sampled corals than juveniles (40.2%), the distribution of age classes varied significantly among genera (MANOVA, Pillai's trace = 0.432, $F_{4,72} = 2.416$, $p = 0.023$) with a higher proportion of juveniles on *Pocillopora* (67%), mostly adults on *Porites* (84%), *Montipora* (77%) and *Acropora* (71%), and a complete absence of juveniles on other genera (Fig. 6).

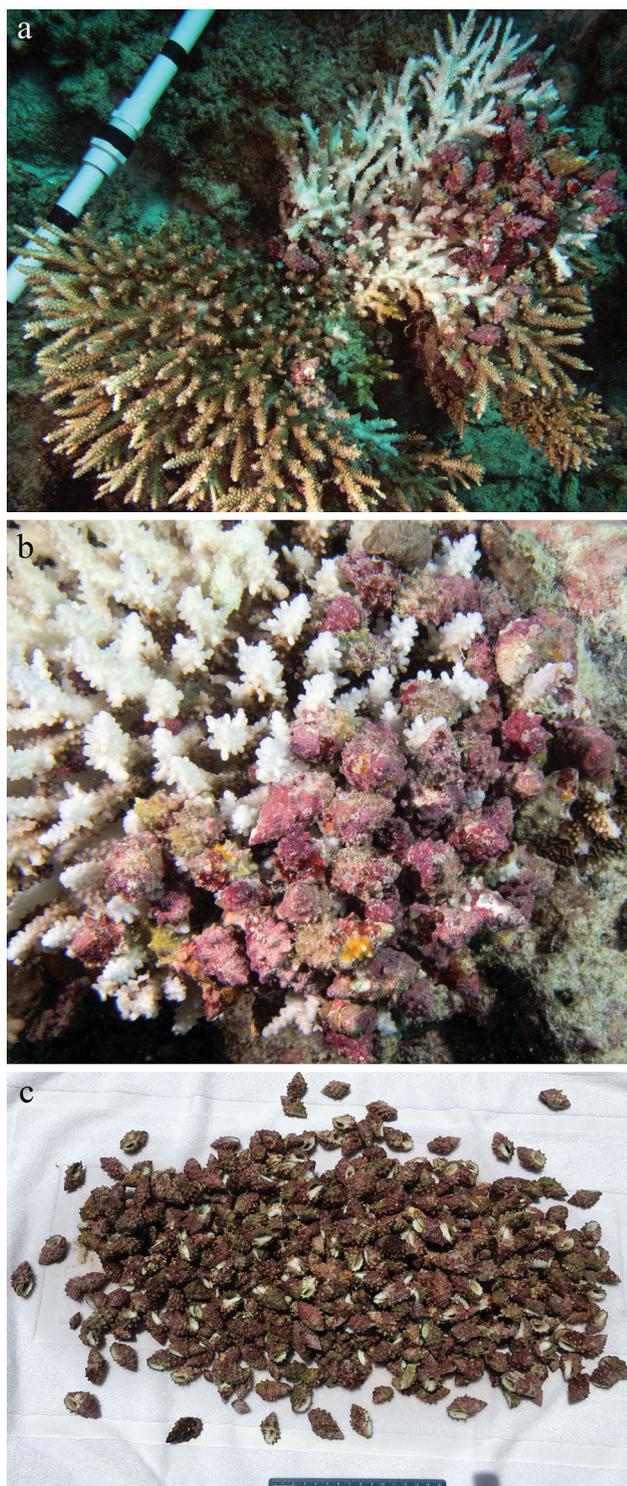


Fig. 2 *Drupella* spp. gastropods on *Acropora*, October 2016, South Malé Atoll, Maldives. **a** Half the colony has been consumed, **b** close-up of an aggregation, **c** specimens of *Drupella* spp. removed from a single small (20 cm diameter) table acroporid (*A. cytherea*). Scale bar is 15 cm

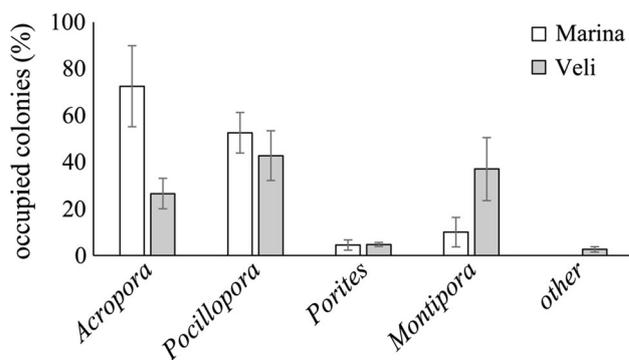


Fig. 3 Percentage of coral colonies of the four dominant genera and all other genera pooled (other) occupied by *Drupella* spp. at Marina and Veli reefs, Maldives, in October 2016

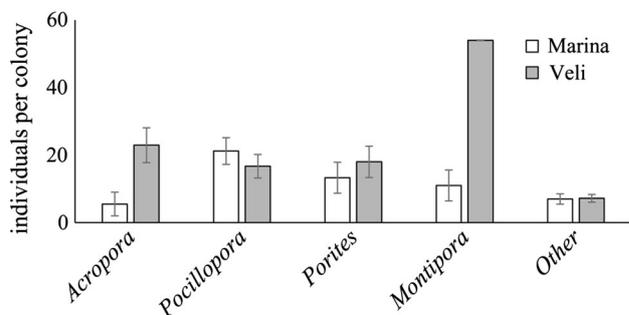


Fig. 4 The mean number (\pm SE) of *Drupella* spp. recorded during October 2016 on the four dominant genera of corals and all other genera pooled (other)

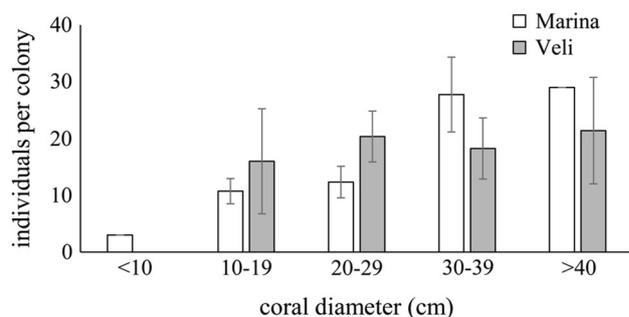


Fig. 5 Mean number of individuals of *Drupella* spp. (\pm SE) per colony in five size classes (diameter) of corals

Discussion

In this study, an abnormally high abundance of *Drupella* gastropods was identified on reefs off South Malé Atoll, Maldives, during October 2016 following a large-scale die-off of corals due to a severe bleaching event. In response to a large reduction in the living cover and abundance of acroporids, *Drupella* extended their range of prey species

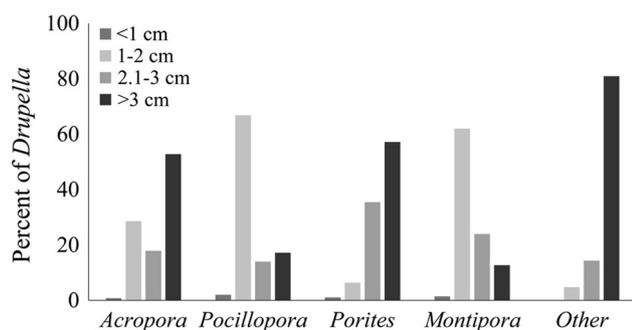


Fig. 6 Size frequency distribution of *Drupella* spp. on the four dominant genera of corals and all other genera pooled (other). *Drupella* spp. are classified into four major size classes (shell length) according to age structure reported by Turner (1994)

compared to their pre-bleaching distribution. The *Drupella* population also showed a strong preference for larger corals, with significant differences in prey noted between life stages.

Large aggregations of *Drupella* were most frequently observed on the competitively dominant coral taxa, *Acropora* and *Pocillopora*, while competitive subdominants such as species of *Montipora*, *Porites* and *Astreopora* were also selected in October, but not April. *Drupella cornus* has been reported to have a strong preference for acroporids (Moyer et al. 1982; Fujioka and Yamazato 1983; Turner 1994; Cumming 1999; Al-Horani et al. 2011), possibly due to a greater surface area, more tissue, and a higher protein and energy content compared to most other coral families (Keesing 1990). They are also noted for their plasticity in prey and are known to exhibit dietary shifts toward less-preferred prey species that are in high abundance if their preferred coral is absent or has declined due to a catastrophic disturbance. For example, *Drupella* were most often associated with branching and massive *Porites* in Kenya (McClanahan 1997), while *Pocillopora* and *Porites* were selected in Hawaii (Robertson 1970). In Thailand, *Drupella* shifted from acroporids to fungiid corals following a bleaching event in 2010, but appeared to avoid fungiidae four years later (Hoeksema et al. 2013; Moerland et al. 2016).

Size structure and age class are also reported to affect prey selection. Juveniles have been found to prefer structurally complex prey species such as caespitose, digitate and tabular growth forms of *Acropora* and branching *Pocillopora* that provide shelter (Forde 1992; McClanahan 1997; Schoepf et al. 2010). On these reefs, the smallest *Drupella* occurred within tightly branched *Pocillopora* colonies, while the largest snails were found on massive and encrusting corals such as *Porites*, *Astreopora* and *Pavona*.

The mean density of 3.4 individuals m^{-2} at South Malé Atoll is much higher than background levels reported from most reefs (Zuschin and Stachowitsch 2007) and is

comparable to the densities reported during recent outbreaks (Shafir et al. 2008). Densities in the Maldives are much lower than those observed during severe outbreaks in Western Australia during the 1980s (up to 19.4 m^{-2} ; Ayling and Ayling 1987; Turner 1994) and Aqaba in the 1990s (12.24 m^{-2} ; Al-Moghrabi 1997), suggesting the high-density aggregations here may represent a different phenomenon than an outbreak (Cumming 2009). An examination of the size structure of *Drupella* (using age estimates of Turner 1994) reveals a population consisting primarily of juveniles (38%) and adults (61%) with very few recruits, suggesting that large numbers of snails have not colonized the reef within the last year. It is more likely that the drastic decline in prey availability as a result of bleaching-related mortality has caused existing snails to aggregate on remaining corals. Habitat containing living corals on these reefs has been greatly reduced, as >99% of the coral that occurred in water shallower than 5 m depth has died and the few remaining corals are concentrated in a smaller area at the seaward edge of the reef flat and on the reef slope.

Drupella are most abundant on shallow reefs (Cumming 2009), which are also the areas most impacted by dive and snorkel tourism, sedimentation and land-based pollution. In the northern Red Sea, Guzner et al. (2010) observed higher snail abundances in areas with high recreational use, which they attributed to mechanical injuries to corals caused by divers. Outbreaks of *Drupella* in the Philippines and Japan were documented on reefs exposed to high levels of siltation associated with shoreline construction and heavy rainfall (Moyer et al. 1982). This suggests that increase in nutrients associated with run-off may promote higher survival of *Drupella* larvae (Turner 1994). In contrast, there was no correlation between snail abundance and human activities in Thailand (Scott et al. 2017). The increase in *Drupella* observed in the present study is also not correlated to human activity. The reefs examined in the Maldives were adjacent to a resort, yet few recreational divers use these areas, sewage is fully treated on shore, and there is no ongoing shoreline construction. There were, however, a large number of fragmented and broken acroporid corals which may have attracted *Drupella*, but colony breakage was attributed to high wave action and not diver damage, as these are exposed outer reefs.

Predator-mediated losses of corals are likely to delay the recovery of these reefs, as more than half of the remaining corals of two genera, *Acropora* and *Pocillopora* had large aggregations of *Drupella* and prominent feeding scars. These genera were the most abundant corals and provided most of the living coral cover on these reefs prior to the bleaching event. They sustained 80–95% mortality in most locations, and the survivors were succumbing to predation by *Drupella*. Furthermore, broken branches and overturned acroporid colonies that had accumulated on the reef slope and were beginning to reattach and produce new growth were affected

by some of the largest aggregations of *Drupella* observed on these reefs. Impacts from *Drupella* are likely to reduce the resilience of these reefs, as many of the corals targeted by the snails were colonies that had resisted bleaching during the periods of high water temperatures.

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