PRIMARY RESEARCH PAPER

Assessing population collapse of *Drupella* spp. (Mollusca: Gastropoda) 2 years after a coral bleaching event in the Republic of Maldives

L. Saponari ⬤ · **I. Dehnert** · **P. Galli** · **S. Montano**

Abstract Corallivory causes considerable damage to coral reefs and can exacerbate other disturbances. Among coral predators, *Drupella* spp. are considered as delayer of coral recovery in the Republic of Maldives, although little information is available on their ecology. Thus, we aimed to assess their population structure, feeding behaviour and spatial distribution around 2 years after a coral bleaching event in 2016. Biological and environmental data were collected using belt and line intercept transects in six shallow reefs in Maldives. The snails occurred in aggregations with a maximum of 62 individuals and exhibited a preference for branching corals. Yet, the gastropods showed a high plasticity in adapting feeding preferences to prey availability. *Drupella* spp. were homogenously distributed in the study area with an average of 9.04 ± 19.72 ind/200 m². However, their occurrence was significantly different at the reef scale with the highest densities found in locations with higher coral cover. The impact of *Drupella* spp. appeared to be minimal with the population suffering from the loss of coral cover. We suggest that monitoring programs collect temporal- and spatial-scale data on non-outbreaking populations or non-aggregating populations to understand the dynamics of predation related to the co-occurrence of anthropogenic and natural impacts.

Keywords Corallivory · Coral · Coral bleaching · Coral recovery · Predation · *Acropora* · *Pocillopora*

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Introduction

Coral reefs are among the most diverse and dynamic ecosystems on the planet, and critically important for providing ecological goods and services to human communities (Williams et al., 2019; Woodhead et al., 2019). Yet, reefs are continuously deteriorating due to anthropogenic and natural disturbances such as global climate change, coral predators, and extreme weather events (De'ath et al., 2012; Hoegh-Guldberg et al., 2017; Hughes et al., 2017a, b; Rice et al., 2019). Knowing the scale of these impacts is essential for driving well-informed management decisions on reef conservation (i.e. Hughes et al., 2017a, b; Shaver et al., 2018). In particular, anthropogenic disturbances are reported to exacerbate the negative effects of coral

predation (Rice et al., 2019). For example, the crown-of-thorns seastar, *Acanthaster* spp., have been reported to cause high coral mortality during outbreaks, reducing coral cover up to 80% (Pratchett et al., 2014, 2017) with an increased effect during temperature-induced coral bleaching (Saponari et al., 2018). Other corallivores have been reported for the reduction in coral cover, among those, *Drupella* spp. feed exclusively on living coral tissue and is known to cause large-scale disturbances to coral reef ecosystems (e.g. Bruckner et al., 2017; Koido et al., 2017).

Drupella is a genus of marine gastropods comprising four species, *Drupella cornus* (Röding, 1798), *D. eburnea* (Küster, 1862), *D. fragum* (Blainville, 1832) and *D. rugosa* (Born, 1778) (Claremont et al., 2011). These tropical gastropods occur on coral reefs of the Indo-Pacific Ocean (Claremont et al., 2011) at low densities (0–2 ind/m^2; Cumming 1999, 2009a), although populations of *Drupella* spp. may display transitions between low density periods with outbreak and/or local aggregation events with up to 20 ind/m^2 or 250 ind/colony, respectively (Cumming et al., 2009a; Bruckner et al., 2017).

Large aggregations of *D. rugosa* have been observed in the Indo-Pacific Ocean and are well documented on the Great Barrier Reef (Cumming, 1999), while outbreaks of *Drupella* spp. were reported from a wide range of regions including Kenya (McClanahan, 1994), Western Australia (Ayling & Ayling, 1987), Hong Kong (Cumming, 1998; Morton and Blackmore, 2009), Red Sea (Antonious, A. & B. Riegel, 1998), Thailand (Scott et al., 2017a, b) and India (Marimuthu & Tripathy, 2018). These events appeared to be caused by overfishing of natural predators, high coral mortality and changes in temperature and salinity (Turner, 1994a, b; Cumming, 2009a, b), although the causes are complex and still not completely understood (McClanahan, 1994, 1997; Lam & Shin, 2007; Ratianingsih et al., 2017). When these events occur, the damage on coral reefs may be severe reducing coral cover by 35 to 70% (Cumming, 2009a, b). Furthermore, impacts mediated by corallivores may synergically act with other coral stressors exacerbating coral mass mortality (Saponari et al., 2014, 2018; Pisapia et al., 2016, 2019) and delay reef recovery (Bruckner & Coward, 2018). Thus, both outbreak and aggregation events may affect coral reef communities by reducing reef resilience and recovery (Lam & Shin, 2007), causing population shifts and

increasing disease incidences (Nicolet et al., 2013, 2018; Scott et al., 2017a, b). The feeding habits of these corallivores may also be influenced by the loss in coral abundance and diversity due to coral bleaching (Rice et al., 2019 and references included). For instance, *Drupella* spp. were reported changing dietary habits from the favourite genera *Acropora* and *Pocillopora* to the less palatable fungiid corals after a major coral bleaching event in Thailand (Hoeksema et al., 2013; Moerland et al., 2016).

Drupella spp. were recently reported to aggregate in the Republic of Maldives concurrent to the coral bleaching event in 2016 by Bruckner et al. (2017), but limited information is available prior to this event (see Taylor, 1978). The Republic of Maldives has been affected by a coral bleaching event in 2016 resulting in a loss of 30% and up to 95% of live coral cover (Perry & Morgan, 2017; Pisapia et al., 2019). In addition, the Maldivian coral reef is threatened by increasing tourism and coastal development (Brown et al., 2017), land reclamation (Fallati et al., 2017) and natural stressors such as diseases (see Montano et al., 2012, 2015a, b, 2016; Seveso et al., 2012). Thus, both coral loss and recovery may vary between and within Atolls based on the different occurrence of disturbances (Zahir, 2000; McClanahan & Muthiga, 2014; Pisapia et al., 2019), and consequently, variation in coral cover may differently influence the ecology and biology of associated organisms, such as corallivores.

The impact of corallivores in Maldives has recently started to attract scientific attention focusing on outbreaks of *Acanthaster planci* (Linnaeus, 1758) (Saponari et al., 2014, 2018), the ecology of *Culcita* spp. (Bruckner & Coward, 2018; Montalbetti et al., 2019a, b) and the population dynamics of *Drupella* spp. after a bleaching event (Bruckner et al., 2017). However, very little information is available on the ecology of *Drupella* spp. in non-outbreaking or non-aggregating populations (Turner, 1994a; Cumming, 1999). Furthermore, the population dynamics of corallivores are still poorly described in the Maldives calling for more in-depth research. Here, we aim to explore the ecological traits of *Drupella* spp. In particular, we surveyed a population around 2 years after a mass coral bleaching event to examine the effects of variation in coral cover on the population structure, feeding behaviour and spatial distribution of *Drupella* snails.

Materials and methods

Biological and environmental data collection

Although both species *D. rugosa* and *D. cornus* are reported from the Maldives (Taylor, 1978) the in-field identification was difficult since the shells of the specimens were often heavily encrusted with coralline red algae and different epifauna. Thus, to avoid misidentification, gastropod snails were identified to the genus level and considered as *Drupella* spp. (Fig. 1).

To examine the effects of variation in coral cover on *Drupella* spp. population structure, feeding behaviour and spatial distribution, we surveyed a total of 6 sites in two different Atolls (3 in Ari Atoll and 3 in Faafu Atoll) in the Republic of Maldives (Fig. 2) between November 2018 and March 2019. Sites were randomly selected according to accessibility and surveyed by snorkelling between 0 and 5 m, in accordance with other studies that found *Drupella* spp. mainly in the shallower reefs (Taylor, 1978; Turner, 1994a; Cumming, 2009a, b; Hoeksema et al., 2013; Bruckner et al., 2017; Koido et al., 2017; Scott et al., 2017a, b; Hamman, 2018; Marimuthu & Tripathy, 2018). To evaluate density variation within and among sites, belt transects of 200 m² (50 × 4 m each) were conducted both on the reef flat (6 transects at 0–2 m) and along the reef crest (6 transects at 2–5 m) in each site. The belt transects were randomly placed parallel to the shoreline and spaced 10–30 m apart. Each snail encountered in each belt transect was counted and removed from the position to avoid recount bias. In addition, size data was collected by measuring the long axis of each shell from the apex to the tip of the siphonal canal. The sizes were measured in the field to the nearest mm, while the analysis and results were presented in cm for consistency with coral size data.

During the survey, the substratum directly beneath the snail was noted specifying the coral genus, size and morphology when the snail was found on a coral colony, or other substrata, such as coral rubble, dead coral or sand. Snails were considered 'preying' when associated with alive coral (i.e. over the living tissue or a dead part of a living coral colony in an aggregation or with a nearby feeding scar). In contrast, snails not associated with alive coral were considered 'moving'
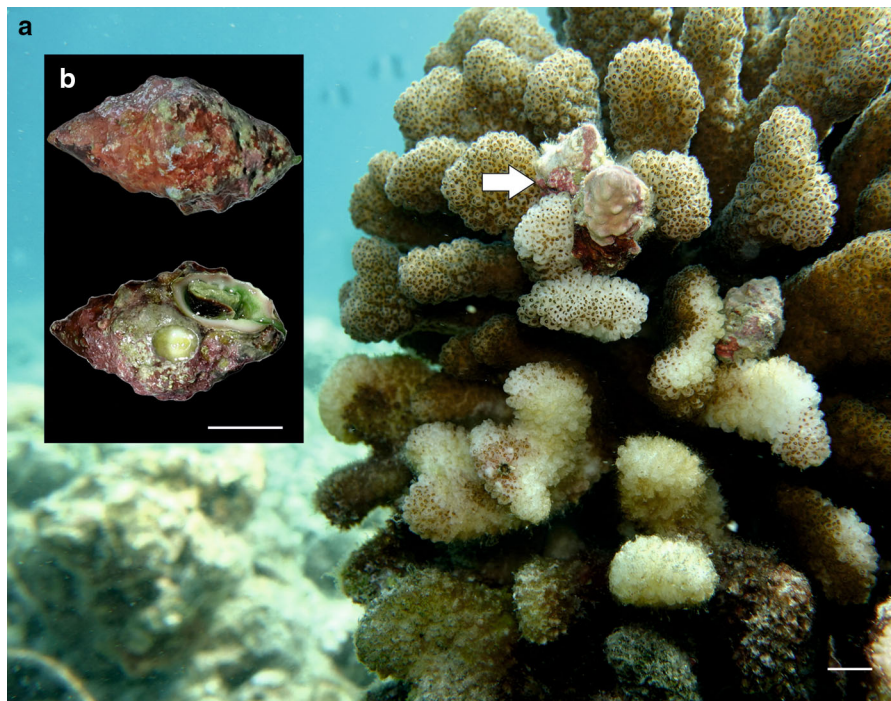

Fig. 1 **a** The picture was taken during the survey in Bathala. The specimens of *Drupella* spp. (highlighted by an arrow) were feeding on a colony of the genus *Pocillopora*. **b** Upper and lower view of *Drupella* spp., bars in **a** and **b** indicate 1 cm
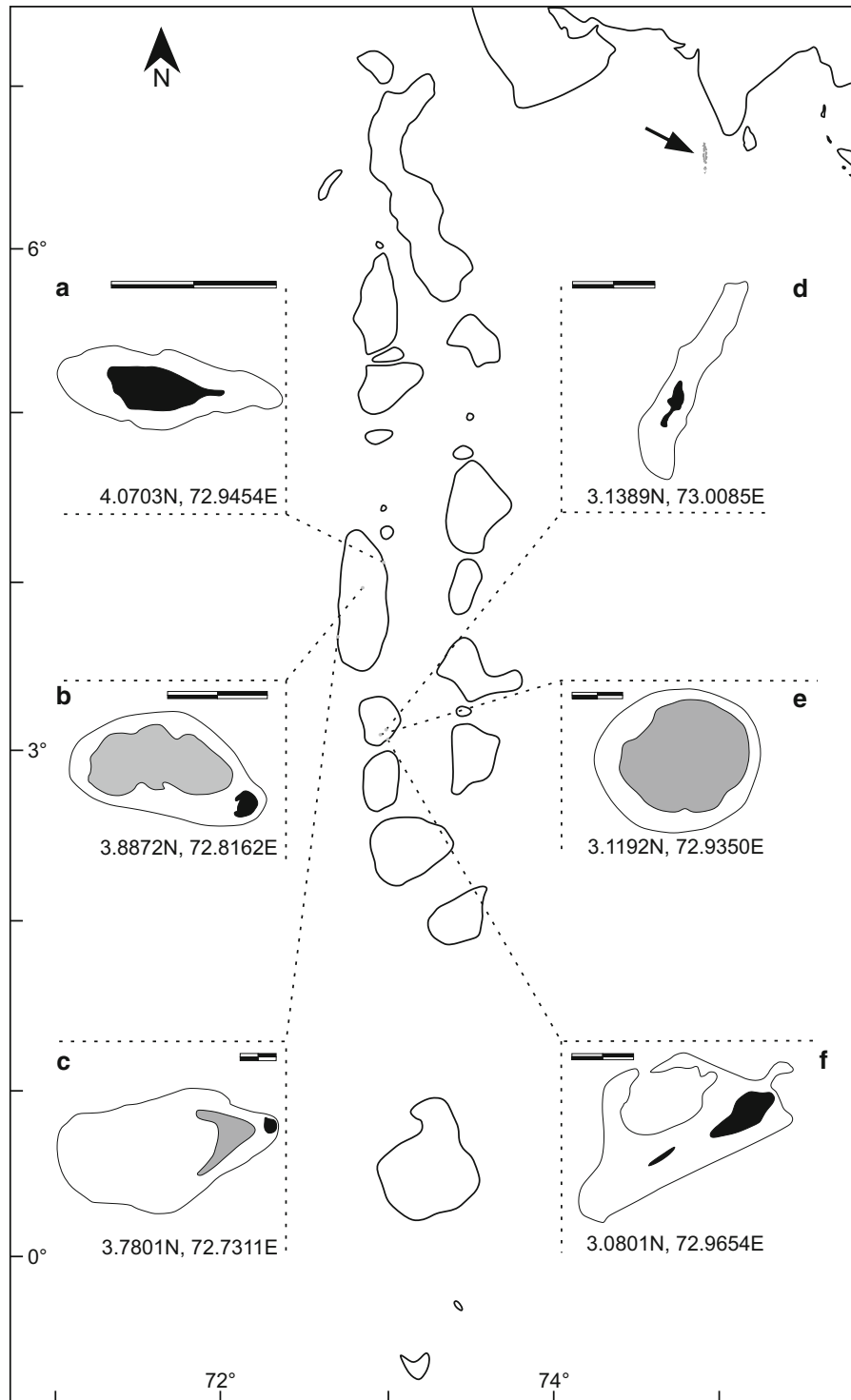
Fig. 2 Map of the study area located in Ari and Faafu Atolls in the Republic of Maldives (black arrow). **a** Bathala, **b** Athuruga, **c** Thudufushi (Ari Atoll), **d** Adhanga, **e** Maaga and **f** Magoodhoo (Faafu Atoll). Solid lines represent reef limits, in black the islands and in grey the closed lagoon. Total scale bars are 0.5 km

based on the concept that they need to move from one coral colony to the other to find shelter and food (Cumming, 1999; Morton et al., 2002). Further, we measured the maximum diameter of the scar area and the coral colony were measured. The scar size was then divided in two categories, specifically > 50% or < 50% of the size of the coral colony. Data for the abundance of corals in the sites was collected by using the Line Intercept Transect (LIT) method with three 10 m long transects spaced 10 m apart, on the same belt transect used for abundance and size structure of *Drupella* spp. Benthic categories were selected following Saponari et al. (2018).

Statistical analysis

Drupella spp. size data was pooled into three classes comprising recruits (< 1 cm), juveniles (1–2 cm) and adults (> 2 cm), following Turner (1994a, b). The Hartigan's dip test (Hartigan & Hartigan, 1985) was used to test the size distribution for unimodality in order to assess the presence of a multiple (i.e. non-unimodal) or single (i.e. unimodal) recruitment event (see Saponari et al., 2018). The statistical analysis was performed using RStudio (R Core Team, 2017) with the dip.test package (Maechler, 2016).

Furthermore, we investigated the feeding preferences of *Drupella* spp. The Ivlev's (1961) electivity index (E_i) was used with the formula:

$$E_i = (r_i - p_i) \div (r_i + p_i).$$

For this equation r_i represents the proportion of prey in the diet and p_i represents the proportion of prey in the environment. Values of E_i range between 1 (maximum preference) and − 1 (maximum avoidance), whereby 0 indicates random feeding. We calculated r_i as the frequency of snails on a specific i genus or family of corals in relation to all the preyed colonies. After, we obtained p_i as the mean relative abundance of each single genus or family of corals in the environment.

Statistical comparisons of the spatial variation, number of snails per aggregation within genera, morphology, locations, differences in shell size between locations and differences in coral cover between locations were analysed using the Mann–Whitney U-test and the Kruskal–Wallis test with Tukey's post hoc test because data failed in meeting the normality assumption (Zar, 1999). Comparisons

within coral genera occupied by *Drupella* spp., the number of snails per aggregations and the occurrence of aggregations on different coral morphologies, genera and locations were analysed with χ^2 goodness-of-fit tests. Spearman's rank correlation was used to examine whether the density of *Drupella* spp. was related to benthic categories and to the number of genera on each location. This allowed us to verify which variables among benthic coral or occurrence of genera drive *Drupella* spp. density. Further, a simple linear regression was used to examine the relationship between coral cover and snail density variation by plotting the number of snails and the average coral cover for each 50 m transect, across sites. Statistical analysis was performed using SPSS ver. 24 (IBM, New York). All data is represented as arithmetic means ± standard deviation.

Results

Drupella spp. population structure

Shell size was measured for all the individuals, ranging from 0.2 to 4.8 cm, and yielding a mean value of 2.62 ± 0.53 cm. The resulting population structure was not unimodal as determined by the dip test ($P < 2.2 \times 10^{-16}$). The snail population was constituted mainly by adults (> 2 cm) with 90.3% of the individuals, while only 9.1% were juveniles (1–2 cm) and 0.6% were recruits (< 1 cm) (Fig. 3). Snail size was significantly larger in Faafu than Ari atoll ($U = 79,998$, $z = 2,383$, $P < 0.001$) as well as on the reef crest compared to the reef flat considering the data pooled ($U = 51,246$, $z = 2,231$, $P = 0.027$). The analysis revealed a significant difference between locations (K–W, $P < 0.001$). The post hoc test suggested that Magoodhoo had bigger snail sizes compared to Bathala, Thudufushi and Adhanga, as well as Adhanga compared to Thudufushi (K–W, $P < 0.05$).

Feeding behaviour

Prey preferences changed in different locations following the availability of coral prey. *Pocillopora* had a positive index value for Bathala, Thudufushi, Adhanga and Maaga, while *Acropora* for Bathala and Thudufushi and *Porites* for Athuruga and Magoodhoo. The genus *Pavona* had a positive index

Fig. 3 Distribution of *Drupella* spp. divided into size classes following Turner ([1994a](#), [b](#))
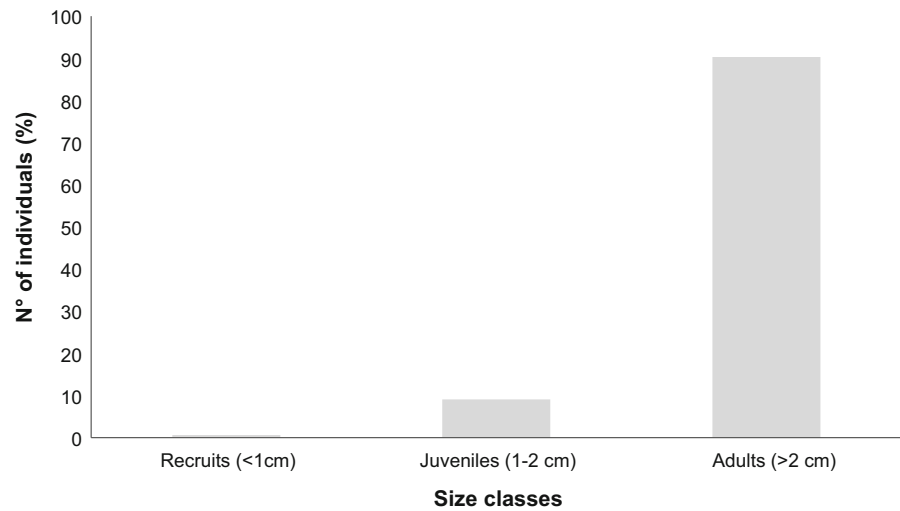
only for Bathala and the genus *Hydnophora* only in Adhanga. In all other cases negative values indicated avoidance (Table 1). Looking at the pooled data, the electivity index (E_i) showed a positive value, by meaning preferred, for the genera *Pocillopora* and *Acropora*, 0.35 and 0.17 respectively, while random choice resulted for *Porites* with an electivity index of 0.002. We observed negative electivity values for *Pavona* and *Hydnophora*, − 0.75 and − 0.79 respectively (Fig. 4). In addition, the predation was not found to be lethal at the moment of the survey, since 82% of the occupied colonies were damaged by less than 50% of the colony size and only 1 colony was found dead.

The size of the preyed upon coral colony varied from 8 to 500 cm in maximum diameter. The size class most represented was 25–35 cm (17.9%), followed by 15–25 and 35–45 cm (15.4% and 10.9%, respectively). Notably, no individuals of *Drupella* spp.

were found preying upon coral recruits < 5 cm in maximum diameter, despite their occurrence in every location.

Individuals of *Drupella* spp. were mostly found on live coral colonies (85.6%), although few individuals were found on dead corals (13.2%) and coral rubble (1.2%). Overall, 92% of the snails were classified as "preying", while the remaining 8% were considering moving, likely searching for other coral colonies. The snails were found on 232 colonies of corals, and considering the whole dataset pooled, the genus *Porites* was the most frequently occupied (43.7%) followed by *Pocillopora* (33.4%), *Acropora* (22.4%), *Pavona* (1%) and only 1 individual was found on a single colony of the genus *Hydnophora* ($\chi^2_{(4)} = 440.708$, $P < 0.001$).

Drupella spp. were found aggregating on 54.7% of the colonies, with a minimum of 2 and a maximum of 62 individuals (Fig. 5), which were found on a single

Table 1 Feeding preferences of *Drupella* spp. according to the Ivlev's Electivity Index (E_i) considering the genera preyed upon at each location

	Porites	*Acropora*	*Pocillopora*	*Pavona*	*Hydnophora*
Bathala	− 0.77	1.00	0.75	0.45	− 1.00
Athuruga	0.79	− 1.00	− 1.00	− 1.00	− 1.00
Thudufushi	− 0.80	0.26	0.44	− 0.39	− 1.00
Adhanga	− 0.24	− 0.02	0.59	− 0.80	0.24
Maaga	− 1.00	− 1.00	0.38	n.d	n.d
Magoodhoo	0.17	− 0.16	− 0.64	− 1.00	− 1.00

The genera *Pavona* and *Hydnophora* were absent in Maaga, thus no data (n.d.) were reported

Fig. 4 Feeding preference of *Drupella* spp. according to the Ivlev's Electivity Index (E_i) for each genera or family pooled in the study area
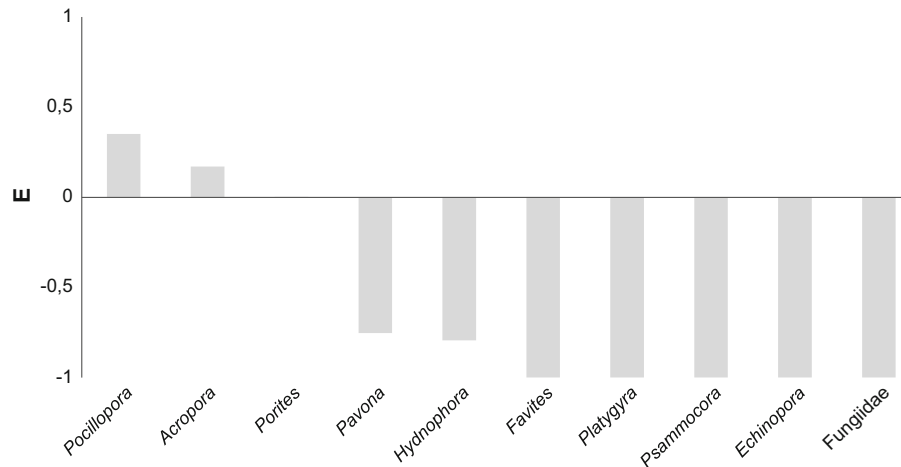

branching colony of the genus *Acropora*. Aggregations constituted of a few individuals, with an average of 5.63 ± 7.1 ind per aggregation and the majority in between 2 and 5 individuals ($\chi^2_{(15)} = 125.455$, $P < 0.001$). The data showed non-significant differences in number of individuals per aggregation within different coral genera (K–W, $P = 0.336$), morphology (K–W, $P = 0.104$) nor for locations (K–W, $P = 0.085$). Thus, the number of individuals was randomly distributed among four genera of corals (*Porites* spp., *Acropora* spp., *Pocillopora* spp. and *Pavona* spp.) and there was no preference in morphology nor in locations. Furthermore, *Drupella* spp. were aggregated more frequently on branching corals (79.8%) than massive (5.6%), digitate (12.4%) or encrusting (2.2%) ($\chi^2_{(3)} = 144.303$, $P < 0.001$). The

aggregations occurred more frequently on *Porites* (49.4%) than *Pocillopora* (33.7%), *Acropora* (14.6%) and *Pavona* (2.2%) ($\chi^2_{(3)} = 46.236$, $P < 0.001$) and more frequently in Magoodhoo ($\chi^2_{(4)} = 75.931$, $P < 0.001$) than other locations.

Spatial distribution

During the study period, the monitoring survey for the population of the snail *Drupella* spp. was performed with a total of 72 transects covering an area of 1.44 ha. We counted 651 individuals of *Drupella* spp. with an overall mean density of 9.04 ± 19.72 ind/200 m^2. The distribution of the snail was homogeneous at a large spatial scale, as highlighted by the *U*-test, which showed non-significant differences in densities
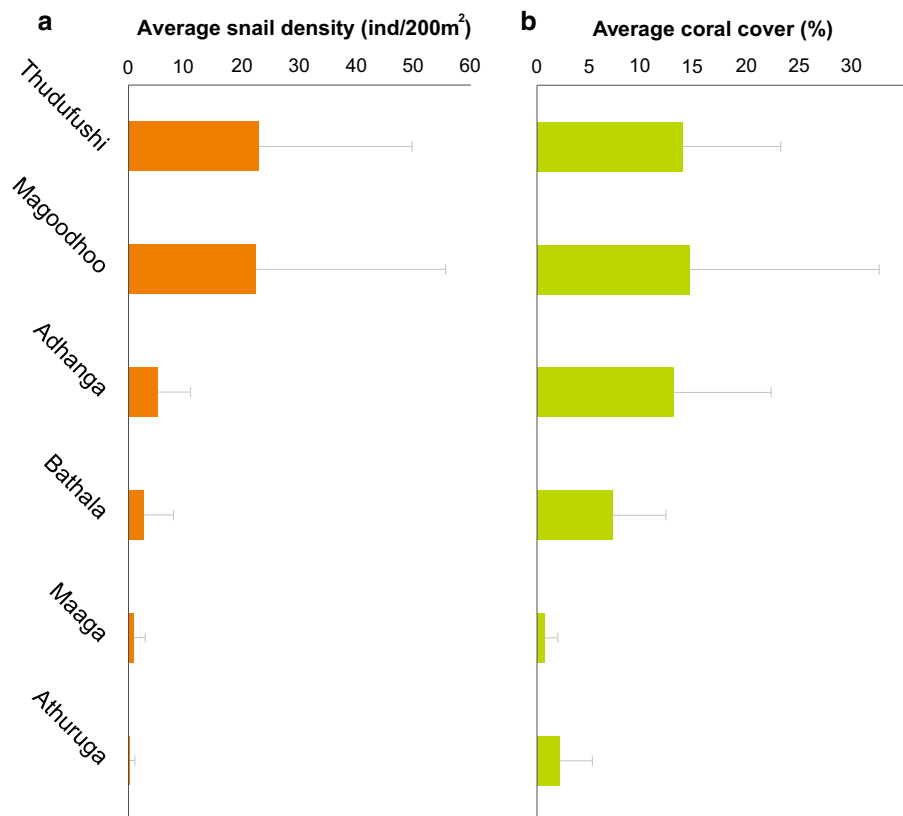
Fig. 5 Distribution of the percentage of aggregations following the number of individuals per aggregation
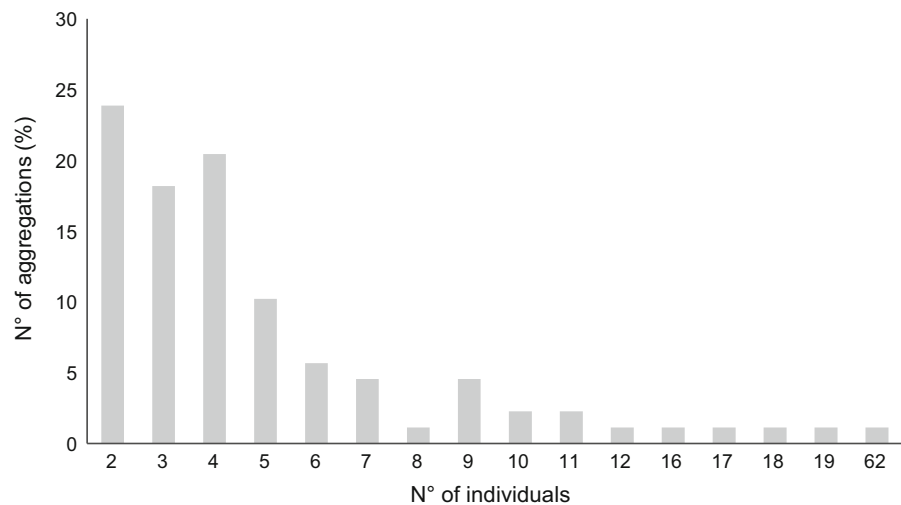
between Ari and Faafu Atoll ($U = 741.5$, $z = 1.103$, $P = 0.270$). Similarly, no significant differences were found comparing the density of individuals on the flat and the crest reef area ($U = 762$, $z = 1.351$, $P = 0.177$) and the comparison within flat and crest area in each location (U-test, $P > 0.05$ for all comparisons). Contrarily, at the location scale, the distribution of individuals varied significantly (Fig. 6a). Thudufushi, Magoodhoo and Adhanga presented the highest densities with 22.8 ± 26.9, 22.3 ± 33.3 and 5.25 ± 5.6 ind/200 m^2 respectively, while *Drupella* spp. occurrence was lowest in Athuruga with 0.25 ± 0.9 ind/200 m^2 (K–W, $P < 0.001$).

The data on coral cover, from 216 LIT pooled, showed that benthic coverage was mostly dominated by dead corals ($50.2\% \pm 29.9$) and coral rubble ($35\% \pm 30.4$) with alive coral coverage accounting for $8.6\% \pm 13.2$. Further, coverage of live coral was significantly different between locations (K–W, $P < 0.001$; Fig. 6b) with Magoodhoo, Thudufushi and Adhanga showing the highest values ($14.5\% \pm 18.1$, $13.9\% \pm 9.4$, $13.\% \pm 9.2$, respectively) and Maaga showing the lowest ($0.7\% \pm 1.3$).

Yet, there was a significant positive correlation between density of *Drupella* spp. and live coral coverage (Spearman's rho $\rho = 0.546$, $P < 0.001$), while, the number of genera in each location did not correlate significantly with the density of *Drupella* spp. (Spearman's rho $\rho = 0.771$, $P = 0.72$). Snail density was also negatively correlated with the presence of macroalgae (Spearman's rho $\rho = -0.330$, $P = 0.005$) and dead coral (Spearman's rho $\rho = -0.266$, $P = 0.024$). Furthermore, a significant regression equation was found ($F_{(1,70)} = 71.393$, $R^2 = 0.5049$, $P < 0.001$, Fig. 7) showing that around 50.5% of the variation in number of snails was explained by the variation in average coral cover per transect, across sites.

Discussion

Drupella spp. population structure

Size structure of the population surveyed revealed a dominant proportion of adults compared to juveniles

Fig. 6 **a** Data showing the differences in snail density for each location and **b** average coral cover in percentage for each location. Bars indicate standard deviation

Fig. 7 Relationship between number of snails and average coral cover per transect, across sites. The dotted line indicates the simple linear regression analysis
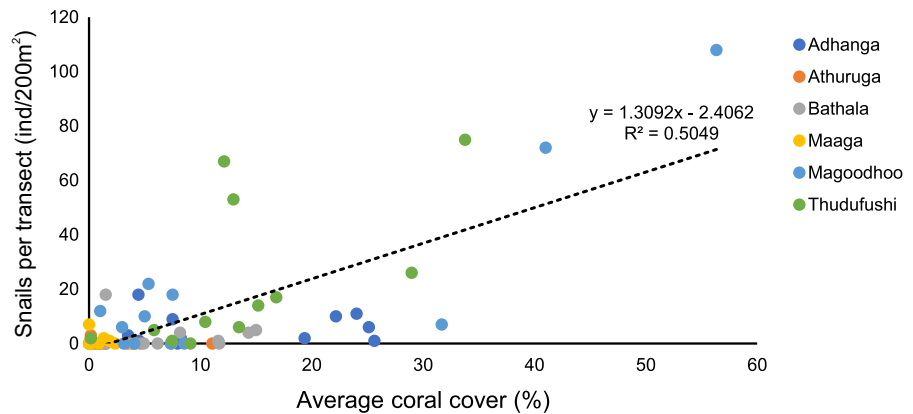
and recruits, with the presence of more than one generation as suggested by the dip test. In a scenario of limited resources, such as a decreased coral cover for food and shelter, aggregations may lead to intraspecific competition where size-dependent density tends to consist of the better competitors with large consequences on population dynamics (De Roos et al., 2003; De Roos & Persson, 2013). In this case, adults may be considered as better competitors dominating the resource and hence causing juvenile mortality (Nicholson, 1954; May et al., 1974; Furness & Birkhead, 1984). An additional explanation may be related to a lower rate of reproduction, as recruits were uncommon. Such limitations in reproduction may be caused by the reduction of substrate for egg capsule attachment. *Drupella* spp. lays egg capsules on the bare skeleton of corals (Sam et al., 2017; Scott et al., 2017a, b), but the reduction of prey presence and the increased competition with algae may lead to a reduction of space for the eggs and hence reduction in reproduction success.

Feeding behaviour

Drupella spp. was found feeding only on scleractinian corals which is in accordance with its ecology as an obligate corallivore (Morton et al., 2002; Rotjan & Lewis, 2008). Few individuals were found on dead corals and coral rubble, probably moving in search for corals following scars or conspecific cues (Morton et al., 2002; Hamman, 2018).

The snails were aggregated mostly on branching corals, particularly of the genus *Porites*, followed by *Pocillopora* and *Acropora*, which also reflects the general prey preferences in the study area, apart from

the genus *Porites* which resulted a random choice. In this study, looking at location scale, *Drupella* spp. feeding preferences changed following coral cover, with preference for *Porites* in locations with low coral cover such as Athuruga and Maaga, while *Acropora* and *Pocillopora* were preferred in locations with higher coral cover such as Thudufushi and Magoodhoo. It is known that acroporids are the favourite prey of *Drupella* spp. (Moyer et al., 1982; Fujioka & Yamazato, 1983; Turner, 1994a, b; Cumming, 1999; Morton et al., 2002; Al-Horani et al., 2011), however, prey preferences may change according to the availability of corals. In Thailand, *Drupella* spp. was reported to shift from acroporids to fungiid corals following a temperature-induced coral mortality event (Hoeksema et al., 2013; Moerland et al., 2016). Also, in the Maldives, the snail was found extending the prey range from *Acropora* and *Pocillopora* to more than 10 genera, including *Porites*, in the aftermath of the 2016 bleaching event (Bruckner et al., 2017). However, we found the snail occupying only five coral genera, likely due to the highest mortality of other genera which may have different susceptibility to heat waves (Pisapia et al., 2016, 2019) and the slower recovery from the mortality event (Pisapia et al., 2016).

Spatial distribution

The population of *Drupella* spp. was monitored and documented around 2 years after the 2016 large scale coral bleaching event. In this study, the total mean density of *Drupella* spp. was much lower than in other studies (e.g. Ayling & Ayling, 1987; Turner, 1994a, b; Al-Moghrabi, 1997; Cumming, 1999, 2009a, b;

Bruckner et al., 2017). Notably, it was around 70-fold less than the density reported by Bruckner et al. (2017), in South Malé Atoll in 2016 (0.045 ind/m^2 in this study, against 3.4 ind/m^2 from Bruckner et al., 2017). This result suggests a possible collapse of *Drupella* spp. population in the aftermath of the bleaching event. Furthermore, no outbreak was reported as the mean density never exceeded the outbreak threshold of > 2 ind/m^2 defined by Cumming (2009a, b). Mean density was lower than the level of 0.62 ind/m^2 suggested by Bessey et al. (2018) as the density beyond which consumption of prey is faster than its growth rate (specifically for *Acropora spicifera*).

Although not in outbreak, the population showed the presence of mainly small aggregations, most of which were found in locations (Magoodhoo and Thudufushi) with the highest coral cover. These sites also had the largest snails observed during the study. Such findings is in accordance with the theory of optimal foraging, which predicts that predators will aggregate most likely in areas with high prey density (see Cumming, 2009a). Generally, the number of aggregations and the individuals per aggregation were lower compared to other studies (Cumming 2009a, b) and especially compared to the findings of Bruckner et al. (2017) who reported aggregations of up to 250 individuals on a single coral colony in South Malé Atoll, Maldives.

It is possible that the population of *Drupella* spp. has decreased compared to the findings of Bruckner et al. (2017). The reduction in live corals caused by the bleaching event in 2016 may have influenced population dynamics of the snail which uses coral colonies as food and shelter (e.g. Ayling & Ayling, 1987; Hamman, 2018). On the other hand, there is evidence that coral predators showing dietary plasticity, like other gastropods and fishes, may prey more heavily on remaining corals (see Pratchett et al., 2004; Cole et al., 2009; Hoeksema et al., 2013; Tsang & Ang, 2014; Zambre & Arthur, 2018). Thus, even if the population was apparently decreased, the dietary plasticity may have pushed the snails to aggregate on remaining corals, increasing local predation pressure. *Drupella* spp. may have even moved to deeper areas of the reef looking for live corals, since the shallow reef was more exposed to the bleaching event, and thus may have had the highest coral mortality (Pisapia et al., 2016, 2019), although more research is needed to

clarify this aspect. Additionally, in response to temperature-induced coral mortality, the snails may be more exposed to predators (Hamman, 2018) and to population decline as also reported for other obligate corallivores such as the coral-dwelling crab *Trapezia cymodoce* (Herbst, 1801) (Stella et al., 2011), butterflyfish (Graham et al., 2009), the filefish *Oxymonacanthus longirostris* (Bloch and Schneider, 1801) (Hobbs et al., 2010) and other coral-dependent fish (Booth & Beretta, 2002).

The snail was homogeneously distributed along the surveyed area at atolls (Ari and Faafu) and the reef scale. Contrarily, differences were found when comparing localities, likely because coral cover was differently affected by coral bleaching in 2016 in different localities (Pisapia et al., 2019). Generally, the density of *Drupella* spp. was higher in locations with higher coral cover, such as in Magoodhoo and Thudufushi, independently from the number of genera. The variability in *Drupella* spp. density was probably due to the plasticity in shifting feeding preferences according to the availability of coral genera.

Drupella spp. is likely to reduce resilience of live corals when acting synergically with other stressors, including temperature-induced mortality, diseases, pollution or other corallivores (e.g. Nicolet et al., 2013, 2018; Bruckner et al., 2017; Scott et al., 2017a, b; Shaver et al., 2018). In addition, co-occurrence of *Drupella* spp. with other corallivores was noted during an ongoing survey (pers. comm.) looking at the presence of three major corallivores in Maldives after the bleaching event in 2016 (the seastars *Acanthaster planci* and *Culcita* spp. and the gastropod *Coralliophila* spp.).

In this study, we showed that 2 years after the coral mortality event, the influence of *Drupella* spp. may be considered lower, possibly due to the collapse of the population. Furthermore, the majority of the corals preyed upon were only partially damaged ($< 50\%$) at the time of the surveys, indicating a lower effect on coral cover. In this condition, the presence of coral guards such as *Trapezia cymodoce* (Samsuri et al., 2018) or the presence of deterring hydrozoans (Montano et al., 2017) may also reduce the predatory pressure, although further research is needed to verify this mechanism. In addition, no coral recruits were preyed upon, despite their presence, indicating that reef recovery is on-going.

Conclusions

Drupella spp. showed a large-scale homogeneity in density and only showed variation dependent on coral cover at the site scale. The population collapsed and showed less aggregations around 2 years after the coral bleaching event in the study area, compared to previous reports in the Maldives. The consequent reduction in predatory pressure may enhance Maldivian reefs resilience, unless other factors will threaten coral survival. Further research should focus on larger geographical areas, including other atolls both in the north and in the south of Maldives and expand to deeper areas of the reef to have a better overview of the snail's spatial distribution. In addition, snail behaviour should be monitored including reefs with pre-bleaching coral cover to clarify the predatory activity and quantify the impacts with a focus on the co-occurrence with other corallivores in the Maldives.

Compliance with ethical standards

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