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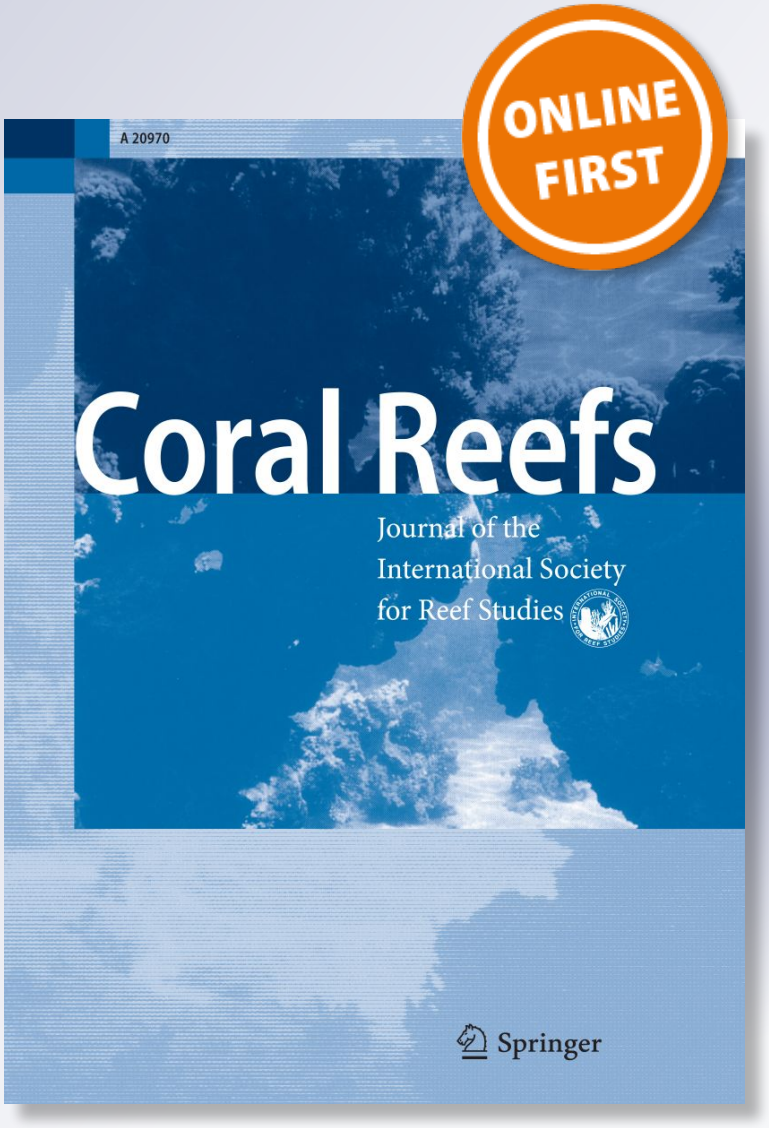

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REPORT

Outbreak densities of the coral predator *Drupella* in relation to in situ *Acropora* growth rates on Ningaloo Reef, Western Australia

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Abstract Outbreaks of coral predators are defined as increases (often rapid) in their abundance above threshold densities that can be sustained by local coral assemblages, which in turn depends on the abundance and turnover of coral prey. To investigate the outbreak densities of the corallivorous gastropod *Drupella cornus,* we conducted both in situ feeding and coral growth experiments at Mandu reef within the Ningaloo Marine Park, Western Australia. Over two 10-day periods, we tagged and photographed feeding scars on colonies of the tabulate coral *Acropora spicifera* that harboured *Drupella* feeding aggregations. We calculated a mean in situ *Drupella* consumption rate of 1.16 ± 1.1 cm^2 coral area $individual^{-1}$ · d^{-1}. We also determined coral growth rates by tagging and photographing 24 colonies of *Acropora spicifera* at time zero and then again 1 year later. We calculated a mean linear extension rate of 7.9 ± 3.7 cm yr^{-1} for actively growing *Acropora spicifera*, which we then used to estimate *A. spicifera* growth rates over a range of coral cover values. This combination allowed us to determine the maximum number of *Drupella* that could be sustained across a range of coral cover. Our data suggest that the outbreak density of *Drupella* at the average level of coral cover for back reef sites at Mandu reef (17.6 ± 13.7%) is approximately 0.95 individuals m^{-2} reef area. At the maximum coral cover observed at Mandu reef (60%), the outbreak density of *Drupella* is estimated to be approximately 2.83 individuals m^{-2} reef area. Establishing *Drupella* outbreak densities assists managers in predicting possible outbreak abundances and in monitoring coral reef health.

Keywords Ningaloo Marine Park · Western Australia · Management · Coral growth · Consumption rate

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Introduction

Drupella is a genus of marine gastropods (Family Muricidae) that feeds almost exclusively on the living tissue of corals (Robertson 1970; Claremont et al. 2011). These generalist corallivores occur throughout the shallow waters of the Indo-Pacific (Claremont et al. 2011). However, excessive densities (outbreaks) of corallivores can result in dramatic and widespread decline in coral cover (Pratchett et al. 2014; Babcock et al. 2016). Outbreaks are defined as increases (often rapid) in the abundance of coral predators above threshold densities that can be sustained by local coral assemblages, which in turn depend on the abundance and turnover of coral prey.

Outbreaks of the coral predator *Drupella* are associated with high coral mortality (Moyer et al. 1982; Fujioka and Yamazato 1983; Ayling and Ayling 1987; Turner 1994; Antonius and Reigl Antonius and Riegl 1997; Shafir and Gur 2008; Cumming 2009a). In Japan, coral degradation

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was associated with large aggregations of *Drupella*, where densities of *Drupella* spp. (mainly *D. fragum*) reached 5.12 individuals m^{-2} (Moyer et al. 1982; Fujioka and Yamazato 1983). In the Red Sea, densities of *D. cornus* were more than 200 individuals per 30-cm-diameter coral colony on multiple genera, resulting in 100% coral mortality at the study site; the southern end of a 150-m artificial limestone quay (Shafir and Gur 2008). Similarly, correlations between declining coral cover and increasing frequency of *D. cornus* had also been observed in the Red Sea by Antonius and Riegl (1997), who reported average densities of up to 12.24 *Drupella* m^{-2} (Al-Moghrabi 1997). On Ningaloo Reef, in Western Australia, *D. cornus* densities of up to 19.4 m^{-2} have been associated with a 75% reduction in coral cover (Ayling and Ayling 1987; Turner 1994). Corals form the basic reef structure that provides habitat for a myriad of organisms, including economically important, iconic, and endangered species. Understanding the densities of *Drupella* that can be sustained based on coral cover and growth is essential information required to help managers monitor and predict possible outbreak abundances.

Drupella feeding rates are a key component in calculating the outbreak densities of *Drupella* that can be sustained by a coral community. Although *Drupella* can forage on a range of coral morphologies (branching, tabulate, massive and encrusting) and genera (*Acropora*, *Astreopora*, *Fungia*, *Millepora*, *Montipora*, *Pavona*, *Pocillopora*, *Porites*, *Seriatopora,* *Stylophora*, and *Turbinaria*) using a specialised radula for scraping (Fujioka and Yamazato 1983; Ayling 2000; Shafir and Gur 2008; Hoeksema et al. 2013), they display a strong preference for the acroporids (mainly *Acropora* and *Montipora*; Boucher 1986; Turner 1994; Cumming 1999; Schoepf et al. 2010; Moerland et al. 2016). *Drupella* tend to create discrete feeding scars and feed at the interface between live and dead corallites during both day and night (although predominantly at night) and show an attraction to stressed or damaged coral (Forde 1992; Turner 1994; Morton et al. 2002; Bruckner et al. 2017). Field experiments report *D. cornus* moving more than 2 m overnight to aggregate on damaged coral, potentially detecting prey species through species-specific chemical substances (Kohn 1961; Turner 1994; Kita et al. 2005). Aquarium experiments estimate *D. cornus* feeding rates at 2.3 cm^2 of coral $individual^{-1}$ d^{-1}, where the average-sized *Drupella* was 28–35 mm (Cumming 2009b) and coral tissue was measured as the total surface area by the paper wrapping method. A 28-mm-long *D. cornus* at Ningaloo Reef is estimated to be between 2.5 and 3.5 years old and reproductively mature (Black and Johnson 1994). *Drupella* coral consumption rates determined in the laboratory are based on measurements of vertical surfaces on branching corals, which are difficult to relate to field monitoring data of coral cover. Furthermore, little is known about in situ *Drupella* feeding rates.

Growth of the preferred prey of *Drupella* is another essential component in calculating the outbreak densities of *Drupella* that can be sustained by the coral community. The growth rates of acroporids, the preferred prey of *Drupella*, can vary depending on growth form, species, and local environment, as well as the method used to quantify their growth (Pratchett et al. 2015; Drury et al. 2017). Obtaining a measure of growth requires direct quantification of colony linear dimensions, area, volume, or weight, taken at various time increments to calculate a time-averaged rate of growth (Pratchett et al. 2015). Linear extension, measured as a change in colony radius over a year, is a common metric of coral growth. There are relatively few studies of coral growth rates in Western Australia. Annual linear extension rates for *Acropora spicifera* are reported as 12.4 ± 1.4 cm at Ningaloo Reef (western side of the North West Cape) and 10.5 ± 1.2 cm at Bundegi Reef, which is located within the Exmouth Gulf on the eastern side of the North West Cape (Stimson 1996). Annual coral growth ranged from 7.3 to 14.6 cm for the closely related species *Acropora hyacinthus* in the Dampier Archipelago (Simpson 1988). Ideally this growth should be expressed as projected surface area, since photographic monitoring of coral typically uses percent cover (e.g. Speed et al. 2013). While linear extension rates may be a more accurate representation of colony growth, these are difficult to determine outside of a controlled laboratory environment and are not typically used in large-scale monitoring programmes.

The goal of our study was to determine the outbreak densities of *Drupella* that can be sustained by a coral community, based on coral cover and growth, in order to help managers predict possible outbreak abundances. We conducted our study in the Ningaloo Marine Park, Western Australia, where previously reported *Drupella* outbreaks have been associated with substantial declines in coral cover (Turner 1994). The purpose of our study was to (1) determine the percent cover of *Drupella* prey (hard coral and preferred prey species *Acropora spicifera*), (2) determine *Drupella* density, (3) determine in situ *Drupella* feeding rates on *A. spicifera*, (4) measure in situ growth rates of *A. spicifera,* and (5) develop estimates of the maximum sustainable density of *Drupella* for maintenance of net coral growth over a range of coral cover, thereby quantifying a *Drupella* outbreak density for Ningaloo Reef.

Materials and methods

We conducted in situ *Drupella* feeding and *Acropora* growth experiments on the back reef near the reef flat margin at Mandu reef (22°03′14.11″S; 113°53′47.80″E) in the Ningaloo Marine Park, located along the north-west coast of Western Australia (Fig. 1). We also determined percent cover of hard coral, and specifically, percent cover of the most abundant coral species within the study area, using pre-existing data from benthic and invertebrate surveys.

Benthic and invertebrate surveys have been conducted annually on 16 back reef sites at Mandu reef most years since 2007. Benthic surveys consisted of two 25-m-long photographic transect lines (English et al. 1997) at each site. Photographs were taken (Canon Powershot G16) every 50 cm along the transect line, at a height of 0.7 m above the substrate (area of photograph is ~ 0.5 × 0.7 cm). To avoid non-independence, 30 randomly selected photographs from each transect were processed using the TransectMeasure (http://www.seagis.com.au) software package. Six fixed points were overlaid on each photograph and the benthic category (rock, rubble, sand, silt, hard coral, algae) underlying each point was recorded (Jonker et al. 2008). Hard coral were further identified to genus or species level and growth morphology using relevant identification texts (Veron 1986). Hard coral cover percent was calculated for all back reef sites at Mandu reef, as well as percent cover of the most abundant coral species. Invertebrate surveys were also conducted along a 5 × 1 m section of the benthic survey transects. Each section was searched for all invertebrates (> 5 mm) and the species were identified and counted, including that of *Drupella*. This method was slightly altered in 2013 onwards to consist of 1 × 1 m quadrats at 5-m intervals along each transect.

Drupella feeding experiments were conducted on 29 coral colonies over two 10-day periods (25 of October 2014 to 4 November 2014; $n = 15$, and 8 to 18 March, 2016; $n = 14$). We tagged, photographed (day 1), and re-photographed (day 10) coral colonies of *A. spicifera* that showed visible signs of *Drupella* feeding (scars), and

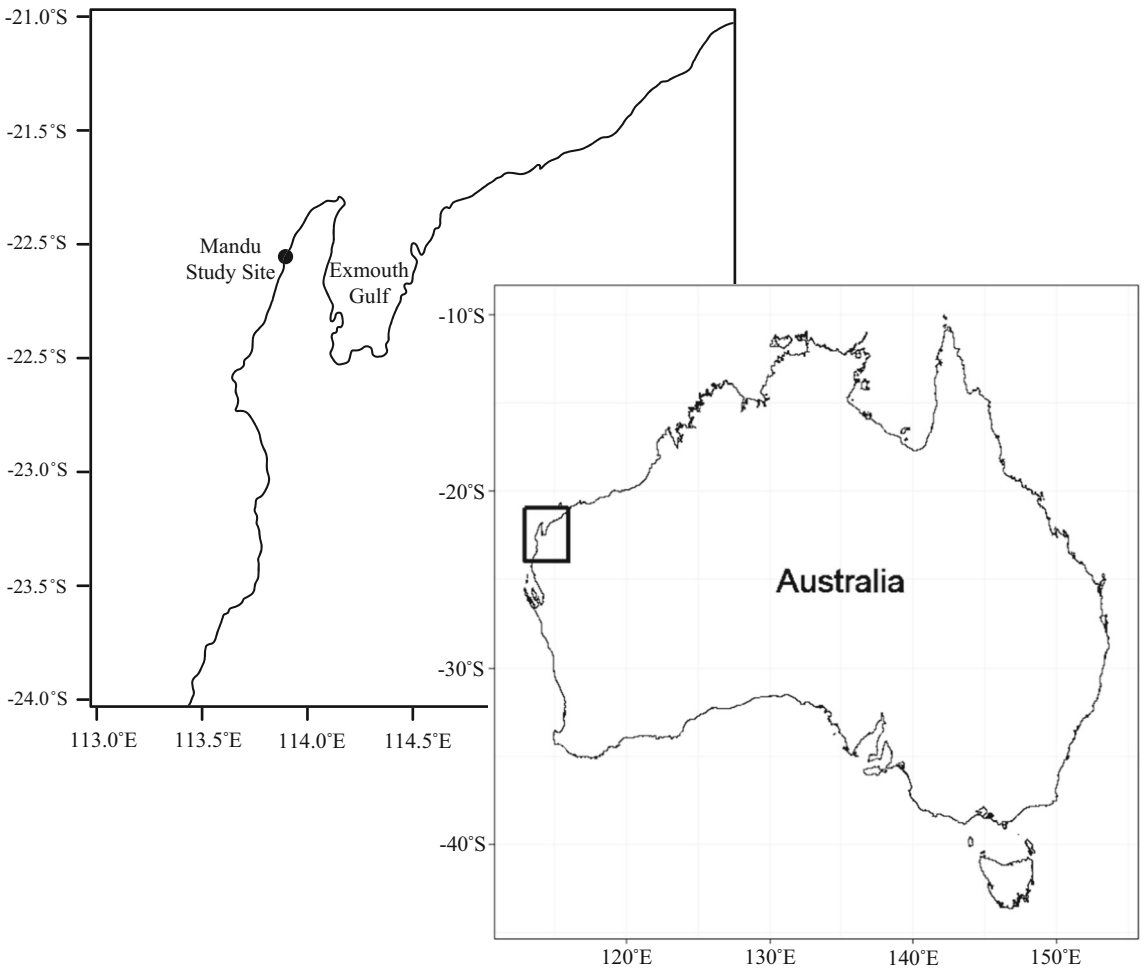

Fig. 1 Location of the study site within the Ningaloo Marine Park, north-west of Western Australia

contained multiple *Drupella* (> 1) on or under the coral colony. Targeting coral colonies with multiple *Drupella* and discrete feeding scars maximised the probability that any tissue loss was due to their feeding behaviour. *Drupella* are generally concealed around the coral base during the day, and emerge at night to feed on living tissue (Turner 1994). The quantity and size class (5-mm increments from 20 to 45 mm) of *Drupella* were determined on day 10 to avoid disturbing the feeding behaviour of the gastropods. Each coral colony was thoroughly searched for all *Drupella*, which were individually removed from the colony by hand and measured.

To determine *Acropora spicifera* growth rates, we used a total of 24 initially healthy (without feeding scars) coral colonies. These colonies were tagged and photographed from a top-down perspective (2014, $n = 11$; 2016, $n = 13$), then re-photographed more than a year later (490 and 372 d, respectively). All corals were tagged with an 8 cm × 3 cm uniquely numbered metal tag, which allowed for identification and provided a scale bar. In instances where the tag had become highly overgrown, as was the case for the growth experiments, the tag was scraped to reveal its number, and an additional scale bar was included in the photographs (30-cm ruler wrapped with black electrical tape at two 10-cm intervals; 0–10 cm and 20–30 cm).

Coral photographs were used to determine colony areas required in calculations. Photographs were analysed using open-source ImageJ software (Schneider et al. 2012) to determine (1) initial surface area of live coral for each tagged coral colony, (2) surface area of dead coral on day one and day 10 for *Drupella* feeding experiments (Fig. 2a, b), (3) linear extension rate of *A. spicifera* colonies (Fig. 2c, d) and (4) final surface area of live coral after 1 year for *A. spicifera* growth observations (Fig. 2d). The known dimensions of the metal tag (or ruler) acted as a scale bar and was used to standardise area by pixels in each photograph. A freehand polygon was then drawn around the area of interest, and a measurement of surface area (cm^2) was obtained. We determined *Drupella* consumption rates using the following equations:

$$\text{Total area consumed}_i\left(\text{cm}^2\ \text{d}^{-1}\right) = \frac{\left(\text{area}_{t2} - \text{area}_{t1}\right)}{10\,\text{d}} \quad (1)$$

$$\text{Drupella consumption rate}_i\left(\text{cm}^2\ \text{individual}^{-1}\ \text{d}^{-1}\right) = \frac{\text{total area consumed}}{\sum \text{Drupella}} \quad (2)$$

where i = each coral colony surveyed, t_2 = day 10, and t_1 = day 1.

We estimated *A. spicifera* growth rates over a range of coral cover values. First, we determined linear extension rates for each *A. spicifera* colony by averaging three measurements of radial growth (Fig. 2). Next, to estimate annual growth in colony area for corals at different densities of overall coral cover, we assumed a community dominated by *A. spicifera* and composed of different-sized circular colonies (5, 10, 20, 100, and 200 cm diameter) at increasing densities (0.1 to 3 m^2). Population size structure was based on the size structure of *A. spicifera* observed in Mandu back reef habitats. Total annual increase in live colony area was calculated as:

$$\text{Total annual increase}_i\left(\text{cm}^2\text{year}^{-1}\right) = \left(\pi(r_{t_0} + x)^2 - \pi r_{t_0}^2\right) \quad (3)$$

where i = each coral colony, r = radius of the coral colony at time t_0, and x = linear extension rate.

These colony growth rates were then summed across the population to estimate the total increase in coral area. The number of colonies in each size class was varied randomly around the seed size class distribution in a Monte Carlo simulation ($n = 1000$) using PopTools Microsoft Excel macro (http://www.poptools.org/), and the mean growth and 95% confidence intervals were estimated. This process was repeated for different levels of coral cover from 4 to 100% to provide estimates of increase in net cover for coral populations across the range of cover values.

Results

Acropora is the dominant coral genus at Mandu reef, and *Acropora spicifera* is the dominant tabulate *Acropora* within the study location (Table 1; Cassata and Collins 2008). *Acropora spicifera* colonies often have irregularly divided plates, with pale borders, and are distinguished from *A. hyacinthus* (Dana 1846), which have smaller and finer branchlets, and from *A. dendrum* (Gassett-Smith 1890), which have prominent corallites and less plate-like colonies (Veron 1986). The average percent cover of hard coral, and specifically *A. spicifera*, at Mandu reef between 2007 and 2016 was 17.6 ± 13.7% (mean ± SD), and 10.0 ± 11.4%, respectively. The minimum and maximum hard coral cover at Mandu reef was 0% and 60%.

In our *Drupella* feeding experiments, we monitored a total of 29 *A. spicifera* colonies which contained 454 *Drupella* individuals with a mean length of 34 mm. A significant positive relationship exists between the number of *Drupella* in a feeding aggregation and the two-dimensional area of coral consumed ($R^2 = 0.48$, $p \leq 0.001$, Fig. 3). The maximum, mean and minimum number of *Drupella* on the coral colonies were 57, 14 and 2, respectively. We calculated a mean individual *Drupella* consumption rate of 1.16 ± 1.1 cm^2 of coral area d^{-1}.

In our growth experiments, we monitored a total of 24 tabulate *Acropora spicifera* colonies, of which 13 showed

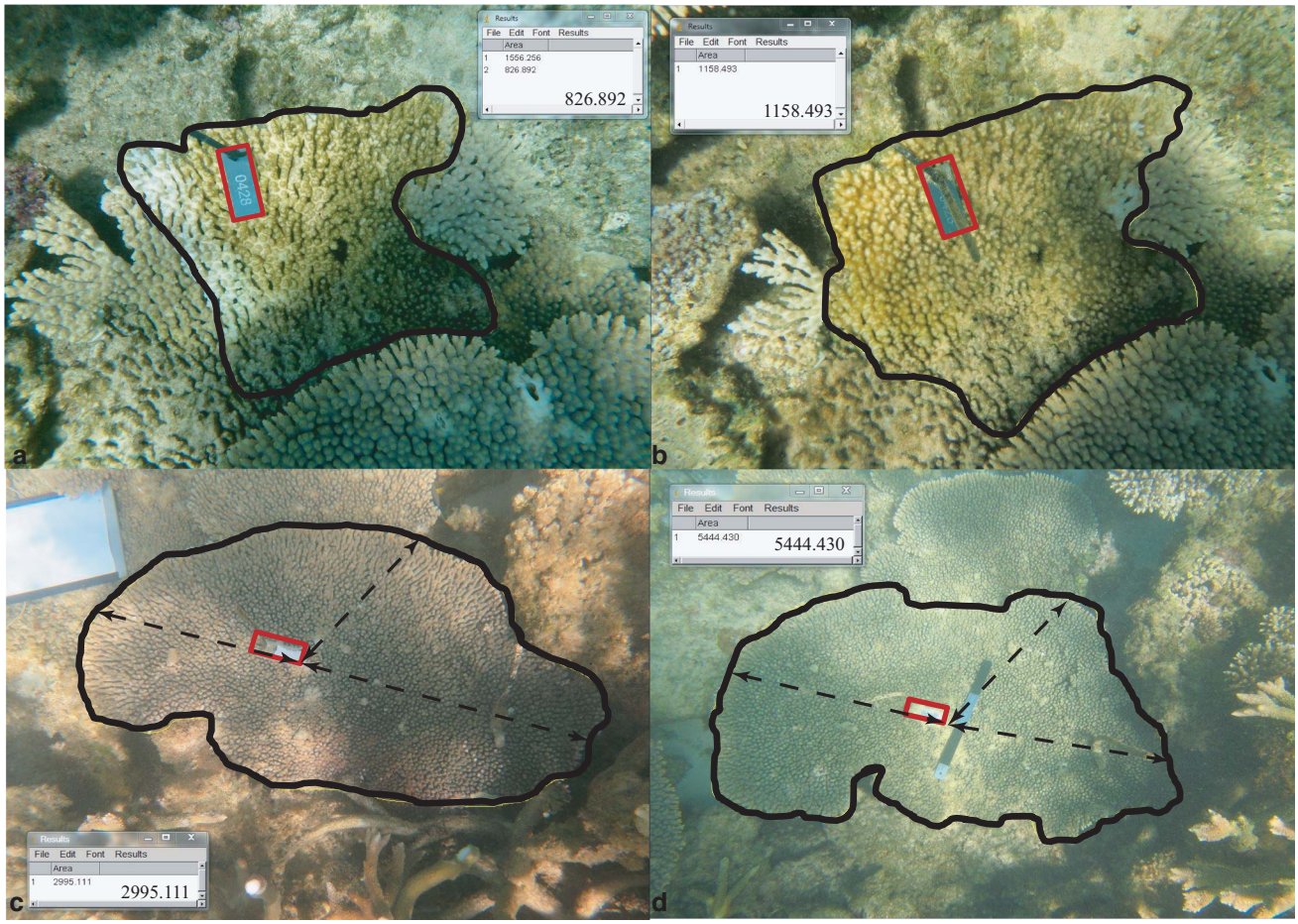

Fig. 2 Determination of dead coral area (cm^2) on day 1 (**a**) and day 10 (**b**) for coral colony #428 observed with multiple *Drupella* (3 × 25 mm, 10 × 30 mm, 5 × 35 mm) under the colony (feeding studies), and the area of live coral for coral colony #427 on day 1 (**c**) and day 372 (**d**) for growth studies. Thick black lines denote the area of coral measured, with ImageJ results inlaid. Inlaid results in (**a**) also contain a measure of total coral colony area. An 8 cm × 3 cm unique identification tag (thick red line) was used to standardise area by pixels in each photograph. Dashed lines denote measurements of radial growth used to obtain linear extension rate

Table 1 Percent cover of hard coral and *Acropora spicifera*, as well as density of *Drupella* measured on Mandu back reef sites from 2007 to 2016

Year	Hard coral cover % (mean ± SD)	*Acropora spicifera* cover % (mean ± SD)	*Drupella* density (mean m^{-2} ± sd)
2007	22.7 ± 14.3	10.8 ± 10.7	0.14 ± 0.29
2008	19.2 ± 13.5	11.7 ± 10.1	0.60 ± 0.40
2009			0.46 ± 0.31
2010			0.23 ± 0.55
2011	18.1 ± 14.4	9.4 ± 9.8	
2013	18.8 ± 13.1	11.2 ± 11.4	
2014	16.0 ± 12.8	8.8 ± 10.6	
2015	14.3 ± 13.2	9.6 ± 12.6	
2016	21.5 ± 14.3	10.2 ± 13.6	0.34 ± 0.68
Grand total	17.6 ± 13.7	10.0 ± 11.4	0.35 ± 0.45

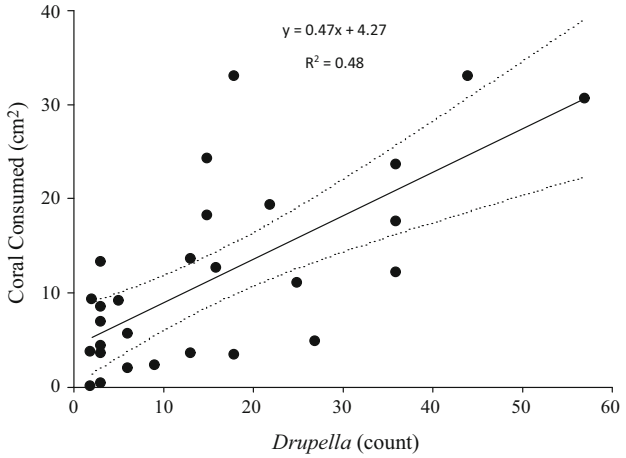

Fig. 3 *Drupella* consumption rates. Total area of *Acropora spicifera* colonies consumed by *Drupella* feeding aggregations of varying sizes, with regression (solid line) and 95% confidence intervals (dashed lines)

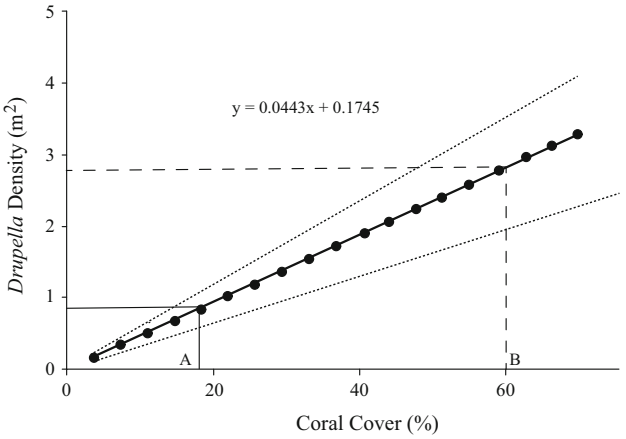

Fig. 4 Outbreak densities of *Drupella cornus*. Outbreak density of *Drupella* as a function of net coral growth over a range of coral cover values. Estimates are based on modelled *Acropora spicifera* growth rates and mean *Drupella* consumption rates (mean relationship represented by thick black line with circles; dotted lines represent 95% confidence interval). Outbreak densities at average (**a**: solid line) and maximum (**b**: dashed line) coral cover for Mandu reef sites on Ningaloo Reef

positive growth and were used to determine growth rates (mean colony size 2783 ± 1168 cm^2). The remaining unused colonies were dead (n = 6), dying/shrinking (n = 4), or appeared healthy but showed no measurable growth (n = 1). In particular, during re-photographing in 2017, there was evidence of two tagged colonies having brown band disease with an additional four colonies in close proximity also showing signs of disease (black lesions). Some of the unused coral colonies had been overturned, but none of these appeared to have active *Drupella* feeding aggregations. We calculated a mean *Acropora spicifera* extension rate of 7.9 ± 3.7 cm yr^{-1}. The average maximum extension rate observed was 12.6 cm yr^{-1}, but the single highest measurement was 20 cm in 1 yr. The combined total area of the tagged corals declined over the monitoring periods due to the complete or partial mortality of some colonies.

Estimates of total growth in coral cover were based on our linear extension rates of actively growing colonies. As total coral cover increased so too did the ability of the coral populations to add area. As a result, the number of *Drupella* that could be supported increased, as did the number that would be required in order to consume coral faster than it could re-grow (Fig. 4). The density of *Drupella*, above which there was net coral loss (outbreak threshold), was determined as the tipping point between net coral growth and net coral consumption over a range of coral cover. The average hard coral cover at our study site was 17.6%, and at this coral cover as few as 0.95 *Drupella* individuals m^{-2} reef area would represent an outbreak density (Fig. 4a), while at the highest observed levels of coral cover (60%), the outbreak densities would be 2.83 *Drupella* individuals m^{-2} (Fig. 4b). The average percent cover for *A. spicifera* at Mandu reef was 10.0%, which indicates that an even lower density of *Drupella* (0.62 individuals m^2) would be required for an outbreak on preferred coral species.

Discussion

Predicting *Drupella* outbreak densities requires information on the density of *Drupella*, as well as growth and cover estimates of coral prey. The densities of *Drupella* reported following outbreaks in Israel, Japan, and Australia range from 5.1 m^{-2} to over 19.4 m^{-2}, with all resulting in substantial coral mortality (Moyer et al. 1982; Fujioka and Yamazato 1983; Ayling and Ayling 1987; Turner 1994; Antonius and Reigl (1997; Shafir and Gur 2008; Cumming 2009a). Here, we show that *Drupella* abundances greater than 0.62 m^{-2} reef area could consume their preferred prey species faster than these corals grow, thereby resulting in erosion of *A. spicifera* coral cover at densities typical of Ningaloo Reef (Fig. 4). Importantly, if abundances of *Drupella* greater than this threshold are sustained over sufficiently large temporal and spatial scales, a net loss to *A. spicifera* could ensue. While previous reports of *Drupella* density on Ningaloo Reef are above the current outbreak density (1.4 ± 1.68 m^{-2}; Armstrong 2009), coral cover on northern and central reefs at Ningaloo Reef were also increasing over that time (Speed et al. 2013). Current densities of *Drupella* on back reefs at Mandu are 0.34 ± 0.68 m^{-2}, but have been reported as high as 0.60 ± 0.40 m^{-2} during 2008 (Table 1). On the Great Barrier Reef, Australia, *Drupella* abundance (for all species combined; *D. cornus*, *D. fragum*, and *D. rugosa*)

typically ranges from 0 to 2 m^{-2}, and no known outbreaks have been recorded (Cumming 2009a).

We determined a mean in situ *Drupella* consumption rate of 1.16 ± 1.1 cm^2 on *A. spicifera* coral cover individual^{-1} d^{-1}. A 1987 preliminary in situ study conducted on Ningaloo Reef reported *Drupella* feeding rates of 2.5 cm^2 individual^{-1} d^{-1} based on surveys of *Acropora* plates over a 7-day period using similar photographic methods (Ayling 2000). Aquarium studies report a similar mean *D. cornus* consumption rate of 2.3 cm^2 individual^{-1} d^{-1}, ranging from 1.79 to 3.36, where the average length of *Drupella* was between 28 and 35 mm (Cumming 2009b). However, these rates were based on total tissue area rather than two-dimensional projected area as in our study. Laboratory studies showed that *D. cornus* grazing rates were positively correlated with seawater temperature, ranging from 0.27 ± 0.11 cm^2 individual^{-1} d^{-1} at 18 °C to 1.31 ± 0.19 at 30 °C, but showed no significant difference in grazing rate in relation to body size (Al-Horani et al. 2011). Consumption rates similar to those reported for *Drupella* have also been reported for another coralllivorous gastropod, *Coralliophilia galea* (Dillwyn 1823). These gastropods show a mean *Acropora* tissue consumption rate of 1.9 cm^2 individual^{-1} d^{-1}, but with a maximum rate of 6.5 cm^2 individual^{-1} d^{-1} in the Caribbean (Bruckner et al. 1997), and an estimated long-term feeding rate of 1.07 cm^2 snail^{-1} d^{-1} for an average 29-mm snail (range: 0.44 to 3.28) in Florida (Baums et al. 2003).

There are a number of important caveats to the outbreak density estimates we present here. While we have measured feeding in > 400 *Drupella* individuals over two separate time periods, actual rates of feeding may be higher or lower than those that we have measured. Published estimates (Ayling 2000; Cumming 2009b) of *Drupella* feeding rates were based on different coral prey species and used quite disparate methods (habitat photographs vs paper wrapping), which are probably not directly comparable. However, if taken at face value, the published estimates of *Drupella* consumption rates would result in an outbreak density around half the level of those presented in this study. It is also important to note that coral communities consist of an array of coral morphologies and species, all of which can result in consumption rates that are different to those of a preferred prey species such as members of the family Acroporidae (Al-Horani et al. 2011).

We determined a mean in situ *Acropora spicifera* extension rate of 7.9 ± 3.4 cm yr^{-1}, with a maximum of up to 20 cm yr^{-1}. Our growth rates are nevertheless slower than those previously observed for *Acropora spicifera* within the Ningaloo Marine Park (annual linear extension of 12.36 ± 1.41 cm at the south central region of the park and 10.52 ± 1.17 cm at Bundegi; Stimson 1996). Indeed, the maximum average rate observed in our current study coincides with the mean growth rate reported for Bundegi. Growth rates reported in our study are more similar to those reported for *Acropora hyacinthus* in the Dampier Archipelago (annual linear extension of 7.3 to 14.6 cm; Simpson 1988), as well as on the Great Barrier Reef (annual linear extension of 0 to 12.5 cm; Pratchett et al. 2015). The reason for high growth rate variability in our study is unclear, although high spatial and temporal variability in coral growth rates is well documented in other locations and attributed to interspecific growth variation as well as light, water quality (e.g. turbidity), temperature and aragonite saturation state (Pratchett et al. 2015). Since tabular *Acropora* species are among the fastest growing of all corals, our estimates of carrying capacity and outbreak densities are likely to be somewhat conservative.

Multiple factors, such as competition, predation, disease, mechanical stability, and disturbances, can all simultaneously limit colony growth (Madin and Connolly 2006; Madin et al. 2014; Pratchett et al. 2015; Drury et al. 2017; Shaver et al. 2017). Although we used idealised coral assemblages that did not suffer mortality and damage to estimate outbreak densities, we found evidence that both disease and disturbance limited the growth of tagged coral colonies in the current study. Consequently, the estimates of outbreak densities are likely to be lower than our idealised estimates. Coral cover on the back reef habitats adjacent to our study site have declined from 2007 to 2015 (22.7 ± 14% to 14.3 ± 13%), but were slightly higher in 2016 (21.5 ± 14%). During this time, the average density of *Drupella* has never exceeded levels that would constitute an outbreak as we have calculated it here. Thus the mean in situ *Drupella* consumption rate determined by our study is consistent with existing data, which do not support a predation-driven decline in overall cover. The observed variability in coral cover is consistent with previously reported dynamic stability of coral communities in northern Ningaloo Reef (Speed et al. 2013). Our estimates are based on standard photographic techniques used to assess community coral cover in broad-scale surveys and can therefore be used more directly in assessing outbreak densities than can data derived from laboratory studies.

Outbreak densities of *Drupella* result in abundances that cannot be sustained by the local coral assemblage. Our study estimates that these outbreak densities are substantially lower than previous conclusions that non-outbreak *Drupella* densities range from 0 to 2 m^{-2} reef area (Cumming 2009a). Cumming (2009a) observed that the majority (69%) of studies reported *Drupella* densities as less than 3 m^{-2}, and that reports of densities > 3 m^{-2} were from outbreak populations. Our current study has been based on a series of highly conservative estimates of feeding rate, and coral growth rates. Consequently, there is a possibility that our outbreak density estimates are upper

estimates and higher than may be required to result in net declines in coral cover.

Understanding the densities of *Drupella* that can be sustained based on location-specific coral cover and growth is essential information required to help managers monitor and predict possible outbreak abundances. Such outbreak densities have been developed for other coral predators, notably the crown of thorns starfish (Keesing and Lucas 1992; Moran and De'ath 1992; Babcock et al. 2014), and are becoming a core part of current coral reef management strategies (e.g. on the Great Barrier Reef; Pratchett et al. 2014). In order to implement any *Drupella* action plan, managers need to be able to distinguish between non-problematic *Drupella* abundances and those that could lead to possible outbreaks situations. Our study, in combination with the previously existing literature, identifies *Drupella* abundances that could lead to a reduction in the preferred prey species of coral. *Drupella* abundances should be closely monitored as part of effective monitoring systems to enable managers to evaluate reef health and make decisions on a dynamic basis.

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Compliance with ethical standards

Conflicts of interest The authors declare no conflicts of interest.

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