Dietary shift in corallivorous Drupella snails following a major bleaching event at Koh Tao, Gulf of Thailand

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NOTE

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Abstract The island Koh Tao in the western Gulf of Thailand suffered severe coral bleaching in 2010. Its mushroom coral fauna of 20 species was surveyed during the bleaching in 2010 and after the bleaching in 2011. Multi-species assemblages of free-living mushroom corals occurred around the island, two of which were invaded by corallivorous *Drupella* snails after the bleaching. Previously these gastropods were known to mainly consume branching corals and hardly any mushroom corals. The snails were found preying on four fungiid species, three of which were susceptible to bleaching. The dietary shift became apparent after populations of preferred prey species (Acroporidae and Pocilloporidae) had died during the bleaching event. It seems that bleaching mortality reduced the availability of preferred prey, causing the corallivores to switch to less preferred species that occur in dense aggregations.

Keywords Coral aggregations · Coral bleaching · Corallivory · Mushroom corals · Predation

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Introduction

Most *Drupella* species (Gastropoda: Muricidae) are obligate coral feeders and may cause severe mortality in Indo-Pacific corals (Turner 1994b; Cumming 2009). They are principally nocturnal predators that usually hide around the bases of branching coral colonies in daylight, although some may forage in the day when present in high densities (Moyer et al. 1982; Boucher 1986; Turner 1994b).

Drupella snails are considered generalist corallivores whose selection of food depends on the availability of potential prey species (Turner 1994b; Morton et al. 2002). Records indicate that they mainly feed on branching corals with small polyps, such as species of *Acropora*, *Montipora*, *Pocillopora*, *Seriatopora*, *Stylophora*, and *Porites* (Johnson et al. 1993; Turner 1994a; Cumming and McCorry 1998; Cumming 1999; Schoepf et al. 2010; Al-Horani et al. 2011). They have been observed to prey on *Echinopora*, *Fungia*, *Galaxea*, *Goniastrea*, *Goniopora*, *Hydnophora*, *Lithophyllon*, *Millepora*, *Platygyra*, *Symphyllia*, and *Turbinaria*, but appear to avoid *Favia*, *Leptastrea*, and *Pavona* (Moyer et al. 1982; Boucher 1986; McClanahan 1994; Turner 1994b; Cumming 1999; Morton et al. 2002; Shafir et al. 2008; Morton and Blackmore 2009).

Reef surveys at Koh Tao, Thailand (Fig. 1), revealed multi-species aggregations of free-living mushroom corals. The occurrence of such large mushroom coral aggregations may be related to the availability of dead coral as substratum for their attached juveniles and their capacity of asexual reproduction through repetitive budding (Hoeksema 2004; Hoeksema and Yeemin 2011). Following extensive bleaching in mid-2010, some of these aggregations were attacked by predatory *Drupella* spp. This is unusual because (1) mushroom corals were previously not recognized as favorite *Drupella* prey, (2) the predators caused substantial damage to the mushroom coral aggregations, and (3) this happened after the bleaching event.

Materials and methods

Coral bleaching was observed around Koh Tao from 19 April until 8 October 2010, peaking around 15 June with 96 % of coral cover fully or partially bleached. *Drupella* abundances were measured prior to the bleaching (2006–early 2010) at two sites in southern Koh Tao (Fig. 1), at 3–10 m depth in four to eight 20 × 5 m quadrats per site. At the end of the bleaching event (12 August–7 October 2010), coral mortality was measured at seven locations around Koh Tao (Fig. 1) using point intercept transects along two permanent lines, one between 3 and 6 m and one between 7 and 10 m. Each line contained four 20-m segments (with a sample point every 50 cm) to yield a total of eight transects per site.

The species richness of mushroom corals was assessed at 13 sites on fringing reefs around Koh Tao 25–30 June 2010, when bleaching was at its peak (Hoeksema and Matthews 2011; Hoeksema et al. 2012a). No *Drupella* spp. were encountered. 5 months after the end of the bleaching event (17–26 February 2011), 13 sites with substantial coral cover were surveyed for presence/absence of fungiid

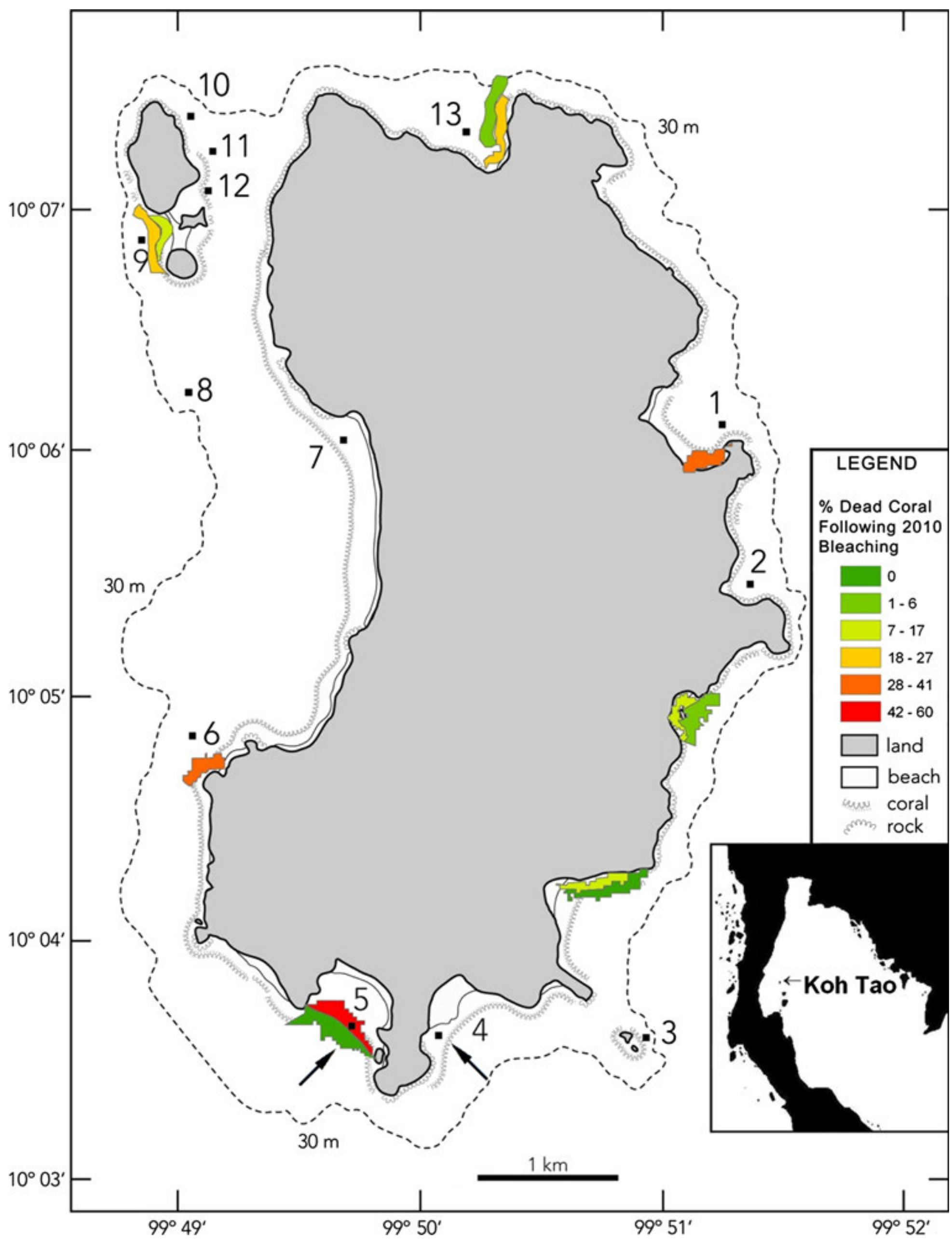

Fig. 1 Map of Koh Tao (after Hoeksema et al. 2012a) showing sample sites listed in Table 1 (February 2011). *Colors* indicate the extent of coral mortality at various sites after the 2010 bleaching event at two depth zones, between 3 and 6 m and between 7 and 10 m. Sites: (1) Hin Wong Pinnacle, (2) Laem Thian Bay, (3) Shark Island, (4) Aow Taa Cha, (5) Chalok Baan Kao, (6) Pottery Pinnacles, (7) Sairee Beach, (8) White Rock, (9) Twin Peaks, (10) Red Rock, (11) Nang Yuan Pinnacle, (12) Japanese Garden, (13) Mango Bay. *Arrows* (sites 4 and 5) indicate observed *Drupella* infestations. Insert: position of Koh Tao in the Gulf of Thailand

species and for *Drupella* spp. (Table 1). In each set of coral surveys, the roving diver technique (Hoeksema and Koh 2009) was used to record the occurrence of species down to the maximum depth per site, but not deeper than 30 m. Each dive was in daytime and lasted approximately 1 h.

Coral identifications were based on a taxonomic revision (Hoeksema 1989) and a phylogenetically adapted classification of the Fungiidae (Gittenberger et al. 2011). Four corallivorous *Drupella* species can be distinguished with the help of molecular evidence (Claremont et al. 2011), but owing to intraspecific variation and encrustations of red calcareous algae on the shells, the snails can be hard to identify in the field. The specimens at Koh Tao resembled *D. rugosa* (Born, 1778) or *D. cornus* (Röding, 1798) (Johnson and Cumming 1995; Claremont et al. 2011).

Results and discussion

Drupella snails were rarely observed on mushroom corals at Koh Tao during surveys conducted prior to the bleaching. At site 4 (Fig. 1), *Drupella* spp. were predominantly observed preying on branching corals from 2006 until 2010, causing substantial loss among tabulate *Acropora* colonies. In 2010 surveys, live coral cover was estimated to be 56 % but had fallen to 8 % in 2011 surveys. At site 5 (Fig. 1), from 2008 until 2010, *Drupella* snails occurred at average densities of 0.5–1.0 m^{-2} on *Acropora* and *Pocillopora* corals and hard coral cover decreased by 60 % at 3–6 m depth (Fig. 1). In 2009–2010, *Drupella* spp. were found on branching corals at sites 1, 3, and 13 but were not observed on mushroom corals. Thus, prior to the 2010 bleaching event, *Drupella* seemed to be confined to non-fungiid prey.

In February 2011, there was little recovery of branching corals, and *Drupella* snails were observed in the two southernmost mushroom coral aggregations (Table 1). At site 4 (Fig. 1), 15 snails were found beneath a single specimen of *Fungia fungites* (ca. 7 m depth). At site 5, several species of mushroom corals were infested by snails (ca. 5–9 m depth). A total of four prey species was recorded (Table 1); *F. fungites* was the most frequently affected ($n = 24$) and *Lithophyllon repanda* was the second-most ($n = 10$). *Ctenactis echinata* and *Pleuractis granulosa* were each represented by a single attacked individual. Since *F. fungites* and *L. repanda* were among

Table 1 Numbers of fungiids observed as infested with *Drupella* spp. in 13 reef sites at Koh Tao in 2011. A zero indicates a site where a fungiid species was present but without infestation; dashes denote sites where the fungiid was not found

Site	1	2	3	4	5	6	7	8	9	10	11	12	13
Mushroom coral species													
Cantharellus jebbi (Hoeksema, 1993)	–	–	–	–	0	–	–	0	–	–	–	–	–
Ctenactis crassa (Dana, 1846)	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenactis echinata (Pallas, 1766)	0	0	0	0	1	0	0	0	0	0	0	0	0
Cycloseris costulata (Ortmann, 1889)	0	0	0	0	–	0	0	0	0	0	0	0	0
Cycloseris mokai (Hoeksema, 1989)	0	0	0	0	0	0	–	0	0	0	0	0	0
Danafungia horrida (Dana, 1846)	0	–	–	–	–	–	0	0	0	0	–	0	0
Danafungia scruposa (Klunzinger, 1879)	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungia fungites (Linnaeus, 1758)	0	0	0	1	24	0	0	0	0	0	0	0	0
Herpolitha limax (Esper, 1797)	0	0	0	0	0	0	0	0	0	0	0	0	0
Lithophyllon concinna (Verrill, 1864)	0	0	0	0	0	–	0	0	0	0	0	0	0
Lithophyllon repanda (Dana, 1846)	0	0	0	0	10	0	0	0	0	0	0	0	0
Lithophyllon undulatum (Rehberg, 1892)	–	0	0	0	–	–	–	–	–	–	–	–	–
Pleuractis granulosa (Klunzinger, 1879)	0	0	0	0	1	0	0	0	0	0	0	0	0
Pleuractis moluccensis (Van der Horst, 1919)	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuractis paumotensis (Stutchbury, 1833)	0	0	0	0	0	0	0	0	0	0	–	0	0
Podabacia crustacea (Pallas, 1766)	0	0	0	0	0	–	0	0	0	0	0	0	0
Podabacia motuporensis Veron, 1990	–	–	–	–	–	–	–	0	–	–	0	0	–
Polyphyllia talpina (Lamarck, 1801)	0	0	0	0	0	–	0	0	0	0	0	0	0
Sandalolitha dentata Quelch, 1884	–	0	–	–	–	–	–	0	0	0	0	–	–
Sandalolitha robusta (Quelch, 1886)	0	0	0	0	0	0	0	0	0	0	0	0	0

the most abundant fungiids in the aggregation, there was no indication that *Drupella* showed a prey preference among mushroom coral species. There were many dead mushroom corals close by that could have been killed by either predation or bleaching.

In several cases, *Drupella* snails were seen on top of fungiids (Fig. 2a, b), indicating some diurnal foraging activity. Corals under attack showed pale radial marks where tissue had been recently removed and bare areas covered by filamentous algae (Fig. 2a, b, d). Infested corals had up to 90 snails hiding beneath them, depending on the prey size (Fig. 2c, e), suggesting that damage is mostly inflicted during nocturnal foraging.

Plague-like outbreaks of *Drupella* have been known to occur since the 1990s and some of these occurred after coral bleaching events (Antonius and Riegl 1998; Baird and Marshall 2002; Morton and Blackmore 2009). High concentrations of coral associates after the occurrence of a coral disease may indicate stress in corals and a decreasing resistance to the settlement of epibionts (Risk et al. 2001; Samimi Namin et al. 2010). However, it is unlikely that mushroom corals at Koh Tao were more susceptible to the *Drupella* attack as a result of bleaching. The corals were already recovering at the time of the second survey, and the greatest number of *Drupella* were found on a specimen of *C. echinata*, a species with low bleaching susceptibility (Hoeksema and Matthews 2011).

A more plausible explanation for the *Drupella* invasion in mushroom coral aggregations is that snails were present on nearby corals before the bleaching started. Many dead *Acropora* corals occurred in close proximity and were not available as prey anymore. Moreover, many snails had shells longer than 2 cm (Fig. 2), indicating that they were over 2-year-old (Black and Johnson 1994) and so would have been present in the vicinity before the bleaching started. After the bleaching, mushroom corals survived (Hoeksema et al. 2012a) and remained available as alternative prey. There are few reports of prey switching in *Drupella* or other non-fish corallivores that eat fungiids (Pratchett 2007; Shafir et al. 2008). Like other generalist corallivores with a preference for prey susceptible to bleaching (Guzmán and Robertson 1989; Berumen et al. 2005; Pratchett et al. 2004, 2009), *Drupella* snails appear to look for an alternative prey when their preferred food

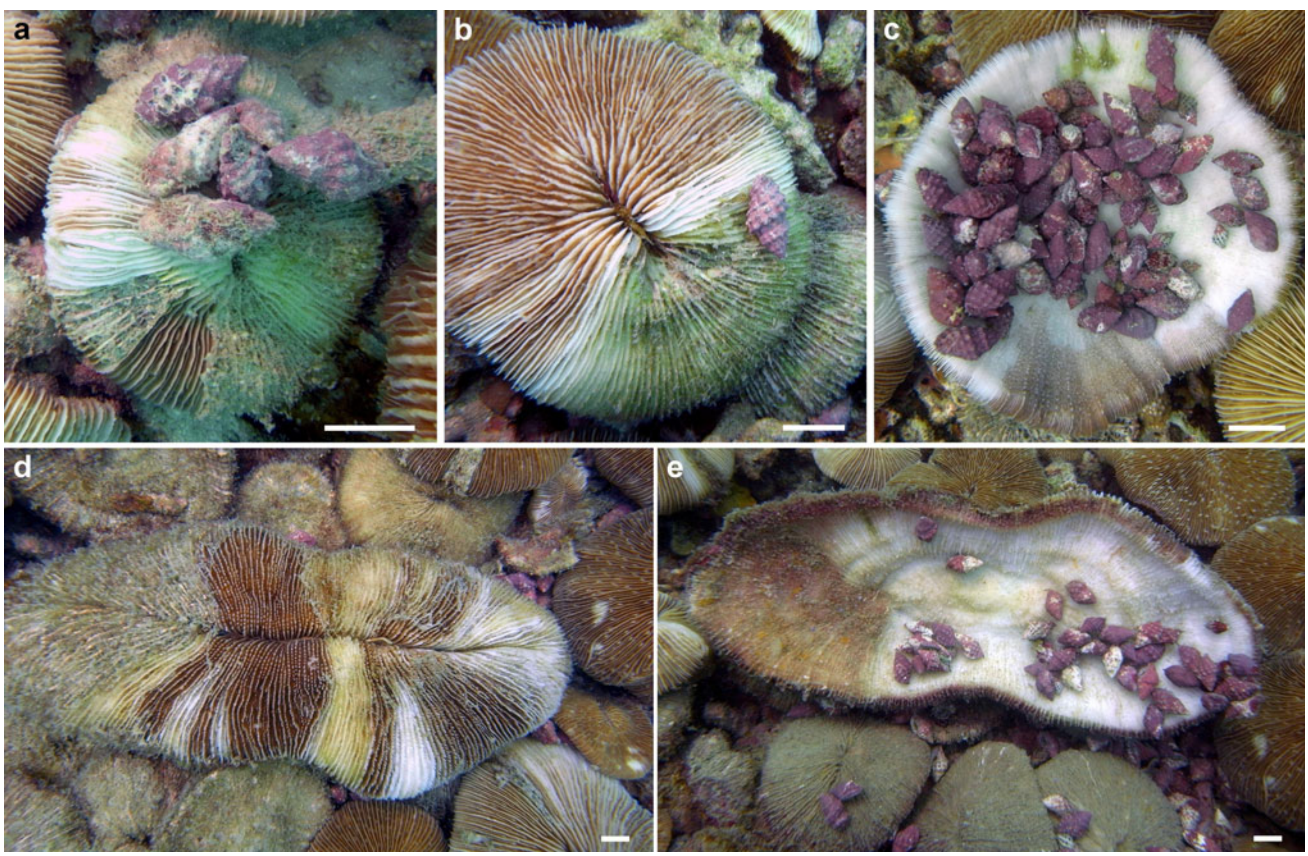

Fig. 2 Mushroom corals under attack by *Drupella* snails (Site 5, 2011). **a** *Pleuractis granulosa* individual in daylight showing six snails and tissue loss on its upper surface. **b** Specimen of *Fungia fungites* in daylight with one snail and tissue loss. **c** *F. fungites* coral turned upside down to show underside with >80 snails. **d** *Ctenactis echinata* coral showing tissue loss in typical radial pattern. **e** Same specimen turned over to show *Drupella* infestation (>90 individuals). *Scale bars*: 2 cm

source has disappeared. Dense aggregations of free-living mushroom corals constitute an ideal habitat for *Drupella* because the snails find shelter underneath their prey (Fig. 2) and can easily move from one coral to another.

Massive predation by *Drupella* has not been seen previously in fungiid assemblages, either during or without bleaching (e.g., Hoeksema and Moka 1989; Hoeksema 1991, 2004, 2012; Hoeksema and Koh 2009; Hoeksema and Gittenberger 2010; Waheed and Hoeksema 2013), but the prey aggregations at Koh Tao were larger and denser than in previous studies. Information on mushroom coral predation is scarce, and they rank among the less preferred coral species (Pratchett 2007). Nonetheless, fungiids host many species of parasitic mollusks (Owada and Hoeksema 2011; Hoeksema et al. 2012b; Gittenberger and Hoeksema 2013), so there is no reason why mushroom coral aggregations should not support *Drupella*, except when more preferred prey species are available.

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