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The outbreak of *Drupella* snails and its catastrophic effects on coral reefs: a comprehensive review

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The recurring outbreaks of *Drupella* snails are a significant threat to coral reef ecosystems on a global scale. However, research on *Drupella* snails is currently very fragmentary. This article explores the ecological impacts and mitigation methods of *Drupella* snails and its outbreaks, and draws the following main conclusions. 1) *Drupella* snails inhabit the tropical oceans of the Indo-Pacific, utilizing their specialized radula to feed on coral polyps, and they predominantly spawn during summer, attaching egg capsules onto coral skeletons. 2) An outbreak of *Drupella* snails is defined by a density of >2 ind/m^2, but large aggregations alone do not necessarily indicate an outbreak. 3) The damage of coral reef ecosystem is the primary cause of *Drupella* snail outbreaks, with the hypotheses of "terrestrial nutrient input" and "overfishing of predator" being widely accepted but not fully explaining all outbreak events. 4) Countering *Drupella* snail outbreaks involves improving the health of coral reef ecosystems, protected areas, biological control and manual removal, though manual removal is the most direct and effective in short-term. 5) The understanding of the physiological and ecological characteristics of *Drupella* snails is inadequate at present, with larval development and population ecology being areas of particular under-investigation. 6) Studies of *Drupella* snail outbreaks have focused mainly on mid-outbreak stages, with little attention to early warnings beforehand or adverse outcomes afterwards. Despite significant challenges, addressing knowledge gaps in the biology of *Drupella* snails is crucial to determine the true causes of their outbreaks and identify corresponding solutions.

KEYWORDS

coral reef deterioration, coral predator, corallivorous gastropod, outbreak hallmark, mitigation strategies

1 Introduction

The coral reef is renowned for being the "tropical rainforest of the ocean" due to its high productivity and immense biodiversity, making it one of the world's most diverse ecosystems (Apprill et al., 2023; Nama et al., 2023). It is not only an essential habitat for marine organisms, but also a significant source of ecological, economic, and cultural value for human societies (Hein et al., 2015; Macneil et al., 2019; Mellin et al., 2020; Apprill et al., 2023). Coral reefs are one of the most vulnerable ecosystems that have been severely damaged by global climate change and human activities such as overfishing and pollution (Dutra et al., 2021; Hill and Hoogenboom, 2022; Ouedraogo et al., 2023; Rahman et al., 2023). While the effects of environmental stressors like temperature and pH on coral reefs are well-studied (Rice et al., 2019), the detrimental impact of corallivores, whose feeding behaviors can cause minor to severe damage, further exacerbates the decline in coral reef health and significantly alters the coral reef ecosystem (Rogers and Plaganyi, 2022). Corals are subject to predation by various macro-consumers, such as fish (Cole et al., 2008), echinodermata, (Kroon et al., 2021) and gastropod (Dalton and Godwin, 2006). For example, coral mortality and a reduction in coral cover of up to 80% have been caused by outbreaks of the crown-of-thorns starfish (*Acanthaster* spp., CoTS) since 1980s (Pratchett et al., 2017). The feeding activity of corallivorous gastropods not only has the potential to damage coral and spread coral diseases but can also worsen the spread of existing ciliates on the coral and create additional infections by providing entry points for pathogens through feeding scars (Montano et al., 2022).

The destructive impact of corallivorous *Drupella* snails has also gradually attracted widespread attention, the high-density presence of these gastropods can decimate vast areas of coral reefs (Boucher, 1986; Cumming, 2009a; Marimuthu and Tripathy, 2018; Thaha and Rathod, 2019). Although climate change threatening coral is widely publicized as a global issue, the havoc wreaked by *Drupella* snails poses an equal danger to coral reef ecosystem. Massive outbreaks of *Drupella* snails have resulted in a decline of over 75% in coral reef coverage in the back-reef areas of Ningaloo Reef, Western Australia (Turner, 1994). Currently, there is limited research on *Drupella* snail outbreaks, leading to an incomplete understanding of the overall situation. This review provides an overview of the existing studies on *Drupella* snail outbreaks and their impacts on coral reefs. It begins by summarizing the physiology and ecology of *Drupella* snails. Subsequently, the outbreak events are examined, and the underlying causes are analyzed. Finally, rational strategies for prevention and mitigation are proposed.

2 Physiological and ecological characteristics of *Drupella* snails

2.1 The taxonomic and morphological characteristics of *Drupella* snails

Drupella snails belong to the family *Muricidae* within the phylum *Mollusca* (Tan, 2000). The main *Drupella* species include *Drupella cornus* (Röding, 1798), *D. eburnea* (Küster, 1862), *D. fragum* (Blainville, 1832), *D. rugosa* (Born, 1778) and *D. margariticola* (Broderip, 1833) (Claremont et al., 2011a) (Figure 1). Studies have documented their average length ranging from 6.4 to 36.3 mm, with average shell and dry body weights of 1335 and 33 mg, respectively (Ismail et al., 2000). The conical shell of *Drupella* snails typically features small, granular nodules on its surface. The small aperture contains a row of teeth along the inner edge of the outer lip. Additionally, the inner lip axis possesses 3-4 rib-like teeth, while surface nodules are prominent (Johnson and Cumming, 1995; Ruan, 2021). Identifying *Drupella* snails in the field proved challenging due to heavy encrustation by coralline algae and assorted epifauna (Saponari et al., 2021). *Drupella* utilizes a distinct radula structure for feeding on coral polyps. Furthermore, some species exhibit sexual dimorphism where males possess more complex radulae and larger rachidian teeth than females (Tan, 2000). *D. rugosa* in particular has specialized oral structures including an externally keratinized proboscis and lateral teeth, providing morphological adaptations against coral nematocysts and efficient feeding (Turner, 1992; Claremont et al., 2011a).

2.2 Habitat and distribution of *Drupella* snails

Drupella snails mainly inhabit tropical oceans within the Indo-Pacific, with some species harming coral reefs. Species within this genus commonly occurs on *Acropora* and *Montipora* corals or hard

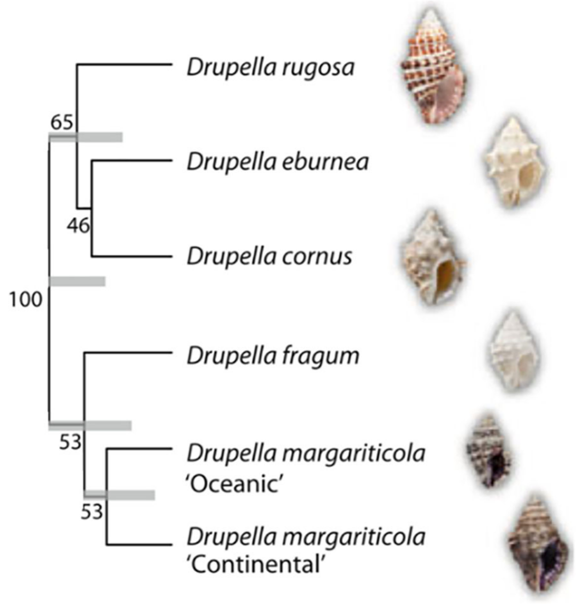

FIGURE 1
BEAST phylogeny of *Drupella* snails. Phylogenetic analysis was conducted based on a combined analysis of the *28S rRNA*, *12S rRNA*, and *cytochrome c oxidase subunit I* genes. Support values are indicated as BEAST posterior probabilities, while grey bars represent the 95% highest posterior density intervals on nodes with support exceeding 50% (Reproduced from ref. (Claremont et al., 2011a), Copyright © 2011, Springer).

substrates in lower intertidal and shallow sublittoral zones (Johnson et al., 1993; Boneka et al., 1999). More sheltered reef slopes favoring branching corals also predominated *D. rugosa* (Cumming, 2009b). The preference for *Acropora* spp. by *Drupella* snails may be linked to their selective feeding on damaged coral tissue (Morton, 2002), fast-growing *Acropora* spp. are prone to damage and breakage, and increased mucus release from these injured corals may attract predators (Johnson et al., 2008). Meanwhile, massive corals like *Platygyra acuta* utilize robust defenses against biological fouling and predation under normal conditions (Tsang and Ang, 2019). However, branching *Acropora* spp. prioritize growth over defenses, resulting in low resistance to predation and disease (Hobbs and Frisch, 2010). Studies found *Drupella* snails aggregating more on larger corals. Coverage on corals ≥30 cm in diameter nearly doubled that of 5-29 cm corals (Bruckner et al., 2017). Predation behavior of *Drupella* snails was generally not found on the coral colonies with a diameter smaller than 5 cm (Saponari et al., 2021). Notably, *Drupella* snails exhibited depth preferences, with most predation recorded at 3 m (Dehnert et al., 2022).

2.3 Reproduction of *Drupella* spp.

Understanding *Drupella* snail reproduction, recruitment, and early life history is essential to monitor and manage their outbreaks. Sexual maturity occurs around 2.5 years, with an expected lifespan of 7-8 years (Turner, 1994; Ismail et al., 2000; Claremont et al., 2011b). *Drupella* snails start as veliger larvae, then metamorphose into crawling juveniles (Holborn et al., 1994). *Drupella* snails lay kidney-shaped egg capsules directly onto dead coral skeletons (D'Asaro, 1986). The embryo development (Sam et al., 2017) and veliger larvae stages (Sam et al., 2016) are critical periods in the lifecycle of *Drupella* snails. However, insufficient research on veliger metamorphosis in labs leads to high mortality (Turner, 1994). Another study found all veligers died within 30 days of hatching under lab conditions (Haslam et al., 2023). Positive phototaxis likely contributed to veliger deaths prior to metamorphosis due to high energy costs of swimming in undefined feeding ecologies and limited nutrients in labs (Turner, 1994).

Understanding spawning times of different *Drupella* snail populations enables targeted larval number control and outbreak management by applying measures during peak periods. Table 1 shows spawning occurs year-round, peaking in summer. In the southern hemisphere, peak spawning is December, in the northern hemisphere it is June. Observations at Rottnest Island, Australia over two consecutive summers (2020-2022) found *D. cornus* laid egg capsules during local summer (January-March) (Haslam et al., 2023). Furthermore, large juvenile aggregations were discovered at Albion, Mauritius in June 2010, supporting reproduction during southern summer (Pillay et al., 2011). The temperature of the water may be the key factor that limits the development of *Drupella* snails, given that research has demonstrated that their embryos can develop normally inside egg capsules, even during the winter season when the water temperature drops to 18°C (Koido et al., 2017). A January-April water temperature reduction also inhibited the spawning of *D. fragum* (Kitamura et al., 2022). Species vary in spawning quantities and embryos per capsule. Specifically, *D. cornus*, *D. fragum*, *D. margariticola*, and *D. rugosa* produce with 596 (Turner, 1992), 106-336 (Sam et al., 2017), 118 ± 18 (Middelfart, 1996), and 67 ± 8 (Sam et al., 2016) embryos per capsule, respectively. *D. rugosa* produces comparatively larger embryos and veligers despite the lowest quantity, this trade-off may be a mechanism to increase the survival rate of the juveniles (Turner, 1992; Sam et al., 2016). Hatching times also differ: 15 days for *D. rugosa*, 22-36 days for *D. fragum*, and 16-23 days for *D. cornus* (Sam et al., 2017). Seawater temperature plays a role in the developmental time of juveniles, as higher temperatures can increase the metabolic rate of embryos and thus accelerate their development (Przeslawski, 2004).

TABLE 1 Spawning behavior of *Drupella* snails.

Species	Site	Time (month)	Substrate	Description of egg capsules	Reference
D. cornus	Obhur Creek, Jeddah, Red Sea (Lab cultured)	peak spawning period (6-7)	/	92.4 ± 38.75 (n=12) eggs within each capsule, average diameter 158.3 µm ± 23.4	(Baomar et al., 2016)
D. fragum	Southwestern Shikoku, Japan	peak spawning period (4-5)	/	/	(Kitamura et al., 2022)
Drupella spp.	Koh Tao, Thailand	4	*Danafungia* spp. skeletons	eggs within each capsule (n=75-85)	(Scott et al., 2017b)
Drupella spp.	Le Bouchon, Mauritius	11	dead fungiid skeletons	96.2 ± 8.9 eggs within each capsule	(Kaullysing et al., 2020)
D. rugosa	Lazarus Island, Singapore (Lab cultured)	3	*Pocillopora damicornis* skeletons	64 (n=3) eggs within each capsule	(Sam et al., 2016)
D. rugosa	Lazarus Island, Singapore (Lab cultured)	3 (averaged 29.5°C)	*P. acuta* skeletons	67 ± 8 eggs within each capsule	(Sam et al., 2017)
D. margariticola	Shirahama, Wakayama, Japan	peak spawning period (6-7)	beds of the mussels	127.9 ± 36.1(n=8) eggs within each capsule	(Ishida, 2004)

Cronia margariticola was assigned to the genus Drupella (Claremont et al., 2011a).

2.4 *Drupella* snails' population dynamics and structure

According to established method, *Drupella* snails can be divided into recruits (<1cm), juveniles (1-2 cm), and adults (>2 cm) based on size (Turner, 1994). Studies have shown that the population structure of *Drupella* snails deviates from the standard unimodal distribution, with over 90% of individuals observed in the survey being adults, which attributed to the cryptic lifestyle of juvenile individuals (Saponari et al., 2021). Small bodies and nocturnal activity further obscure juveniles (Furushima et al., 2012; Tsang and Ang, 2019). Habitat preferences may also differ between juveniles and adult snails. Large gatherings of juvenile *Drupella* snails have been reported forming clusters among *Acropora* coral debris on a shallow fringing reef in Puerto Galera, Mindoro Island, Philippines, at a depth of 1-2 meters, while adults inhabit reef flats and slopes (Cumming, 2009b). Dwindling coral and constrained living space may exacerbate intraspecific rivalry and confer larger *Drupella* snails a competitive benefit across generations (De Roos et al., 2003). Species-specific structures also exist. Few juveniles characterize *D. rugosa* and *D. cornus* populations, whereas juveniles comprise half of *D. fragum* populations (Cumming, 1999). *D. rugosa* is predominantly found on sheltered reef slopes and *D. fragum* is mostly found on exposed reef crests, and the unique environmental conditions in these habitats such as eddying currents and restricted water flow across coral branches can influence the larvae's dispersal and settlement choices, thereby resulting in distinct population structures (Cumming, 1999). The aggregation of *Drupella* snails is influenced by the season, with notably higher densities in summer potentially relating to breeding behavior (Morton and Blackmore, 2009).

3 The outbreaks of *Drupella* snails

3.1 The threshold of outbreaks

The outbreak criteria for *Drupella* snails, although challenging to define solely based on density, play a crucial role in understanding their impact on coral reefs. The threshold for the outbreak of *Drupella* snails is defined as > 2 ind/m^2, based on their feeding rate and the growth rate of coral (Cumming, 2009b). Studies have shown that for *Drupella* snail species with a strong preference for feeding, such as *A. spicifera*, an outbreak is considered to have occurred when the density of *Drupella* snails exceeds 0.62 ind/m^2. At this density, their feeding rate on corals surpasses the growth rate of corals, causing a negative growth rate in corals (Bessey et al., 2018). Furthermore, *Drupella* snails exhibit heterogeneity and high levels of clustering in their distribution, with their density potentially exceeding the outbreak threshold only in certain belt transects, while the average density across the entire reef area is significantly lower than the outbreak threshold (Lei et al., 2022). While the outbreak criteria of *Drupella* snails are difficult to quantify due to the differences in coral coverage and dominant species across various reef areas, the density of *Drupella* snails can still serve as a useful indicator to some extent.

3.2 Overview of *Drupella* snail outbreaks

Drupella snail outbreaks have occurred worldwide, impacting coral reefs in different regions. Massive outbreaks in the South Pacific Ocean and Asia-Pacific have been documented, with population densities reaching millions of individuals (Table 2). Four major outbreaks of *Drupella* snails have occurred in South Pacific Ocean, in 1983, 1989, 1993, and 2014-2016, respectively. The coral reef of Ningaloo Marine Park, spanning 2,240 km^2, once saw a population of up to 500 million *D. cornus* individuals (Ayling and Ayling, 1987). The multi-year intervals between outbreaks may be attributed to the recovery rate of coral reefs. Furthermore, the outbreak patterns of *Drupella* snail and CoTS show a degree of coincidence, suggesting different corallivorous species may interact to exacerbate coral degradation (Pratchett, 2010). *Drupella* snail outbreaks have occurred in several areas within the Asia-Pacific region. In November 2006, a total of 300 colonies of *P. acuta* and *P. carnosus*, covering an area of 700 m^2, were discovered to have suffered severe bioerosion at their bases by *Drupella* snails at Coral Beach in Hoi Ha Wan Marine Park, Hong Kong (Lam et al., 2007). After a severe coral bleaching event in Koh Tao Island in the western Gulf of Thailand in 2010, a large-scale outbreak of *Drupella* snails was detected in the same area in 2011 through local monitoring (Hoeksema et al., 2013). Under certain extreme conditions, the outbreak density of *D. cornus* can reach as high as 3000 ind/m^2 (Moyer et al., 1982). While mass gatherings of *Drupella* snails have also been documented in Hainan Island, China, with a maximum of 38 individuals found on a single coral species (*A. hyacinthus*), the density of *Drupella* snails (0.09 ± 0.03 to 1.78 ± 0.39 ind/m^2) did not reach the so-called outbreak threshold (Lei et al., 2022). Outbreaks of *Drupella* snails have also impacted various regions within the Indian Ocean. The extensive coral bleaching that occurred in South Male', Maldives in April/May 2016 resulted in the loss of up to 80% of live coral, facilitating a massive subsequent outbreak of *Drupella* snails with densities of up to 250 individuals recorded per surviving coral colony (Bruckner et al., 2017). A large-scale outbreak of *Drupella* snails also occurred in the reef areas of Mauritius between 2010 and 2016, with higher average outbreak densities during the summer months compared to winter. In 2016, the outbreak density was as high as 158.14 ± 13.85 ind/m^2, which may be related to the continuous decline in local coral reef health and climate change (Kaullysing et al., 2016; Kaullysing et al., 2017). Density disparities of *Drupella* snails likewise exist between sites within reef systems.

Existing statistical results indicate that the major species involved in outbreaks are *D. cornus* and *D. rugosa*. The consumption rates of corals by different types of *Drupella* snails vary. Reports indicated that each individual of *D. cornus* can consume 2.6 cm^2 of live branching coral per day, with the consumption rate increasing with temperature, although body size associated feeding rates did not exhibit a significant difference (Turner, 1992; Al-Horani et al., 2011). Consumption rates of coral tissue also differed between *D. rugosa* (1.81 cm^2 per day) and *D. margariticola* (0.51 cm^2 per day) (Samsuri et al., 2018). Similar results have also been detected in other studies on coral-feeding snails. Marine gastropod consumption of *Acropora* tissue averages

TABLE 2 The outbreak of *Drupella* snails.

Species	Year	Site	Density (ind/m^2)	Reference
D. cornus	1983	Ningaloo Reef, Western Australia	19.4	(Ayling and Ayling, 1987)
D. cornus	1989	Bundegi Reef, Western Australia	2.9	(Forde, 1992)
Drupella spp.	1993	Lizard Island, Great Barrier Reef, Australia	exposed reef crests: 2.55	(Cumming, 1999)
			sheltered reef slopes: 2.08	
D. cornus	1997	Gulf of Aqaba, Red Sea, Jordan	upper reef slope: 12.24	(Al-Moghrabi, 1997)
			lower reef slope: 2.73	
Drupella spp.	2000	Hoi Ha Wan, Hong Kong, China	2	(Morton and Blackmore, 2009)
D. cornus	2004	Northern Gulf of Eilat, Red Sea, Israel	200 ind/30 cm diameter	(Shafir et al., 2008)
Drupella spp.	2003	Chinwan Inner Bay, Penghu, Taiwan, China	5.5	(Hsieh et al., 2011)
	2009		22.7	
D. rugosa	October, 2010	Chalok Ban Kao, Thailand	7.9	(Scott et al., 2017a)
	February, 2011		5.6	
D. cornus	2010	Mauritius (20°17’ S, 57°35’ E)	S:17.60 ± 2.71, W:6.40 ± 0.98	(Kaullysing et al., 2016)
	2011		S:17.00 ± 2.63, W:6.20 ± 1.59	
	2012		S:30.60 ± 1.21, W:6.20 ± 0.98	
	2013		S:17.4 ± 2.16, W:5.20 ± 0.86	
	2014		S:19.6 ± 2.25, W:5.40 ± 0.92	
D. rugosa	April-June, 2014	Koh Tao, Thailand	>3	(Moerland et al., 2016)
D. cornus	2014&2016	Mandu reef, Ningaloo Marine Park, Western Australia	2.83	(Bessey et al., 2018)
Drupella spp.	2016	South Male Atoll, Maldives	outer fore reef: 3.1 ± 1.5	(Bruckner et al., 2017)
			channel reef: 3.8 ± 1.3	
D. cornus	November, 2016	Mauritius (20.20° S, 57.50° E)	158.14 ± 13.85	(Kaullysing et al., 2017)

1.9 cm^2 per individual per day, but peaks at 6.5 cm^2 for some Caribbean species (Bruckner et al., 1997). In Florida, the estimated long-term feeding rate for marine snails (average length 29 mm) was 1.07 cm^2 of tissue per individual per day (Baums et al., 2003). In addition, it is worth noting that coral communities contain various coral morphologies and species, and the consumption rates of *Drupella* snails may vary with the preferred prey species selection.

3.3 Outbreak mode of *Drupella* snails

The limited research on the outbreak mode of *Drupella* snails underscores the importance of understanding their outbreak patterns for effective management, as the factors triggering the initial onset of outbreaks can be subtle and challenging to detect. Given their comparable feeding habits, living environments, planktonic larval stage and metamorphosis, insights from the better-studied outbreak mechanism of CoTS can provide valuable information on potential *Drupella* snail outbreaks. The CoTS outbreak is categorized into primary and secondary outbreaks. Primary outbreaks are characterized by a multimodal distribution of individual sizes and a large variation in size. On the other hand, secondary outbreaks exhibit a unimodal distribution of population size, with individuals of similar size comprising the outbreak population (Birkeland et al., 1990; Pratchett, 2005; Pratchett et al., 2014). It is likely that the outbreak of *Drupella* snails falls under the secondary outbreak category. Studies indicate that *Drupella* snail populations primarily consist of mature individuals of comparable sizes, possibly originating from either a single large-scale recruitment event or the gradual accumulation of snails from multiple cohorts (Saponari et al., 2021). Another plausible explanation was that smaller individuals grow rapidly in the early stages of the outbreak, and most current research focused on the middle stages of the outbreak when juvenile individuals were already similar in size to adults. For example, *Drupella* snails that were 15 mm long grew by 5.2 mm over six months at a site in the early stages of an outbreak, whereas at a site with an established outbreak, they only grew by 3.8 mm (Black and Johnson, 1994). Snails that were larger than 35 mm showed very little growth.

3.4 Drivers of *Drupella* snail outbreaks

Marine ecosystems are complex and dynamic, and the outbreak of *Drupella* snails is a multifaceted issue that has been studied extensively. The causes of *Drupella* snail outbreaks are not yet fully understood, but various factors have been suggested as possible contributors, including terrestrial runoff, overfishing of *Drupella* predators, and increased reef damages (Turner, 1994). The following hypotheses have gained the most widespread acceptance.

3.4.1 Terrestrial nutrient input hypothesis

Coastal runoff containing nutrients can drive *Drupella* snail outbreaks by stressing corals through lowering salinity and increasing nutrients, thus developing conditions favorable for snail proliferation. *Drupella* snails were notably more drawn to corals that were experiencing stress and exposed to low salinity water, the formation of feeding aggregations can explain the outbreaks of *Drupella* snails previously reported in Hong Kong (Morton, 2002). The phenomenon of increased phytoplankton levels due to warmer temperatures and nutrient pollution potentially enhancing the survival and growth of *Drupella* larvae and juveniles, and contributing to outbreaks, has also been proposed as a contributing factor in outbreaks of CoTS (Kamya et al., 2018). An ample supply of phytoplankton ensured that veligers of *Drupella* snails had enough energy to complete metamorphosis and transform into crawling juveniles (Turner, 1994). Furthermore, high nutrient input exacerbates the overgrowth of macroalgae (Leckraz, 2015). The macroalgae's (*Padina boryana*) attachment to and overgrowth of *A. muricata* releases organic carbon that promotes microbe proliferation, weakening the coral's resistance and reducing the photosynthesis efficiency of its zooxanthellae by 56% (Kaullysing et al., 2016). Other researcher also identified the synergistic impact of corallivorous *Hermodice carunculata* and macroalgae *Halimeda opuntia* on reef-building coral *Orbicella faveolata* in the Caribbean, potentially inducing coral predation and tissue decay (Wolf and Nugues, 2013). As the health condition of corals deteriorates, their resistance and immunity decrease, making *Drupella* snails more easily capture and prey on coral tissues and leading to their rapid reproduction and outbreak on a large scale (Morton, 2002).

3.4.2 Overfishing of predator hypothesis

Overfishing that reduced balistids, labrids and invertebrate predators may have contributed to higher *Drupella* snail populations regionally by lifting controls on their numbers. Predators of *Drupella* snails, such as the fish *Coris aygula*, were seldom observed in investigated region, which may account for the behavior of *Drupella* snails foraging on the upper surfaces of branching corals and exposed massive or encrusting corals during the daytime, without being constrained by "top-down" control (Shafir et al., 2008). Napoleon wrasses (*Cheilinus undulatus*), considered one of the natural predators of *Drupella* snails, can suck the snails out of coral and crush their hard shells using pharyngeal bones (Ratianingsih et al., 2017). However, another study has shown a significant decline in Napoleon wrasses populations in coral reefs (Sadovy et al., 2003). The decline of herbivorous fishes further exacerbates the overgrowth of macroalgae, resulting in the deterioration of coral reef ecosystems (Leckraz, 2015). Corals can also be protected from attack to some extent by other small predators, such as *Alpheus lottini* and *Cymo andreossyi*, as their larger claws can crush the shells of *Drupella* snails (Williams et al., 2001; Gokul and Venkataraman, 2010).

3.4.3 Climate change hypothesis

Climate change impacts like thermal-stressed bleaching and extreme weather events may contribute to *Drupella* snail outbreaks through weakened coral resilience. Reports of high densities of *Drupella* snails have risen in recent years, notably after thermal stress triggered mass bleaching events (Bruckner et al., 2017). The cyclical occurrence of *Drupella* outbreaks indicates a possible correlation with oceanographic oscillations (e.g., El Niño) (Turner, 1994). In a similar vein, *Drupella* snails had a more significant impact on corals that were damaged by cyclone Ivor in 1990 on the Great Barrier Reef (Ayling and Ayling, 1992). Periodic climate change may also be responsible for the cyclical occurrences of *Drupella* outbreaks. Other studies have suggested that as early as the 1940s, there were large populations of other corallivorous animals present, which implies that the cyclical outbreaks may have existed even in the absence of significant human impacts on the marine environment (Pratchett et al., 2014).

In addition, other factors have also exacerbated the outbreak of *Drupella* snails. The high amount of visitation to dive sites has exacerbated the damage to corals, and the mucus secreted by broken coral fragments has attracted *Drupella* snails to feed, leading to significant aggregations of *Drupella* snails and contributing to outbreaks to some extent (Armstrong, 2009). Studies have shown that areas with higher levels of human disturbance tend to have greater densities of *Drupella* snails, while less impacted areas generally show lower abundances (Boneka and Mamangkey, 2013). While the outbreak of *Drupella* snails can be attributed to both human-induced environmental degradation and cyclical climate change, the precise mechanisms underlying these outbreaks remain unclear. Therefore, further research is necessary to obtain a better understanding of this phenomenon and its impact on marine ecosystems.

4 Coral destruction induced by *Drupella* snail outbreaks

4.1 Direct destruction for corals

Widespread coral predation by *Drupella* snails can severely degrade reefs through slowing coral growth and directly reduce coral coverage (Figure 2). The outbreak of *Drupella* snails has brought devastation to coral reefs, destroying 35 m^2 of coral reef on Great Barrier Reef in just two months, resulting in extensive coral rubble areas and a shift from coral-dominated to macroalgae-dominated distribution (Cumming, 2009b; Kayal et al., 2012). Moreover, *Drupella* snails will move on to nearby coral reefs to cause destruction after completely devastating a coral reef (Shafir et al., 2008). CoTS (*A. planci*) is widely acknowledged as a coral predator. The outbreak of CoTS in Moorea Island from 2003 to 2010 led to a drastic decline in live coral cover in an area of 132 km^2, from over 40% to less than 1%, causing approximately 96% of coral mortality in the region (Kayal et al., 2012). The destructive capacity

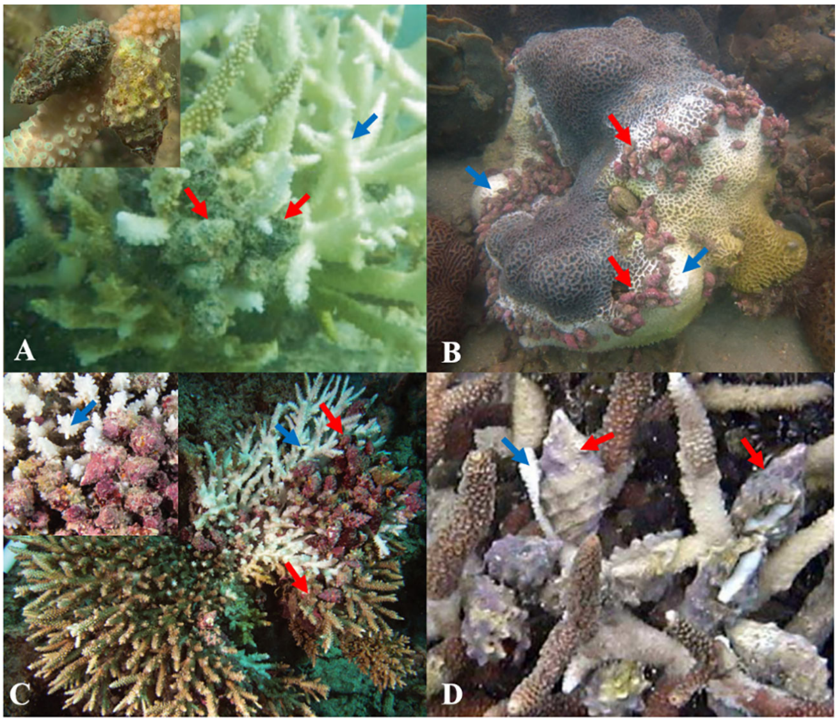

FIGURE 2
The devastation of corals amid *Drupella* outbreaks. **(A)** indicate *D. rugosa* predation on *A. formosa* in the Van Phong Bay, Vietnam (Reproduced from ref. (Bettarel et al., 2018), Copyright © 2018, Springer). **(B)** indicate aggregation of *D. rugosa* on an *P. acuta* colony in Hong Kong (Reproduced from ref. (Tsang and Ang, 2019), Copyright © 2019, Elsevier). **(C)** indicate *Drupella* spp. consuming half colony of *Acropora* in Maldives (Reproduced from ref. (Bruckner et al., 2017), Copyright © 2017, Springer). **(D)** indicate the aggregation of *D. cornus* (Reproduced from ref. (Kita et al., 2005), Copyright © 2005, Elsevier). The red arrows point to the snails, and the blue arrows point to the coral ailment.

of *Drupella* snails on coral reefs is no less than that of CoTS, 0.9 *Drupella* snails per m^2 was equivalent to 10 CoTS per hectare, calculated using regression relationships between coral-grazing surface area of reef and surface area of coral branches (Cumming, 2009b). Between 1987 and 1989, the live coral cover along a 280 km stretch of Ningaloo Reef in Western Australia decreased by up to 75% due to predation by *Drupella* snails (Baird, 1999). Following the *Drupella* snails attack, the survival rate of *A. formosa* decreased to 66%, while that of *P. damicornis* dropped to 79% (Pillay et al., 2011). Different species of *Drupella* snails show varying feeding rates on corals, with *D. rugosa* consuming coral tissue at a significantly higher rate (1.81 ± 0.95 cm^2/day) than *D. margariticola* (0.51 ± 0.75 cm^2/day) (Samsuri et al., 2018).

By using their specialized radula to rasp live tissue from the coral skeletons, these snails create grazing scars that have the potential to significantly impact the growth rate and overall health of the corals. On the one hand, *Drupella* snails inflicted injuries cause coral colonies to prioritize tissue regeneration over colony growth, and prolonged or recurrent injuries may ultimately result in colony mortality (Pillay et al., 2011). On the other hand, the disruption of the bacteriome and virome by *Drupella* snails ultimately leads to a reduction in the coral's overall fitness (Bettarel et al., 2018; Nguyen et al., 2023). *Drupella* snails can create feeding scars and disrupt the coral's superficial mucus layer, which can provide an environment conducive to the growth and spread of pathogens that cause diseases (skeletal eroding, band disease) (Lamb et al., 2014). Therefore, the occurrence of *Drupella* snails has been linked to a number of coral diseases (Widiastuti, 2019), such as white syndrome (Antonius and Riegl, 1998), skeletal eroding band disease and black band disease (Onton et al., 2011), and brown band disease (Nicolet et al., 2013; Nicolet et al., 2018). The gastropod *Drupella* snails, which feeds on coral, proved to be a highly efficient carrier of brown band disease, as it infected over 40% of the experimental colonies (Nicolet et al., 2013). Studies have also demonstrated that *Drupella* snail predation can alter the composition of the coral's symbiotic microbial community, leading to an increase in the abundance of potentially harmful bacteria (Bettarel et al., 2018). Specifically, the community composition of active epibiotic bacteria has shifted towards more pathogenic taxa, including those belonging to the *Vibrionales*, *Clostridiales*, *Campylobacterales* and *Alteromonadales* orders (Bettarel et al., 2018). Likewise, the feeding behavior of *Drupella* snails also has an impact on the reproduction of corals. The removal of coral recruits by *Drupella* snails (10%) underscored the importance of coral recruitment in maintaining the population structure of adult corals and promoting the recovery of coral reefs following disturbances (Tsang et al., 2018).

Coral reefs affected by coral diseases or large-scale bleaching are particularly vulnerable to further degradation, and the feeding of corallivorous animals hinders the recovery of coral reefs (Bruckner et al., 2017). *D. cornus* exhibit a greater attraction to conspecifics than to undamaged coral, and even show a preference for corals damaged by conspecifics over those damaged artificially (Hamman, 2018). Under the threat of climate change, outbreaks of *Drupella* snails may devastate the resilience of coral reefs. The ongoing predation by *Drupella* snails may lead to the extinction of once-dominant coral species, including genets that have tolerance to higher sea water temperatures (Bruckner et al., 2017). The presence of *Drupella* snails is likely to diminish the resilience of these reefs, as many of the corals that are targeted by *Drupella* snails were previously able to withstand bleaching during periods of elevated water temperatures.

4.2 Indirect destruction

Drupella snails can strongly impact reefs through selective yet adaptive feeding that facilitates coral composition shifting. *Drupella* snails' feeding behavior is selective, with a preference for branching corals over massive corals during the initial outbreak (Saponari et al., 2021). Their selective feeding can cause changes in the composition and diversity of coral communities (Lachs et al., 2019). *Drupella* snails exhibit strong adaptability and modify their feeding preferences based on the availability of food (Hoeksema et al., 2013; Moerland et al., 2016). After their preferred species are depleted, they continue to feed on other species, ultimately leading to the death of most corals. However, the decrease in coral coverage has minimal impact on the distribution of *Drupella* snails (Saponari et al., 2021). After a major coral bleaching event in Thailand, there have been reports of *Drupella* snail shifting their dietary preferences from their favored genera *Acropora* spp. and *Pocillopora* spp. to less palatable fungiid corals (Hoeksema et al., 2013; Moerland et al., 2016). After the massive death of corals, the coverage of macroalgae rapidly increases due to the enlarged living space, and occupies the ecological niche of corals, hindering coral recovery (Lesser, 2021). Therefore, the outbreak of *Drupella* snails indirectly alters the community structure of coral reef ecosystems, reduces their recovery capacity, and indirectly leads to the reduction or even disappearance of certain coral reef fish species.

5 Strategies to address *Drupella* snail outbreaks

Recurrent outbreaks of *Drupella* snails significantly contribute to the degradation of coral reef ecosystems. However, limited documentation exists regarding methods to control *Drupella* snails. By implementing effective management strategies, it is possible to mitigate the risk of *Drupella* outbreaks and protect coral reef ecosystems. Here are strategies that can be employed.

5.1 Protection of coral reef ecosystems

Reducing anthropogenic impacts and promoting the health of coral reef ecosystems are key to mitigating future *Drupella* snail outbreaks and maintaining their overall well-being (Armstrong, 2009; Boneka and Mamangkey, 2013). By improving water quality in the Great Barrier Reef, such as through the reduction of agricultural runoff, it is possible to reduce macroalgal cover by an average of 39% and increase the richness of hard corals and phototrophic octocorals (De'ath and Fabricius, 2010). Increasing the richness of coral can enhance the resilience and stress resistance of coral reef ecosystems. For example, the presence of *P. cylindrica* has reduced the predation of *Drupella* snails on *P. frondifera* to some extent (Lachs et al., 2019). Enhancing the protection of coral reef fish and increasing their abundance and diversity, especially herbivorous fish, can control the growth of macroalgae, improve the health and resilience of coral reef ecosystems, and promote their resistance to *Drupella* snail outbreaks (Balasubramanian et al., 2014; Sheppard et al., 2023). Additionally, no-take marine protected areas can contribute to the well-being of coastal societies and the sustainability of coral reef ecosystems by increasing the abundance of reef organisms and protecting key ecosystem functions (Graham et al., 2011). The development of habitat connectivity restoration technology has the potential to enhance the connectivity of indigenous marine biological communities, promote nutrient cycling and material flow across multiple ecosystems, and improve the health and organization of coral reef ecosystems while also boosting biological abundance and diversity (Wang et al., 2022).

5.2 Biological control

Biological control methods can be utilized to manage *Drupella* snail outbreaks. Certain organisms can act as predators or competitors of *Drupella* snails, helping to control their population. The giant triton snail (*Charonia tritonis*) is considered a predator of various corallivorous harmful organisms (Bose et al., 2017; Ratianingsih et al., 2017). The Australian government has invested $568,000 in studying the reproductive biology of giant triton snails and successfully bred 100,000 juveniles, which will be used for the biological control of corallivorous harmful organisms (Chadwick, 2017). The coral guard crabs (*Trapezia* spp.) are commonly found among the branches of live *Acropora* spp. and *Pocillopora* spp. colonies, and they exhibit high levels of territorialism and aggression towards corallivores. They effectively discourage the invasion of *A. planci* by clipping and pinching the soft tissues of intruders (Glynn, 2013). The feeding rate of *D. rugosa* was reduced by 22.9% in the presence of the coral guard crab (*Trapezia cymodoce*) (Samsuri et al., 2018). It is important to exercise caution during biological control and conduct a comprehensive assessment of the selected species to prevent ecological disasters in coral reef ecosystems.

5.3 Manual removal

Manual removal is a recommended method for controlling *Drupella* snail outbreaks under current conditions. Manual removal, which involves clearing both juveniles and adults, the former involves inspecting exposed coral skeletons on the reef for early detection of *Drupella* snails' egg capsules and removing them to decrease the likelihood of outbreaks. Moreover, manual removal has been implemented successfully in various regions. According to other researchers, it is advisable to carry out extermination activities in southwestern Shikoku (Japan) between February and March, prior to the spawning season (Kitamura et al., 2022). By implementing the extermination program of *Drupella* snails, Japan effectively controlled the number of *Drupella* snails, causing the density of *Acropora* spp. to remain high even in the cold winter, despite *Acropora* spp. being more sensitive to low temperatures and more prone to predation under cold stress conditions. This precisely illustrated the importance of manually removing *Drupella* snails (Kimura et al., 2005). The local government is employing methods like manual removal of *Drupella* snails and implementing restrictions on human activities to assist in the restoration of coral reefs (Lam et al., 2007). The manual removal of 14,000 individuals by volunteer divers effectively mitigated the outbreak of *Drupella* snails in Thailand, resulting in a significant decrease in *Drupella* snails density from 7.9 ind/m^2 in October 2010 to 5.6 ind/m^2 in April 2021 (Scott et al., 2017a). Removing a distinct species of corallivorous snail, *C. abbreviata*, from coral reefs resulted in a significant increase in the area of live coral tissue in comparison to areas where the snail clusters were left untouched (Miller, 2001). Manual removal is the most immediately effective method in the short term. However, it also has certain restrictions. For example, it can only temporarily alleviate the damage caused by outbreaks and cannot solve the issue fundamentally. Manual removal is expensive, and its operational depth is limited, making it impossible to remove snails in deeper waters. Additionally, its effectiveness in controlling widespread outbreaks of *Drupella* snails is not significant.

5.4 Alternative methods and perspectives

In addition to the aforementioned strategies, alternative methods can be utilized for the control of *Drupella* snails. For example, a Japanese research team has developed specific antibodies for the planktonic larvae of *Drupella* snails, which can be used for low-cost and rapid on-site detection. This can help better monitor the population dynamics of *Drupella* snails and predict their outbreaks (Kitamura et al., 2021).

To address the outbreak of *Drupella* snails in the long term, further research and comprehensive studies are necessary. Exploring the physiological and reproductive characteristics of different species of *Drupella* snails can provide a basis for early outbreak management. Initially, researchers believed that only a single species was responsible for the outbreaks. However, as knowledge advanced, it was discovered that sometimes multiple species of *Drupella* snails were involved in the outbreak, and there were significant physiological differences among different species of *Drupella* snails. For example, *D. margariticola* does not have specialized mouth structures and can only feed on coral that has already been attacked by other *Drupella* species (Claremont et al., 2011a). Therefore, understanding the physiological and reproductive characteristics of different species of *Drupella* snails, especially the duration of their planktonic larvae, metamorphosis, and feeding habits, can provide a basis for early outbreak management. Additionally, establishing population dynamic models, identifying environmental triggers, and studying the interactions between *Drupella* snails and their predators will contribute to developing more effective control strategies.

Furthermore, based on the aggregation characteristics of *Drupella* snails, it is possible to identify the main components of specific pheromones (such as mucus released during conspecific feeding, coral fragment secretions, etc.) associated with *Drupella* snails' aggregation. By analyzing the main components, targeted trapping devices can be designed (Kita et al., 2005). Additionally, *Drupella* snails possess the characteristic of evading areas with natural predators. By analyzing the main components of pheromones released by their natural predators, it is feasible to create dispersal devices that may serve as potential control strategies for outbreaks.

Notably, it is crucial to raise awareness among local communities, policymakers, and stakeholders about the ecological importance of coral reef ecosystems and the impacts of *Drupella*

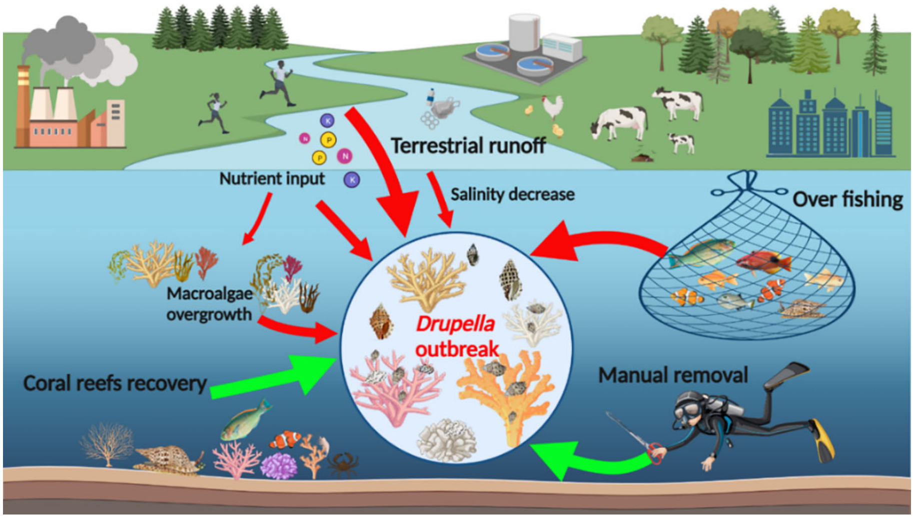

FIGURE 3
A schematic diagram of *Drupella* snail outbreaks and mitigation strategies.

snail outbreaks. Education and outreach programs can promote sustainable practices and encourage community involvement in the conservation and restoration of coral reefs.

6 Conclusion

Addressing the recurrent outbreaks of *Drupella* snails requires a multifaceted approach (Figure 3). Protecting coral reef ecosystems, implementing biological control methods, utilizing manual removal, and exploring alternative techniques are all important strategies. Additionally, conducting further research, raising awareness, and promoting community involvement will contribute to the long-term management and conservation of coral reef ecosystems affected by *Drupella* snail outbreaks.

Author contributions

FZ: Conceptualization, Data curation, Validation, Writing – original draft. XJ: Validation, Writing – review & editing. ZL: Validation, Writing – review & editing. YJ: Validation, Writing – review & editing. MQ: Conceptualization, Funding acquisition, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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