

BRIEF REPORT

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First reported field observations of *Drupella* spp. feeding on milleporids in Indo-Pacific reefs

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Abstract

Outbreaks of the corallivorous gastropod *Drupella* spp. are increasingly recognised as a major driver of coral reef degradation across the Indo-Pacific. While *Drupella* is typically associated with predation on scleractinian corals, particularly *Acropora*, interactions with milleporids remain understudied. Here, we report the first observation of *Drupella* feeding on *Millepora* spp. in the Indo-Pacific, based on field observations from shallow reefs (1–4 m) at Gili Asahan, Lombok, Indonesia (8.739482 N, 115.890852 E). During a 90-minute survey, *Drupella* snails were observed within six colonies of *Millepora dichotoma*, *M. tenera* and *M. intricata*. Adult snails were found in deep skeletal recesses, with white scars directly underneath the snails suggesting active feeding. Occasional spillover of *Drupella* aggregations onto adjacent *Acropora* colonies was also observed. The predominance of adult *Drupella* within *Millepora* colonies may suggest an ontogenetic shift in habitat use and prey choice, likely driven by feeding plasticity, refuge availability and energetic demands. We propose that the complex skeletal structure of *Millepora* provides both shelter and an alternative prey source, facilitating *Drupella* persistence under variable resource conditions. This interaction may have cascading ecological consequences, as milleporids provide important habitat for reef-associated fauna and are vulnerable to climate change. These findings highlight an underappreciated local corallivore-hydrozoan interaction and emphasise the need for targeted monitoring of *Millepora* during *Drupella* outbreaks in Lombok to better understand emerging reef trophic dynamics.

Keywords Corallivory, Indonesia, *Drupella*, *Millepora*, Prey switching

1 Introduction

Outbreaks of *Drupella* spp. in the Indo-Pacific have been documented since the 1980s [2, 31], but research interest has only increased substantially in the past decade. Recent research from India, Australia, Mauritius, and Thailand has advanced our understanding of these corallivorous snails and their role in coral reef degradation [15, 17, 19, 28]. The ecological consequences of these outbreaks can be severe. For instance, in the Ningaloo Marine Park in Western Australia, extensive grazing by *Drupella* has been linked to massive coral loss along at least 100 km of reef, with mean reductions of 86% in reef flat and back-reef coral cover from 1980 to 1987, and a 47% decline at a monitored fore-reef



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slope [2]. In addition to direct tissue removal, *Drupella* snails facilitate the transmission of coral diseases by inflicting wounds through feeding which allow pathogens to infect coral and further compound mortality during outbreaks [33]. Multiple anthropogenic stressors appear to drive population explosions. Overfishing reduces *Drupella* predators such as members of Labridae (wrasses), Ballistidae (triggerfish), Lutjanidae (snapper), and Diodontidae (pufferfish), while climate change further destabilises coral communities by weakening coral resilience to stressors such as elevated sea surface temperature, nutrient enrichment, sedimentation and pollution. These stressors compromise coral health and recovery capacity, thereby creating conditions conducive to *Drupella* outbreaks [29, 52]. A growing concern is *Drupella*'s ability to switch prey when its preferred prey (i.e., acroporid corals) declines. Following bleaching-induced *Acropora* loss, *Drupella* snails have been observed feeding on previously avoided taxa such as fungiid corals and *Pavona* spp. (Hoeksema et al. [17], Shafir [44]; Toofany et al., under review). This demonstrates considerable feeding plasticity, enabling the survival of the snails, while imposing new predation pressure on corals typically not preyed upon by *Drupella*. As a result, regular monitoring and targeted culling efforts are becoming increasingly urgent on affected reefs.

Milleporidae (Order: Anthoathecata, Class: Hydrozoa), also known as fire corals, are abundant in the Indo-Pacific, where their rapid growth and high fecundity allow them to compete effectively for space, often outperforming many scleractinian corals [9, 25]. Although both milleporids and scleractinian corals contribute to reef building, they differ functionally within reef ecosystems. Scleractinian corals are considered the primary long-term reef builders due to their calcium carbonate skeletons and relatively slower growth [51], whereas milleporids typically function as fast-growing opportunistic space competitors that rapidly colonise available substrate and interact aggressively with neighbouring benthic organisms [25]. Their ability to overgrow neighbouring corals can cause stress and partial mortality, representing an important mechanism of spatial competition in reefs [9]. Of the 16 *Millepora* species recognised globally, six are found in Indonesian waters [39, 50]. Beyond their competitive dominance, milleporids play a vital role in the reef community by providing habitat and refuge for a wide range of marine organisms, including providing nursery habitat to fish [23] and hosting symbiotic invertebrates [13, 16, 42, 46]. *Millepora* possess nematocysts, which deliver painful stings and can offer protection against certain predators [34]. This defensive capability can partly explain why they are favoured as a habitat by many invertebrates [10, 25]. Collectively, these findings demonstrate the ecological significance of milleporids that support diverse reef-associated communities. While corallivores usually feed on scleractinian corals such as *Acropora*, *Porites*, *Montipora*, and *Pocillopora* [26, 40], interactions with milleporids are increasingly documented. In the U.S. Virgin Islands, the opportunistic fireworm, *Hermodice carunculata*, caused substantial damage to *M. complanata* by grazing on the branch tips, reducing their growth rate [49]. Similar predation has been recorded on *M. alcicornis* in Brazil [37]. In the same region, eight reef fish species, six of which were juveniles, have been recorded feeding on milleporids, including the parrotfish *Sparisoma axillare*, the butterflyfish *Chaetodon striatus*, and the damselfish *Stegastes rocasensis* [36]. Although the crown-of-thorns seastar, *Acanthaster planci*, typically avoids preying on milleporids [20, 21], it will consume *Millepora* spp. when preferred prey is scarce [5, 11], with direct predation also photographed in the field [45].

Similar prey switching from scleractinian corals to milleporids was also observed in corallivorous snails. In the Gulf of Eilat, large aggregations of *Drupella cornus* initially fed on their usual prey, *Acropora* spp. and *Pocillopora damicornis* before shifting to *M. dichotoma* and other unusual prey species [44]. Earlier observations in the Red Sea also recorded *D. cornus* occurring on reef slopes dominated by *Acropora-Millepora* assemblages [53].

2 Materials and methods

2.1 Sampling site

Gili Asahan (8.739482 N, 115.890852 E, Fig. 1), located within the Gita Nada Marine Protected Area in Lombok, Indonesia, supports a shallow reef system (1–4 m depth), followed by a slope and with a sandy bottom of 14–16 m. The site has a reef cover of approximately 40–60% [18] dominated with acroporids and poritids, with high scleractinian diversity of 136 morphologically identified species throughout the site, though actual diversity may be higher [14]. The site has a history of overfishing and pearl farming, with ongoing coral restoration efforts by SeaChange Indonesia (a marine conservation NGO) that include targeted *Drupella* removal from scleractinians.

2.2 Sampling method

On 4 July 2025, corallivorous snails were recorded on six *Millepora* colonies during a 90-minute survey conducted using SCUBA. *Millepora* colonies (minimum diameter of 50 cm) were haphazardly inspected across the shallow reef flat (1–4 m depth) for the presence of corallivorous snails. The six colonies of *Millepora* sampled were identified as *Millepora dichotoma*, *M. tenera* and *M. intricata* (Supplementary Fig. S1), based on morphological descriptions by Razak and Hoeksema [39]. The corallivorous snails were identified to the genus *Drupella* based on external shell morphology during the field survey. Species-level identification was not attempted as several *Drupella* species exhibit

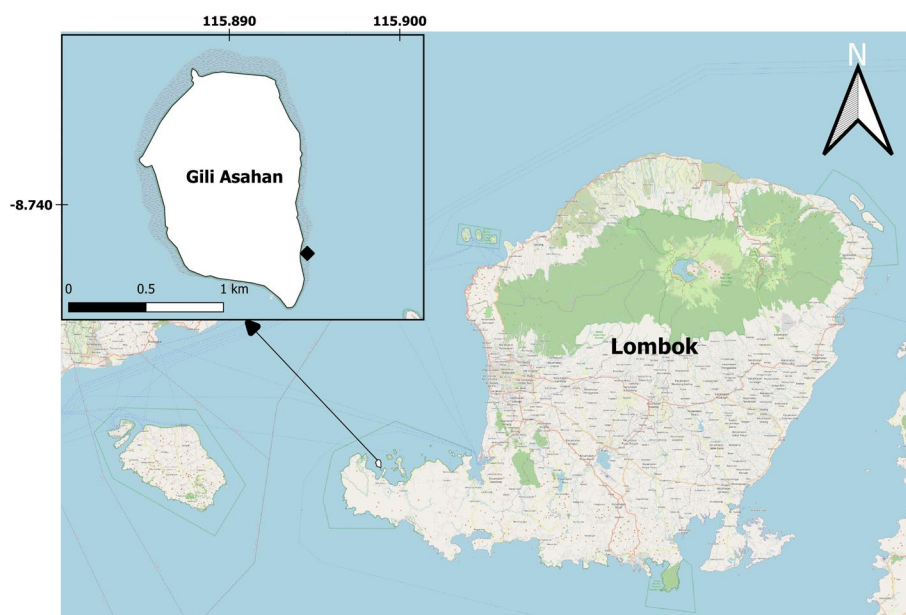


Fig. 1 Map showing the location of Gili Asahan, off the southwest coast of Lombok. The sampling area is indicated with a black diamond

highly similar shell characteristics, and reliable identification often requires detailed taxonomic examination or molecular analysis.

A two-person buddy-team sampling approach limited search efforts to a maximum of 20 min per colony or until no additional snails were detected. *Drupella* were removed from the colonies using scissors and long tweezers to avoid breakage of the *Millepora* branches. Adult snails (> 2 cm shell length; [47, 52]) were found within milleporid structures, including deep recesses with exposed coral skeletons directly underneath snails suggesting active feeding (Fig. 2a). Other adults were found on exposed surfaces without visible feeding scars. In two cases, aggregations were hypothesised to spill from the *Millepora* onto nearby *Acropora* spp. (Fig. 2b), where active feeding was documented. The direction of movement was inferred as *Drupella* were found throughout the *Millepora* colony, and only at the corner of the *Acropora* colony facing the *Millepora*; however, continuous behavioural observations were not conducted, and thus movement direction could not be definitively confirmed. Following collection, the snails were bleached to remove encrusting organisms, measured using a vernier calliper, and photographed to document morphological variation (Supplementary Fig. S2). Shell length was defined as the maximum linear distance from the tip of the apex to the distal end of the siphonal canal, measured along the central axis of the shell [15].

2.3 Statistical analyses

Due to the limited number of colonies observed for each *Millepora* species, occurrences were reported descriptively and no species-level statistical comparisons were conducted. Figure 4 was created using R Version 4.5.2 [38].

3 Results

All collected corallivorous snails were identified as belonging to the genus *Drupella*. A total of 122 *Drupella* spp. from six *Millepora* colonies were collected for this study in a 90-minute period (Table 1). *Millepora* colonies were classified as mature as they had a minimum width of 50 cm and their horizontal surface area (length * width of colony) was calculated to enumerate *Drupella* density in each colony. As an added measure, ellipsoid colony volume of *Millepora* ($(\pi * \text{length} * \text{width} * \text{height of colony})/6$) was calculated and was found not to correlate with the number of *Drupella* found in the colonies ($R^2 = 0.0252$).

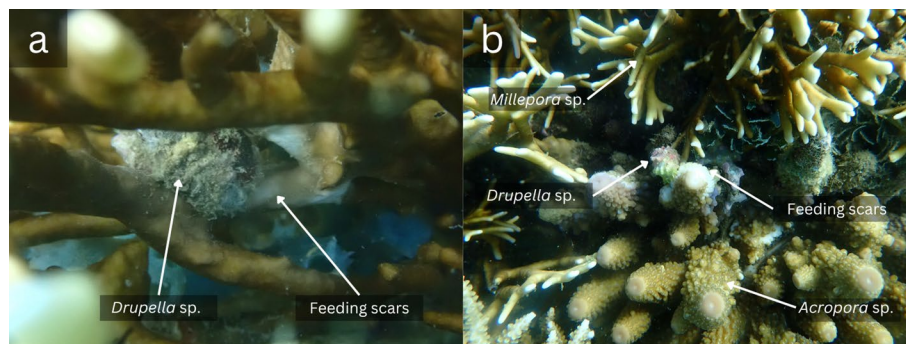


Fig. 2 a *Drupella* snails feeding scar observed within a *Millepora* colony; b Spillover of *Drupella* snails from the *Millepora* onto nearby *Acropora* colony

Table 1 Summary of *Millepora* colonies sampled, with approximate horizontal surface area (length * width of colony; SA), ellipsoidal volume ((π * length * width * height of colony)/6; V), number of *Drupella* spp. individuals removed, presence of feeding scars on the colony, and observation notes of each colony

Colony no.	Colony species	Colony SA (m ²)	Colony V (m ³)	No. adults	No. juveniles	Total	Density (ind. m ²)	Feeding scars on colony	Observation notes
1	<i>M. intricata</i>	0.7	0.15	37	3	40	57.14	Yes	Isolated colony
2	<i>M. tenera</i>	2.16	0.68	7	0	7	3.24	Yes	On restoration frame, near other colonies; spillover to <i>Acropora humilis</i>
3	<i>M. intricata</i>	1.26	0.40	16	3	19	15.08	No	Adjacent to <i>Acropora florida</i> ; no spillover
4	<i>M. intricata</i>	4.8	2.01	20	1	21	4.38	No	Adjacent to <i>Pocillopora</i> sp.; no spillover
5	<i>M. dichotoma</i>	1.4	0.37	16	5	21	15	No	Adjacent to <i>Dipsastraea</i> sp.; no spillover
6	<i>M. intricata</i>	0.77	0.16	11	3	14	18.18	Yes	Adjacent to <i>Porites</i> sp.; no spillover

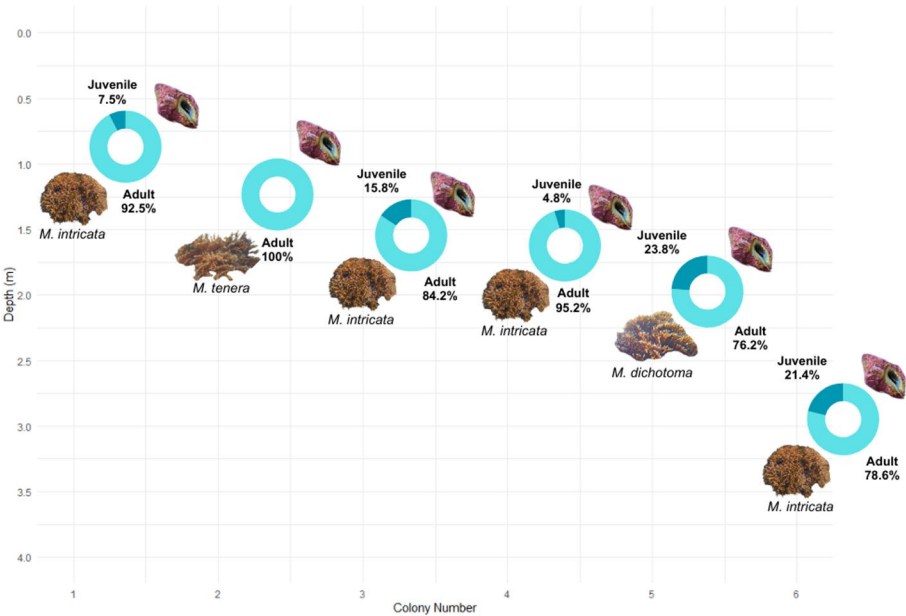


Fig. 3 Percentage of adult vs. juvenile *Drupella* snails observed in the six colonies of *Millepora dichotoma*, *M. intricata* and *M. tenera* at varying depths (1–4 m)

3.1 Possible ontogenetic segregation and prey choice

A majority of the *Drupella* collected during this study were adults (Figs. 3 and 4; Table 1), comprising the dominant life stage across all sampled colonies. Juveniles were present in five of the six surveyed colonies but consistently occurred in lower proportions. Shell-length distributions overlapped substantially among *Millepora* host species, with comparable median values across colonies (Fig. 4). Most adult snails measured between 20 and 25 mm in shell length, with the largest individual reaching 28 mm. Juveniles ranged between 17 and 19 mm, with the smallest individual measuring 14 mm. Although the number of *Drupella* varied among colonies (Fig. 4), visual comparison did not reveal a clear host-specific trend. Given the limited replication, these observations are presented descriptively.

4 Discussion

4.1 Microhabitat characteristics of *Millepora* as potential refugia

These observations, to our knowledge, represent the first reported case of *Drupella* feeding on *Millepora* in the Indo-Pacific. The predominance of adult *Drupella* within

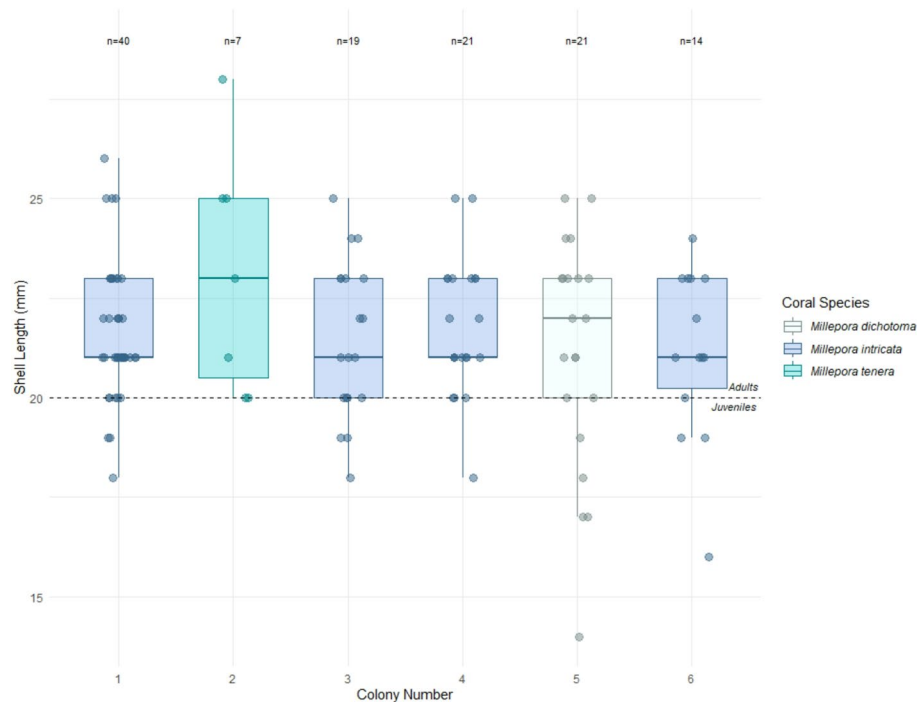


Fig. 4 Distribution of shell length in mm of collected *Drupella* snails in the six colonies of *Millepora dichotoma*, *M. intricata* and *M. tenera*

Millepora colonies, coupled with the low number of juveniles, suggested a size-based host association possibly driven by ontogenetic shifts in feeding behaviour, refuge use, energetic requirements and feeding plasticity. The complex reticulate skeleton of *Millepora* has deep cavities that may offer adult *Drupella* shelter from predators and protection from hydrodynamic exposures. The snails are known to exhibit short-term residence, moving between colonies and leaving each site before the colony is fully eaten [7]. Adult *Drupella* may therefore exploit *Millepora* both as a habitat and as a secondary prey source. This dual use is consistent with reports from the Gulf of Eilat and Red Sea, where *Drupella* have been observed within *Millepora* colonies during periods of prey scarcity [44, 53]. In contrast, *Drupella* sampling in the present study did not coincide with periods of siltation or thermal stress, suggesting that *Millepora* use in this report was not driven by the absence of preferred prey.

Larger, and possibly more resilient, *Drupella* adults may therefore exhibit greater feeding plasticity, allowing them to better exploit less-preferred coral species while benefiting from the structural protection provided by *Millepora*. In contrast, juveniles, which have higher energetic requirements for growth and survival, may preferentially target more nutritious prey such as *Acropora* [1, 24, 43]. Juvenile *Drupella* are shown to exhibit distinct prey preferences and occupy different coral hosts, revealing an ontogenetic shift in feeding behaviour [3, 43]. Ontogenetic differences in movement behaviour are well documented, and studies on gastropod movement suggest that body size strongly influences foraging behaviour under resource limitation, which may have occurred in this instance.

Repeated movement of *Drupella* between the coral genera is likely influenced by chemical cues. Competition and reduced food availability are known to trigger dispersal in sea snails [4], and density-dependent movement has been reported in other snail

species such as the limpet, *Cellana tramoserica* [27]. Similarly, *Boonea impressa* was observed moving frequently among different aggregates on its oyster host, with up to 20–30% of individuals moving around every day [48]. Investigations of *Drupella* movement and residence times likewise showed frequent relocation both within and between coral colonies, sometimes within a few days, resulting in highly dynamic group sizes [7]. Together, these patterns may explain the crowding-dispersal strategy in the observed *Drupella*, with individuals shifting between *Millepora* to *Acropora* in response to local density and resource conditions.

4.2 Potential behavioural mechanism linking adult occupancy and movement

Movement of *Drupella* between *Millepora* and adjacent *Acropora* may be influenced by short-range behavioural cues rather than broad-scale habitat selection alone. Chemical cues from stressed or competitively overgrown *Acropora* are known to attract corallivorous gastropods [22, 30], and *Drupella* snails have been shown to move more than 1 m overnight in response to such cues [12]. *Millepora* are widespread in the island of Gili Asahan, and individual colonies tend to form bushes (30–150 cm wide) that grow beside scleractinian corals in the shallows (1–5 m). The occasional observations of aggregations spilling from *Millepora* onto neighbouring *Acropora* suggest that adult *Drupella* may use *Millepora* as refuge or staging habitat before exploiting nearby, chemically detectable prey.

In this context, the competitive dominance of *Millepora* in the site may further reinforce these dynamics. Overgrowth-induced stress in adjacent acroporids could enhance chemical signalling, increasing their susceptibility to corallivory while indirectly facilitating *Millepora* expansion. However, this advantage may be short-lived, as continued *Drupella* predation on milleporids could ultimately offset any competitive gains.

4.3 Ecological implications for *Millepora* and associated reef communities

Active feeding by adult *Drupella* on *Millepora* may represent a previously underappreciated trophic interaction. As *Millepora* often serve as nursery habitats for juvenile fishes and host diverse symbiotic invertebrates, increased corallivore pressure may reduce habitat availability for associated taxa. Given the vulnerability of *Millepora* to thermal stress and the limited long-term persistence of *Millepora*-dominated phase following heatwaves [8], additional mortality from *Drupella* could pose added risk to these reef communities. The presence of *Drupella* snails within milleporids colonies thus may have cascading ecological consequences. Beyond partial mortality, *Drupella* increases biotic pressure through prey switching or feeding plasticity, further compounding existing climate-drive stressors such as elevated temperatures and ocean acidification [32, 41].

Reports from multiple regions suggest that *Millepora*-dominated reef states are often transient. In the U.S. Virgin Islands, a marine heatwave eliminated 84% of the newly established milleporid community following a post-disturbance dominance [8]. In the Maldives, *Millepora*-dominated zones were lost during the bleaching event of 1998 and have only recently reemerged in the northern most regions [35]. Anecdotal observation from Gili Asahan suggest a different trajectory: following the 2016 mass coral bleaching event, scleractinian-dominated reefs south of the study site were reportedly replaced by *Millepora*. The *Drupella*-*Millepora* associations described here may have indirectly

contributed to such phase shift through prey-switching during stressful periods and subsequent overgrowth of scleractinians by *Millepora*.

Although the long-term impacts of *Drupella* predation on milleporids remain unclear, this added corallivore pressure may accelerate declines in already vulnerable *Millepora* populations. Observations from Gili Asahan highlight the feeding plasticity of *Drupella*, underscoring the potential risk to newly exploited prey species and their associated communities.

5 Conclusion

This study documents a potential emerging *Drupella*-*Millepora* interaction in Lombok, characterised by size-linked habitat and prey associations. While these observations suggest that *Drupella* may exploit an expanded range of prey taxa under contemporary disturbance events, the findings should be interpreted with caution due to the limited sample size and qualitative nature of the observations. Further research is therefore needed to quantify the prevalence, severity and feeding rates of *Drupella* on *Millepora* across broader spatial scales. Future studies should also incorporate nocturnal surveys to better capture snail foraging behaviour, given that *Drupella* snails are primarily active at night [6] and examine the potential interactions with other coral prey and competitors. Moreover, genetic or morphometric identification of collected snails will help clarify species-level patterns as the taxonomy of *Drupella* remains under revision [15]. Continued monitoring is needed to assess the broader ecological implications and to inform targeted removal efforts where appropriate.

Acknowledgements

The authors would like to thank Oceanway for providing SCUBA support and Niek Wassink for assisting with sample collection.

Author contributions

The study was conceptualised by Febrianne Sukiato and Kok Lynn Chew. Data collection was conducted by Febrianne Sukiato. Data analysis and visualisation was performed by Tanya Toofany. The first draft of the manuscript was written by Tanya Toofany with inputs by Febrianne Sukiato and Kok Lynn Chew. Febrianne Sukiato: Conceptualization, Methodology, Investigation, Resources, Writing- Reviewing and Editing. Kok Lynn Chew: Conceptualization, Methodology, Writing- Reviewing and Editing. Tanya Toofany: Software, Formal Analysis, Data Curation, Writing- Reviewing and Editing, Visualization.

Funding

Open Access funding enabled and organized by Projekt DEAL. The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Data availability

The data collected during this study will be made available on reasonable request. Please contact author FS (febri.suki@gmail.com) for raw data used in this study.

Declarations

Permits

This study was conducted under Indonesian permit Persetujuan Kesesuaian Kegiatan Pemanfaatan Ruang Laut (PKKPRL) no. 02092410515200007.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Received: 28 January 2026 / Accepted: 15 April 2026

Published online: 27 April 2026

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