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RESEARCH ARTICLE

Distribution and Population Structure of Corallivorous *Drupella* Snails in the Coral Reefs of Kenting in Taiwan

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Abstract

The corallivorous *Drupella* snails are common predators of living hard corals in the Indo-Pacific Ocean, and they can significantly threaten coral reef ecosystems when outbreaks occur. In Taiwan, a *Drupella* outbreak, which resulted in the dramatic decline of *Acropora* and *Montipora* corals, was reported in Penghu in 2002–2009. However, the *Drupella* species involved was not identified, and no further research has been conducted. To obtain current knowledge on the predation pressure of corallivorous snails on hard corals, we investigated benthic communities and the distribution and population structure of *Drupella* snails in the coral reefs of Kenting, Taiwan. The composition of benthic communities revealed hard coral coverage ranging from 28.7 to 72.1% among the three surveyed sites at depths of 3–5 and 8–10 m. *Drupella cornus* (n = 326) and *Drupella fragum* (n = 6) had shell lengths of 13.6–40.1 and 8.0–17.8 mm, respectively. The density of *Drupella* snails among sites varied from 0.07 to 2.07 ind/m^{2}, with no clear trend observed with water depth. Eight percent of the 1424 hard coral colonies contained *Drupella* snails; most patches only had one individual (48.2%). More snail patches were found in areas with more *Montipora* and *Pocillopora* colonies. Moreover, *Porites* corals were the avoided prey of *Drupella* snails. Although most *Drupella* snails formed a small patch (1–4 individuals) in this region, due to the current density being five times higher than in 2013 (i.e., 0–0.37 ind/m^2) and the existence of two *Drupella* species, we recommend broadening the survey areas better to understand the population dynamics of these corallivorous snails for local coral reef governance.

Keywords: *D. cornus*, *D. fragum*, Prey preferences, *Montipora*

1. Introduction

The corallivorous *Drupella* snails are common predators of living hard corals distributed in the Indo-Pacific Ocean and Red Sea, including Australia, Kenya, Thailand, Vietnam, Jordan, Hong Kong, Hainan Island, Mauritius, and Taiwan [1–11]. In the field, they are usually associated with coral species of *Acropora*, *Pocillopora*, *Montipora*, *Porites*, *Stylophora*, etc. [3, 12–16]. Laboratory tests also confirmed that *Drupella* snails preferred to prey on branching *Acropora* corals [6, 17]. *Drupella* snails can significantly threaten coral reef ecosystems when outbreaks occur. An outbreak occurs when populations increase to elevated, abnormal densities, significantly threatening coral reef ecosystems. Cumming reviewed the literature on population densities of *Drupella* spp. in coral reefs in Australia, Hong Kong, Japan, Jordan, and Sudan and proposed normal (or non-break) populations as having densities in the range of 0–2 individuals (ind)/m^2 [1]. Besides, the *Drupella* outbreak is also defined as the feeding rate of the predatory *Drupella* snails exceeding the growth rate of their prey corals. Bessey et al. proposed a linear relationship where outbreak densities ranging from 0.95 to 2.83 ind/m^2

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corresponded to coral coverage of 17–60% [18]. Recently, Zhang et al. summarized outbreak densities of *Drupella* snails, ranging from 2 to 158 ind/m^2 [19]. They suggested that the composition of predatory species, local coral assemblages, and environmental conditions all play crucial roles in determining the outbreak threshold density of snails.

There are six recorded *Drupella* species in the world, i.e., *Drupella cornus* (Röding, 1798), *Drupella rugosa* (Born, 1778), *Drupella eburnea* (Küster, 1862), *Drupella fragum* (Blainville, 1832), *Drupella margariticola* (Broderip, 1833), and *Drupella minuta* (Fujioka, 1984) [20,21]. Adult *D. cornus* are usually found individually, in pairs, or in small groups (<10), but large aggregates of up to 200–300 individuals have been reported during outbreaks [1,22–24]. Aggregation in hundreds to thousands was also reported on species of *D. rugosa* and *D. fragum* [7,15,25]. *Drupella* aggregation has generally been observed on corals under environmental stress, such as disease, bleaching, siltation, predation, low salinity, breakage, overfishing, anthropogenic pollution, or thermal stress [12,22,26–29]. The release of chemical cues by damaged coral tissues may be responsible for such aggregations to be formed and maintained [22,26,29–32].

So far, information on species diversity and population structure of *Drupella* snails is scarce in Taiwan. The density data of *Drupella* snails was obtained ten years ago, i.e., 1.7–22.7 and 0.01–0.37 ind/m^2 in the coral reefs of Penghu and Kenting, respectively [10,11]. Hence, we provide recent observations of the predation pressure of *Drupella* snails on reef-building corals in the Kenting area of southern Taiwan.

2. Materials and methods

The study locations were selected in the Kenting area, namely Hejie (HJ), Houbihu (HB), and Outlet (OL) (Fig. 1). Hejie is situated on the west coast of Kenting. Houbihu and Outlet are upwelling-influenced sites in a bay [33]. Moreover, OL is also affected by cooling discharge water from the Third Nuclear Power Plant, where its water temperature is 1–2°C higher than that of background environments.

The survey was conducted in July 2023 by SCUBA. To investigate the benthic communities and abundance of *Drupella* snails, we applied three 15-m transect lines laid out in shallow (3–5 m) and deep (8–10 m) waters at each location. The substrata of the transect lines had no sand or reef trench, and the distance between lines was at least 5 m apart.

We used a video transect line method to examine benthic communities. Thirty 35 × 35 cm quadrats were placed on either side of the transect line at least 50 cm apart, and photographs were taken of each quadrat.

To analyze the image data, we uploaded the pictures to the CoralNet website (https://coralnet.ucsd.edu/) [34]. Fifty points were stratified and randomly assigned to each photograph. Each point was identified and classified into seven categories: hard coral (HC), soft coral (SC), macroalgae (MA), tufted algae (TA), crustose coralline algae (CCA), bleached or diseased coral (DC), and other fauna and substrate (Others). Points assigned to shadows, blurred areas,

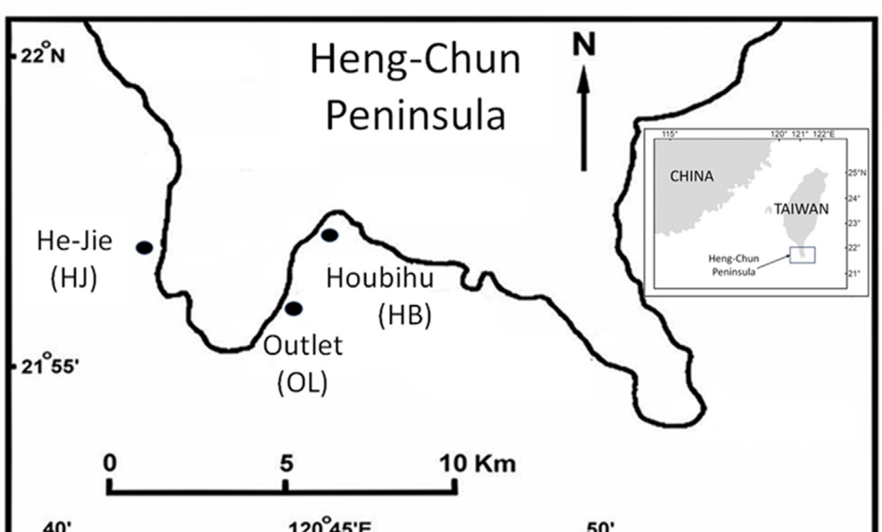

Fig. 1. The survey sites with both deep and shallow sampling zones in Kenting, Taiwan.

and human-made objects in the photographs were excluded from the analysis. The results of point identification were summarized to calculate the coverage of each benthic type. In addition, the number of discrete hard coral colonies was counted and classified at the genus level, including Scleractinia corals, *Millepora*, *Heliopora*, and *Tubipora*.

We examined the abundance of *Drupella* snails within a meter of each transect line's left and right sides in a total area of 30 m^2. We recorded all the patches and individuals in each patch. The genus of those inhabited corals was also investigated. A patch was defined as an aggregate of snails ranging from 1 to several hundred individuals. In cases where large corals grew in overlapping layers extending up to 5−6 m long, such as *Montipora* corals, a 1 m^2 area along the transect was considered one coral colony. The snails were collected using forceps and kept in zipper bags. In the laboratory, *Drupella* species and their shell length were determined.

The shell of *Drupella* snails is usually obscured by calcareous incrustation [35]. The adult size of *Drupella conus* is 20−35 mm. The shell is white, and its shape is from fusiform to cylindrical. The interior of the outer lip has 6−7 moderate denticles, the upper one larger than the lower. The columellar lip has 2−4 folds. The adult of *D. fragum* is 15−27 mm. It is white and ovoidal in shape. Interior of the outer lip has 5−7 denticles. The columellar lip has 3−4 folds.

Data on the composition of benthic communities and hard corals were analyzed separately by two-way crossed ANOSIM and global tests to assess differences among sites and depth. Pairwise Global R-values in ANOSIM give an absolute measure of separation for all groups. The density and shell length of *Drupella* snails among sites were analyzed by a one-way ANOVA and Tukey's post-hoc tests. All univariate and multivariate analyses were performed using PRIMER 6.0 [36]. The Pearson correlation was used to estimate the preference of preyed corals of *Drupella* snails. The Real Statistics Resource Pack software (Release 8.9.1) for Microsoft Excel, developed by Charles Zaiontz (www.real-statistics.com), was used for the analysis.

3. Results

The composition of benthic communities revealed hard coral coverage ranging from 28.7 to 72.1% among sites (Table 1 & Fig. 2). Macro algae were 25.1 and 19.1% at HJ_S and OL_S. Other sites were covered by 1.0−8.1%. The coverage of turf algae was from 18.1 to 39.9% among sites. Crustose coralline algae (CCA) were 3.0−7.6% in deep waters and 2.0−3.4% in shallow waters. The genera of hard corals of the surveyed sites were summarized in Fig. 3. HJ_D had the highest amount of hard coral genera and colonies, i.e., 12 and 291, respectively. Two-way crossed ANOSIM tests revealed significant effects of site and depth on both benthic composition and genera of hard corals, respectively (Table 2). Depth was more important in explaining variation than site based on R values of benthic composition (i.e., 0.605 vs. 0.547) and genera of hard corals (i.e., 0.955 vs. 0.840), respectively. The lowest similarity between sites for benthic composition was HB and OL ($R = 0.556$), for the genera of hard corals being OL vs. HJ ($R = 0.833$).

A total of 332 *Drupella* snails were recorded comprising *D. cornus* and *D. fragum* (Table 3 & Fig. 4). *D. cornus* was prominently abundant, with densities ranging from 0.07 to 2.07 ind/m^2 among sites. More *Drupella* snails inhabited HB_D than at other sites (Table 3). *D. fragum* was only found at OL_D, with a density of 0.07 ind/m^2.

The sizes of *D. cornus* and *D. fragum* ranged from 13.6 to 40.1 and 8.0−17.8 mm, respectively (Fig. 5). Their mean shell lengths were 33.1 ± 5.2 ($n = 326$) and 13.1 ± 1.4 mm ($n = 6$), respectively (Table 3). Six juvenile *D. cornus* from 13.4 to 14.9 mm were observed at OL_D (Fig. 5) inhabiting *Acropora* corals. The six *D. fragum* were juveniles. Four of them lived

Table 1. Benthic composition of the survey sites in Kenting, Taiwan. CCA: crustose coralline algae; HB: Houbihu; HJ: Hejie; OL: Outlet; D: deep water; S: shallow water.

Site	Benthic structure types						
	Hard coral (%)	Soft coral (%)	Macro algae (%)	Turf algae (%)	CCA (%)	Bleach & Diseased coral (%)	Other fauna & Substrate (%)
	Mean ± Se	Mean ± Se	Mean ± Se	Mean ± Se	Mean ± Se	Mean ± Se	Mean ± Se
HB_S	72.10 ± 1.8	0.6 ± 0.1	1.0 ± 0.2	21.2 ± 1.1	2.1 ± 0.4	0.2 ± 0.1	2.9 ± 0.9
HB_D	65.90 ± 1.9	5.6 ± 3.2	2.3 ± 0.5	18.1 ± 3.0	3 ± 0.8	2.4 ± 1.1	2.8 ± 1.0
OL_S	57.30 ± 3.4	0.6 ± 0.4	19.4 ± 2.6	19.1 ± 1.9	2 ± 0.6	1.4 ± 0.3	0.2 ± 0.1
OL_D	44.20 ± 4.0	8.7 ± 3.9	1.9 ± 0.7	36.3 ± 7.1	7.6 ± 1.4	0.8 ± 0.4	0.5 ± 0.3
HJ_S	28.70 ± 1.9	1.1 ± 0.2	25.1 ± 1.2	39.9 ± 0.7	3.4 ± 0.2	1.0 ± 0.3	0.8 ± 0.1
HJ_D	46.40 ± 5.3	2.1 ± 0.1	8.1 ± 1.4	34.1 ± 3.5	5.9 ± 0.4	2.5 ± 1.2	1 ± 0.1
All	52.50 ± 3.7	3.1 ± 1.0	9.6 ± 2.3	28.1 ± 2.8	4 ± 0.6	1.4 ± 0.3	1.4 ± 0.3

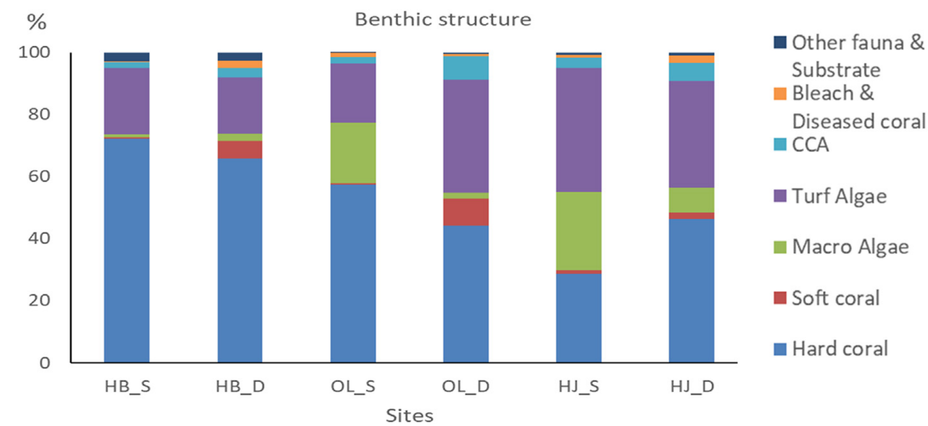

Fig. 2. Benthic composition of the survey sites in Kenting, Taiwan. HB: Houbihu; HJ: Hejie; OL: Outlet; D: deep water; S: shallow water.

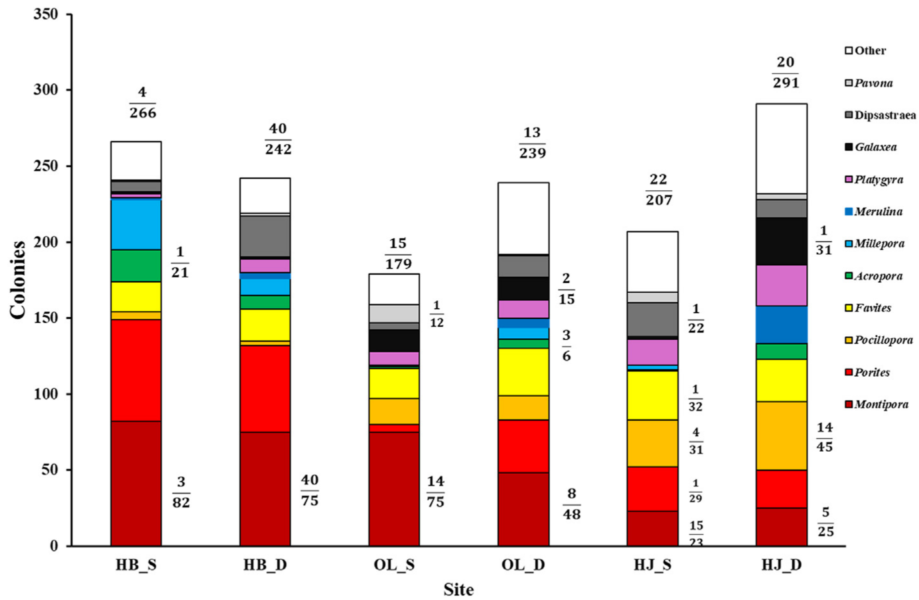

Fig. 3. Genera of hard corals and total number of coral colonies with Drupella snail patches in surveyed sites. Numerator: colony with snails; Denominator: total colonies; HJ: Hejie, HB: Houbihu; OL: Outlet; S: shallow waters; D: deep waters.

Table 2. Results of global tests from the 2-way crossed ANOSIM tests for differences among sites and depth for benthic compositions and genera of hard corals respectively. R: ANOSIM statistic; p: probability level.

Group level	Site		Depth	
	R	*p*	*R*	*p*
Benthic composition	0.547	0.002	0.605	0.01
HB/OL	0.556	0.02		
HB/HJ	0.741	0.01		
OL/HJ	0.611	0.02		
Genera of hard corals	0.840	0.002	0.955	0.001
HB/OL	1	0.01		
HB/HJ	1	0.01		
OL/HJ	0.833	0.01		

with five *D. cornus* juveniles in an *Acropora* colony. Two other patches had single individuals inhabiting the *Acropora* and *Montipora* corals.

Most snail patches only had one individual (48.2%) (Fig. 6). The greatest patch had 16 samples inhabiting a *Montipora* colony. Four patches contained more than ten snails, all at HB_D. Only one patch had a mixture of *D. cornus* and *D. fragum*.

The proportion of coral colonies with *Drupella* patches in the surveyed sites ranged from 1.5 to 16.5% (Fig. 3), with an average of 8% across the total colonies (n = 1424) (Fig. 6). The number of snail patches on preyed corals generally correlated with

Table 3. Densities (ind/m^2 ± Se) and shell length (mm ± Sd) of Drupella cornus and D. fragum found at study sites. HB: Houbihu; HJ: Hejie; OL: Outlet; D: deep water; S: shallow water; n: sample size. Letters A, B, and C indicate significant differences by one-way ANOVA and Tukey's post-hoc test ($p < 0.05$).

Site	Average Density (ind/m^2±Se)			Average Shell length (mm ± Sd)	
	D. cornus (n = 326)	*D. fragum* (n = 6)	All species (n = 332)	*D. cornus*	*D. fragum*
HB_S	0.07 ± 0.04^{C}	0	0.07 ± 0.04	$29.9 \pm 1.3^{A,B}$	
HB_D	2.07 ± 0.11^{A}	0	2.07 ± 0.11	34.0 ± 3.5^{A}	
OL_S	$0.20 \pm 0.08^{B,C}$	0	0.20 ± 0.08	31.5 ± 2.6^{A}	
OL_D	$0.20 \pm 0.07^{B,C}$	0.07 ± 0.12	0.27 ± 0.13	26.9 ± 7.9^{B}	12.8 ± 2.6
HJ_S	0.69 ± 0.24^{B}	0	0.69 ± 0.24	27.2 ± 3.9^{B}	
HJ_D	$0.40 \pm 0.24^{B,C}$	0	0.40 ± 0.09	26.8 ± 4.4^{B}	
All	0.60 ± 0.17	0.01 ± 0.01	0.61 ± 0.17	31.3 ± 5.2	12.8 ± 2.6

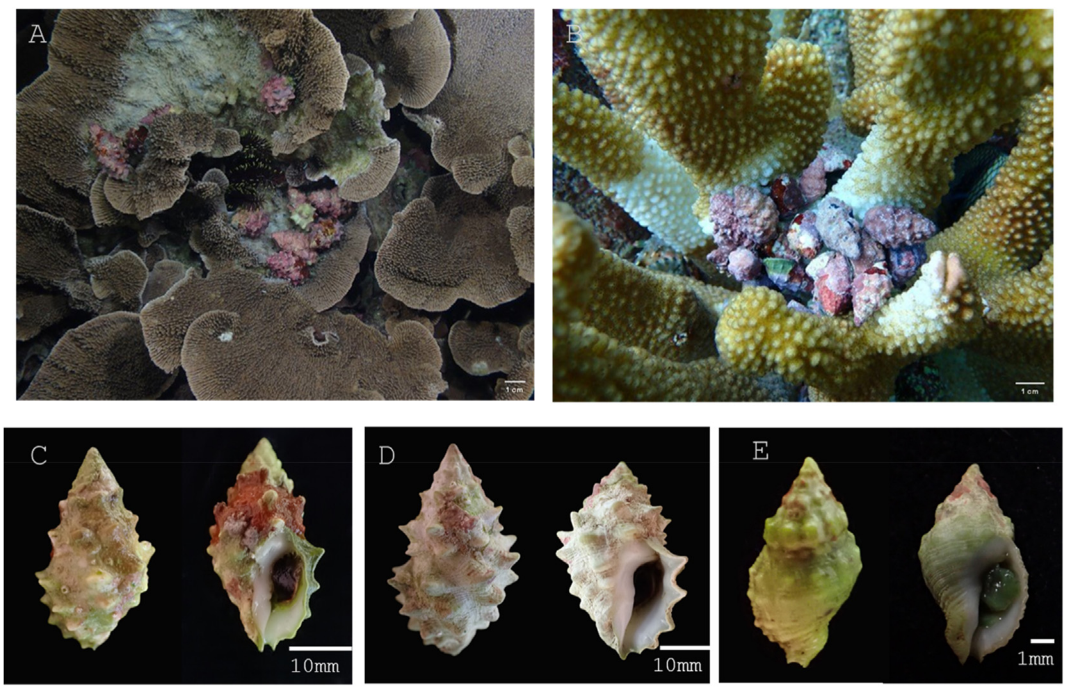

Fig. 4. Drupella snails inhabiting hard corals in Kenting, Taiwan. A: Montipora sp.; B: Pocillopora sp.; C and D: D. cornus; E: D. fragum.

the abundance of the coral genera (Pearson's coefficient = 0.701, $p < 0.05$). For example, *Montipora* was the most abundant genus at HB and OL, with coverages of 20.9–41.9%. The preyed proportion was 3.7–53.3%. *Pocillopora* was the most abundant coral genus at HJ_D (15.5%), and its preyed proportion was 31.1%. Notably, the coverage of *Acropora* corals was 0.5–7.9%, and their preyed proportion was 0–50% across all sites. By contrast, *Montipora* corals had more snail patches than others at HJ_S, although it ranked fourth among hard corals, i.e., *Favites* (32) > *Pocillopora* (31) > *Porites* (29) > *Montipora* (23), respectively. Another common phenomenon was that *Porites* corals were typically disliked by *D. conus* despite being the second most abundant corals at HB_D, HB_S, and OL_D.

4. Discussion

This study investigated the distribution and population structure of *Drupella* snails in the coral reefs of Kenting. Two species were recorded, i.e., *D. cornus* and *D. fragum*. The density of *Drupella* species ranged from 0.07 to 2.07 ind/m^2 among sampling sites with no clear trend concerning water depth. Among the 1424 coral colonies, 8% had *Drupella* snails. Snail patch size varied from 1 to 16 individuals. High abundant hard corals generally were inhabited by more *Drupella* patches except for *Porites* corals.

The predation pressure of *D. cornus* on hard corals was more severe than those in 2013, i.e., 0.07–2.07 vs. 0–0.37 ind/m^2 [11]. The density ranged in the

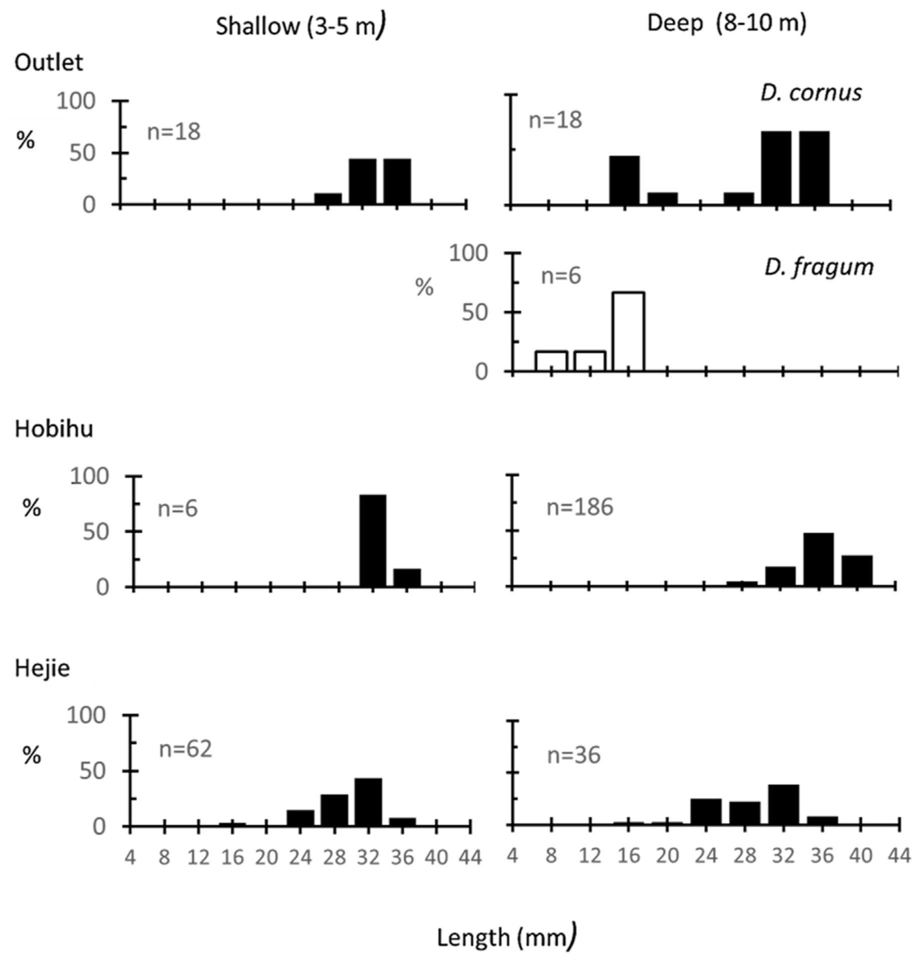

Fig. 5. Size-frequency distributions of Drupella cornus and D. fragum collected from the study sites in Kenting, Taiwan. n: sample size. Black bar: D. cornus; White bar: D. fragum.

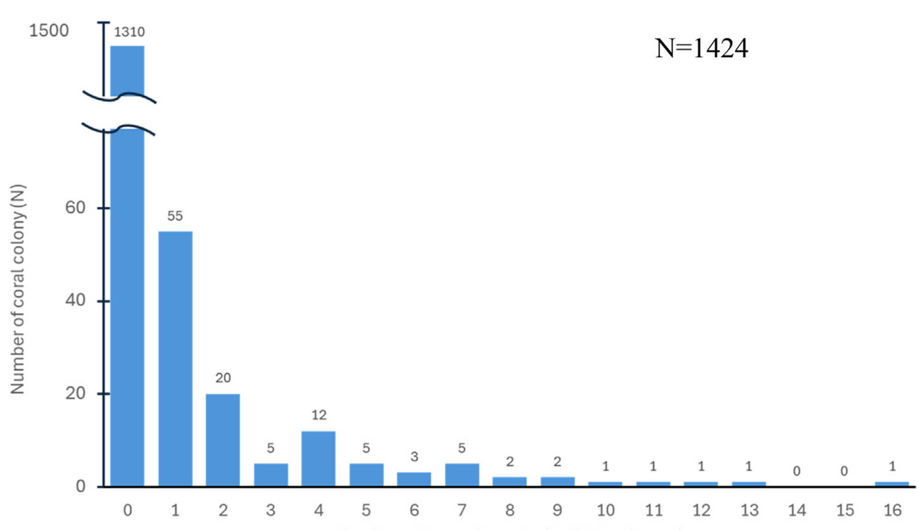

Fig. 6. The number of patches with Drupella snails in surveyed coral colonies. Data were collected from Hejie (HJ), Houbihu (HB), and Outlet (OL) in July 2023.

non-outbreak category (<2 ind/m^2) proposed by Cumming [1]. However, according to the outbreak density derived from the relationship between the *D. cornus* feeding rate and *Acropora* growth rate [18], the density of this study exceeded the outbreak threshold, i.e., 0.61 vs. 0.53 ind/m^2. Moreover, *D. fragum* was found in Kenting for the first time with a density of 0.07 ind/m^2.

Based on the population structure and mark-recapture studies of *D. cornus* in Western Australia [24,37], the size of recruit, juvenile, and adult was categorized as <1.0, <2.0, and >2.0 cm, respectively. In the present study, the size ranges of *D. cornus* and *D. fragum* were 13.6–40.1 and 8.0–17.8 mm, 95% of which were adult except for *D. fragum*. The size-frequency distributions revealed *D. cornus* contained recruits, juveniles, and mature individuals. Thus, it is worth monitoring the *Drupella* populations and taking necessary action to prevent an outbreak in Kenting.

Our surveys indicated that adult *Drupella* spp. preferred *Montipora* and *Pocillopora* corals, while *Porites* was disfavored (Fig. 3). This finding was consistent with studies by Boneka et al. [23] and Schoepf et al. [22] as *Montipora* was the most abundant genus in our study sites of HB and OL. However, more snail patches were found on the fourth-ranked *Montipora* at one of the surveyed sites (i.e., HJ_S), which had the lowest coverage of hard corals (28.7%) compared to the others (44.2–72.1%) (Fig. 2). *Porites* corals appear to be avoided by *Drupella* spp. However, their abundance was the second at sites of HB_D, HB_S, and OL_D (Fig. 3). In the investigation conducted in southern Bunaken Island in Indonesia, the abundance of *D. cornus* was following the occurrence order of coral genera, i.e., *Montipora*, *Acropora*, and *Porites*, respectively [23]. Another case was in the northern Red Sea, where the most dominant *Acropora* corals were preferred by *D. cornus* [22]. The distribution of *Drupella* spp. and their feeding ecology were investigated in the southeastern Hainan Island [8]. The coverage of living hard corals ranged from 0.8 to 37.5%. In general, the preferred prey corals of *Drupella* species were correlated with abundance, with the Acroporidae being the most abundant and preferred. *Drupella* spp. had a positive tendency to prey on *Porites* corals at one of the five surveyed sites on Hainan Island. The authors also pointed out that the favored coral prey generally contained relatively high nutritional value, e.g., high protein content, lipid content, and tissue thickness.

In Taiwan, the *Drupella* outbreak at Chinwan Inner Bay of Penghu caused a significant decline in coral coverage from 80.8% in 2001 to 34.1% in 2003 and further to 16.3% in 2008 [10]. The *Drupella* inhabiting *Galaxea fascicularis*, *Montipora cactus*, and *Acropora muricata* were 48.1, 37.0 and 7.4%, consistent with the coverage trend of the corals in 2001 (i.e., 25.5, 16.7, and 6.7%, respectively), but not in the year 2003 (i.e., 5.2, 3.7, and 13.3%, respectively). This phenomenon may suggest that *Drupella* is significantly shaping the coral community. The prey preference of *Drupella* spp. may exhibit dietary plasticity, which relates to the overall coverage of living hard corals, the abundance of each coral taxon, their nutrition value, or their tissue thickness [8,22]. These clues can be applied in this research to elucidate why *Drupella* snails avoid *Porites* corals.

Our study revealed that an average of 8% of prey corals were inhabited by *Drupella* snails, most harboring small patches (1–4 individuals). Therefore, a slight portion of prey colonies were damaged by *Drupella* grazing since adult snails devour 1.8 cm^2 of coral tissue per night [38]. However, due to a severe massive coral bleaching event that occurred in 2020 [39] and the presence of two *Drepella* species in the reef regions of Kenting, we recommend that large-scale monitoring programs assess the spatial trends better to understand the population dynamics of these corallivorous snails for local government policy-making and management.

Ethics approval

Ethical approval was not applicable for the present study because this study did not involve human or vertebrate experiments.

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Conflict of interest

The authors declare no conflicts of interest associated with this paper.

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