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EDITED BY
Dilip Kumar Jha,
National Institute of Ocean Technology, India

REVIEWED BY
Xinqing Zheng,
State Oceanic Administration, China
Wentao Niu,
Ministry of Natural Resources, China
Jiayuan Liang,
Guangxi University, China

*CORRESPONDENCE
Guowei Zhou
zhougw@scsio.ac.cn
Hui Huang
huanghui@scsio.ac.cn

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Spatial variability in the abundance and prey selection of the corallivorous snail *Drupella* spp. in the southeastern Hainan Island, China

Xinming Lei[1,2,3], Chengyue Liu[1,2,3], Yuyang Zhang[1,2,3], Xiaolei Yu[1,3], Jianhui Yang[1,3], Yong Luo[1,3], Guowei Zhou[1,3*] and Hui Huang[1,2,3*]

[1]CAS Key Laboratory of Tropical Marine Bio-Resources and Ecology, Guangdong Provincial Key Laboratory of Applied Marine Biology, South China Sea Institute of Oceanology, Innovation Academy of South China Sea Ecology and Environmental Engineering, Chinese Academy of Sciences, Guangzhou, China, [2]Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou, China, [3]CAS-HKUST Sanya Joint Laboratory of Marine Science Research and Key Laboratory of Tropical Marine Biotechnology of Hainan Province, Tropical Marine Biological Research Station in Hainan, Chinese Academy of Sciences, Sanya, China

Global climate change has caused extensive loss of biodiversity and ecosystem function globally, particularly in coral reefs in shallow tropical waters. As the corallivorous snails represent considerable disturbances to coral reefs across Indo-Pacific region, it is becoming a threat to coral health and recovery in the Hainan Island, South China Sea, but current-knowledge gap remains on the spatial distribution, prey preferences, and the influence factors related. Thus, we investigated the abundance distribution of *Drupella* spp. in relation to coral-prey selectivity, availability, and nutritional value. The snail density was heterogeneously distributed in the study area with an average of 0.72 ± 0.32 ind m^{-2} (varying from 0.09 ± 0.03 to 1.78 ± 0.39 ind m^{-2}), and the snail density was found generally higher in locations with higher coral cover, which resulted in much lower density where their preferred corals became scarce. Despite the snails showing a positive preference for Acroporidae corals, they displayed dietary plasticity by changing with prey abundance and availability. Further, we found the electivity index of the coral prey related to the substrate types, and the nutritional value of prey was an additional important determinant in the prey preference, suggesting that the specific reef habitat and environmental context may alter the prey preference of *Drupella* spp. Combined, these results provide preliminary evidence that *Drupella* spp. is among the common corallivories in the reef regions of Hainan Island, and we recommend that large-scale monitoring programs assess the spatial-temporal trends to better understand the dynamics of predation linked to both anthropogenic and natural impacts.

KEYWORDS

Corallivory, coral, prey selection, spatial variation, *Drupella*

Introduction

Coral reefs are highly biodiverse but are among the most threatened habitats on Earth, facing unprecedented risk from global climate change, overfishing, and pollution (Hughes et al., 2018; Wolff et al., 2018; MacNeil et al., 2019). Due to these anthropogenic and natural disturbances, coral reefs are continuously deteriorating across the world (Gardner et al., 2003; Hoegh-Guldberg et al., 2007; Hughes et al., 2017). Although individual environmental threats (e.g., temperature, pH) to coral reefs have been well studied, the negative effect of corallivores could aggravate the reef degradation process (Rice et al., 2019). To mitigate losses in coral cover, it is essential to seek to identify the ecological processes and make well-informed conservation decisions that promote coral survivorship.

Feeding activities of corallivores have negative effects on coral growth and fitness, varying from minor to lethal damage and subsequently leading to fundamental changes in the reef state (Turner, 1994b; Rotjan and Lewis, 2008; Rice et al., 2019). For instance, an outbreak of crown-of-thorns starfish (*Acanthaster* spp., COTS) has caused high-coral mortality and reduced coral cover by up to 80% (Pratchett et al., 2017). High densities of other corallivores such as *Coralliophila* spp. and *Drupella* spp. have been reported to impact corals strongly in the Indo-Pacific, Western Indian Ocean, and Asia (Moyer et al., 1982; Boucher, 1986; Mcclanahan, 1994; Bruckner et al., 2017).

The genus *Drupella* is among the well-known corallivores occurring on coral reefs of the Indo-Pacific Ocean (Turner, 1994b; Claremont et al., 2011). Generally, these corallivorous gastropods are found in coral reef regions at a low density of 0–2 ind m^{-2} (Cumming, 1999; Cumming 2009a), while the outbreak of *Drupella* could reduce the live coral cover by more than 75% in the coral reef areas with a mean density of 14.73 ± 4.37 ind m^{-2} (Turner, 1994a; Turner 1994b). There were large aggregation or outbreak events of *Drupella* spp. have been observed in various regions, including Western Australia (Ayling and Ayling, 1987; Turner, 1994b), Great Barrier Reef (Cumming, 1999), Red Sea (Antonius and Riegl, 1998), Kenya (Mcclanahan, 1994), Thailand (Moerland et al., 2016; Scott et al., 2017), Maldives (Bruckner et al., 2017) and Hong Kong (Cumming and McCorry, 1998; Morton and Blackmore, 2009). Both anthropogenic (overfishing of natural predators, coral reef damage, and terrestrial run-off) and natural (changes in temperature and salinity) causes have been proposed to explain these events (Turner, 1994b; Turner, 1994a; Cumming, 2009b; Cumming, 2009a).

Previous studies have reported that these corallivorous snails display significant feeding selectivity and are affected by the relative abundance of each coral taxon (Morton and Blackmore, 2009). Many corallivores exhibit high dietary plasticity with respect to their coral prey, feeding on less preferred corals when their favored corals are not abundant. For instance, *Drupella* spp. had shifted their dietary preference for coral species of Acroporidae and Pocilloporidae to the less preferred fungiid corals after a major coral bleaching event in Thailand (Hoeksema et al., 2013; Moerland et al., 2016). Nevertheless, Morton et al. (2002) found that the snails of *D. rugosa* still preferred the low-abundance coral *Acropora* spp. in the reefs of Hong Kong despite being primarily dominated by massive corals. Hence, the coral assemblage composition might influence their diet varies as well. Additionally, the importance of the nutritional value of the prey species to prey preference has received attention in COTS (Pratchett et al., 2014; Keesing, 2021), while the data on the food selectivity of *Drupella* spp. is scarce.

In recent years, the aggregations of four species of *Drupella* spp., named *D. cornus*, *D. rugose*, *D. fragum*, and *D. margariticola* (Zhang and Zhang, 2007; Peng et al., 2014), have been constantly observed in the reef regions of Hainan Island. However, information regarding the snail aggregation and the coral status in these reef regions is still limited. Furthermore, the coral reefs in Hainan Island have suffered more from coastal development, pollution, overfishing, and destructive fishing practices than climate change (Hughes et al., 2013), which resulted in the live coral cover of the fringing reefs declining by more than 80% up to now. Nevertheless, both coral loss and recovery vary between each reef due to the different occurrence of disturbances (Lian et al., 2010; Zhang et al., 2016; Huang et al., 2020), and consequently, variation in both coral species abundance and cover may influence the ecology of the related organisms such as corallivores, in different ways.

The impact of corallivores in Hainan Province has recently attracted scientific attention, focusing on the outbreaks of *A. planci* (Li et al., 2019a; Li et al., 2019b). However, no information is available on the spatial distribution of *Drupella* spp., and the feeding ecology of these corallivorous snails is still poorly described in Hainan Island. The study aimed to investigate the distribution patterns and prey selection of *Drupella* spp. and the associated factors influencing its feeding preference in the southeastern Hainan Island. In particular, we tested the hypotheses that (1) the abundance distribution of *Drupella* spp. varies with coral abundance; and (2) reef substrate types and the nutritional value of coral prey are related to the prey selection of the corallivores.

Materials and methods

Study area

A field study was conducted from July 2019 to December 2020 along the coast of the southeastern Hainan Island, South China Sea. Our study area included five locations (Figure 1) with the intensive distribution of reef coral communities to enable convenient sampling and detection of *Drupella* spp. (Mollusca, Gastropoda, Muricidae).

Xiaozhou Island (XZD) and Xiaodonghai (XDH) are located at the east and west sides of the Luhuitou Peninsula of Sanya, respectively, and the marine environments are significantly affected severely by intensive human activities (e.g., coastal works, tourists activities, sewage discharges) (Titlyanov et al., 2019). Wuzhizhou Island (WZZ) is a small uninhabited island located about 2.7 km off the northern coast of Sanya. However, the marine environments are influenced by direct human activities (e.g., constructions, marine traffic, diving activities) (Huang et al., 2020). Fenjiezhou Island (FJZ) is a small island located at the junction of Lingshui County and Wanning City, and 2.2 km off the east coast of Hainan Island. Due to its exceptional coastal and diving tourism resources, the marine environment of this uninhabited island is affected by coastal construction, tourist activities, and disordered harvesting of marine resources, etc. (Bai et al., 2016). Dazhou Island (DZD) is another uninhabited small island located about 11 km away from the coast, and it has been the National Marine Ecological and Climatic Nature Reserve since September 1990. There are no constructive activity being conducting on it. Therefore, there are two types of sample sites among the five research stations: inshore sites (XZD and XDH) and offshore sites (WZZ, FJZ, and DZD).

Biological and environmental data collection

The shells of the snails are often encrusted with crustose coralline algae and other epifauna, which makes their *in situ* identification difficult. To avoid misidentification, the snail taxa were identified to the genus level and pooled as *Drupella* spp.

To examine the effects of variation in coral cover, abundance, and substrate pattern on the population structure, prey preferences, and spatial distribution of *Drupella* spp., we surveyed five locations along the southeast coast of Hainan Island. According to the accessibility of each site, three replicate belt transects of 20 m in length and 2.5 m on either side, lying parallel to the shoreline, were randomly selected at a depth of 1–3 m at each sample station. The survey depth was set in accordance with the previous studies, which reported that *Drupella* spp. is mainly distributed in shallower reef areas (Turner, 1994a; Cumming, 2009a; Scott et al., 2017; Hamman, 2018).

The benthic reef community composition was determined by the linear point intercept (LPI) method (Nadon and Stirling, 2006)

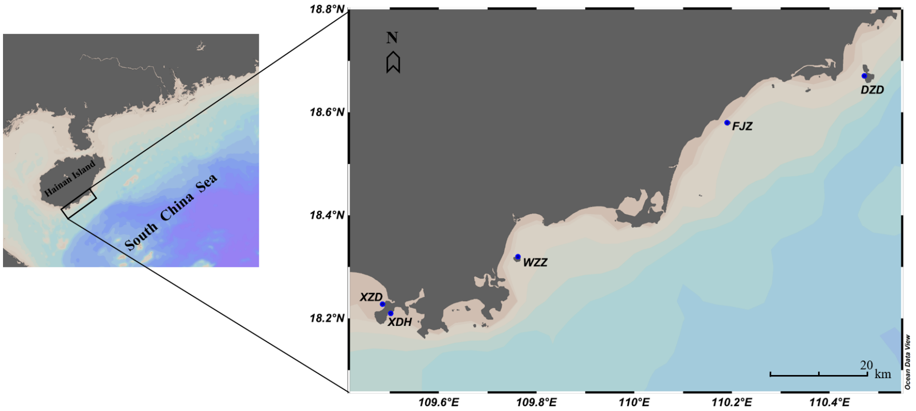

FIGURE 1
Research stations along the southeastern part of Hainan Island.

on the same belt transects. Within each transect, types of substrate were identified as live coral, dead coral, rock, sand, macroalgae, and other sessile invertebrates. During the survey, special emphasis was given to the substrate directly under the *Drupella* individuals, while the corals were identified to species level to study the detailed prey preference and to broad categories for all other substrate types. *Drupella* spp. was considered relating to corals whether they were in an aggregation over the living tissue or a dead part of a living coral colony or near the feeding scar, because they should move from one coral colony to another to find food or shelter (Cumming, 1999; Morton et al., 2002).

Statistical analysis

Statistical comparisons of the spatial variation of the predator density and percentage of live coral cover between stations were analyzed using the permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. Furthermore, the feeding preferences of *Drupella* spp. were investigated using the Ivlev (1961) electivity index (E_i). E_i was estimated using the formula:

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

For this equation, r_i represents the proportion of prey in the diet and p_i represents the proportion of prey in the environment. Values of E_i range between 1 (maximum preference) and −1 (maximum avoidance), whereby 0 indicates random feeding. We calculated r_i as the frequency of corallivorous snails on a specific i species or genus of coral in relation to all the preyed colonies within each station.

The distribution and abundance of coral species, especially the species used as prey by *Drupella* spp., are likely to influence the distribution and abundance of the predator. Therefore, the similarity of coral species distribution for stations was analyzed using the ANOSIM test based on the Bray–Curtis similarity coefficient (Clarke and Gorley, 2015). Non-parametric multi-dimensional scaling (nMDS) ordinations were used to visualize the similarities and dissimilarities in coral community composition between stations, with a bubble plot showing the coral species preyed upon by *Drupella* spp. ($E_i > 0.5$) in each sample station. We took the percentage of live coral cover as the relative abundance of corals at every station.

To explore the relationship between the electivity of coral prey and the benthic variables at each study station, we employed a nonparametric distance-based linear model (DISTLM) along with distance-based redundancy ordination analysis (dbRDA). The DISTLM models the relationship between these variables mentioned and the multivariate E_i of the coral dataset based on a multiple regression model as a way to determine the linear combination of variables that explains the greatest amount of variation in the elected coral community dataset, and it examines the amount of variance explained by each variable. Before analysis, benthic variable data were averaged, and a Draftsman plot was used to assess the collinearity between variables. Variables with a high degree of collinearity (Spearman's correlation coefficient $|r| > 0.85$) were removed from the DISTLM analyses. Additionally, DISTLM was initially used to analyze the marginal effects of each variable, followed by the application of the "best" model building process with a R^2 selection to identify the best set of factors explaining the variation in the preferred coral community.

Additionally, principal component analysis (PCA) was used to investigate the features of the nutritional value of prey of the coral genus. The PCA multivariate analysis of the coral genera nutritional value of prey data, including lipid content (mg cm^{-2}), protein content (mg cm^{-2}), tissue biomass (ash-free dry weight, mg cm^{-2}), *Symbiodinium* density ($\times 10^6$ cells cm^{-2}), Chlorophyll-a content (Chl-a, µg cm^{-2}), tissue thickness (mm), and polyp density (polyps cm^{-2}). These data were obtained from the Coral Trait Database (Madin et al., 2016) and some published studies (Achituv et al., 1994; Loya et al., 2001; Anthony and Hoegh-Guldberg, 2003; Leuzinger et al., 2003; Edmunds et al., 2014; Qin et al., 2020; Keesing, 2021). The obtained species data were averaged as genus values, and the missing values were filled out using linear regression (Table S2).

All analyses were performed using PRIMER v7 software, including the PERMANOVA+ add-on package (Anderson et al., 2008; Clarke and Gorley, 2015).

Results

Abundance and spatial distribution

During the survey period, we counted individuals of *Drupella* spp. with an overall average density of 0.72 ± 0.32 ind m^{-2}. Snail density was higher at the offshore sites (WZZ, FJZ, and DZD) compared to the inshore sites (XZD, XDH) (Figure 2A). The variation of snail densities among the stations was found to be statistically significant ($p<0.05$), with mean densities ranging from 0.09 ± 0.03 ind m^{-2} at station XDH, up to 1.78 ± 0.39 ind m^{-2} at station DZD. Similarly, the percent live hard coral cover varied significantly among the stations as well ($p<0.05$), with the mean value ranging from 0.83 ± 0.60% at station XDH, up to 37.52 ± 0.07% at station WZZ (Figure 2B). The mean number of individuals per aggregation was 4.56 ± 1.28 for all *Drupella* spp. individuals pooled together; ranging from a minimum of 1 to a maximum of 38 individuals found on a single coral species, *Acropora hyacinthus* (at DZD).

There were 70 coral species in the total found among the five research stations (Table S1), of which 30 species belonging to 10 genera were preyed on by *Drupella* spp. (Tables 1, 2). The number of coral species ranged from four at XDH to 38 at WZZ, and the other benthic reef substrate variables showed

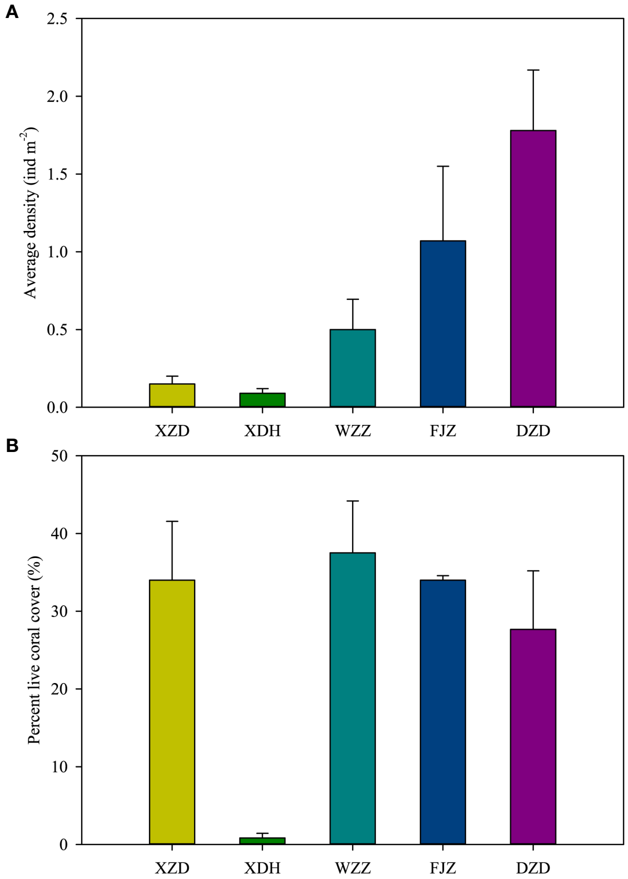

FIGURE 2
Spatial differences in **(A)** average snail density and **(B)** average percent live coral cover for each station. Bars indicate standard error.

significant differences among the research stations, except for sand, macroalgae, and the other sessile invertebrates (Table 3). The top three genera with the highest proportion at each station were *Favites* (30.39%), *Acropora* (25.00%), and *Platygyra* (15.20%) in XZD, *Oulastrea* (40.00%), *Montipora* (20.00%), and *Favites* (20.00%) in XDH, *Porites* (32.16%), *Acropora* (24.78%), and *Montipora* (13.19%) in WZZ, *Galaxea* (37.09%), *Porites* (24.48%), and *Platygyra* (7.09%) in FJZ, *Acropora* (22.29%), *Favites* (17.47%), and *Acanthastrea* (12.05%) in DZD, respectively. The coral community structure varied significantly among the research stations (ANOSIM, global R = 0.62, p = 0.001) (Figure 3).

Prey selection and preferences

Prey preference varied at different stations according to the availability of coral prey. Coral species belonging to the family Acroporidae (*Acropora* and *Montipora*) were all preferred positively by *Drupella* spp. among the sample stations. Considering the preferred coral prey (E_i >0.5 at any station) of the snail, there were 20 coral species, and the abundance and distribution of these species were different in the sample stations (ANOSIM, global R = 0.52, p = 0.001), with species *A. gemmifera*, *Montipora* sp., and *P. lobata* being more abundant in the stations XZD and DZD, while the other eight species (*A. cytherea*, *A. formosa*, *A. hyacinthus*, *A. intermedia*, *Acropora* sp., *G. fascicularis*, *Goniastrea* sp., and *Porites* sp.) were more abundant in the stations WZD and FJZ (Figure 3, Table 1).

Species belonging to the genera *Acropora*, *Echinophyllia*, *Favites*, *Montipora*, and *Pocillopora* had positive values of the electivity index (E_i) in the five sample stations, while the other species had at least one negative value of the index in all stations (Table 1). At the genus level, all the genera of coral prey had positive values of E_i in the sample stations, except for the genera of *Galaxea*, *Porites*, *Platygyra*, and *Lobophyllia*, which were the avoided prey by *Drupella* spp. in the station FJZ (Table 2).

TABLE 1 Feeding preferences of *Drupella* spp. according to the Ivlev's electivity index (E_i) considering the coral species preyed upon at each station.

Species	XZD	XDH	WZZ	FJZ	DZD
Acropora cytherea	–	–	0.79	–	–
Acropora digitifera	–	–	–	–	1.00
Acropora formosa	–	–	0.79	–	1.00
Acropora gemmifera	–	–	1.00	–	–
Acropora hyacinthus	–	–	–	–	1.00
Acropora intermedia	–	1.00	0.74	–	1.00
Acropora microclados	–	–	–	–	1.00
Acropora robusta	0.09	–	–	–	–
Acropora sp.	–	–	1.00	0.77	–
Echinophyllia aspera	–	–	–	0.58	–
Favites abdita	0.18	–	–	0.58	–
Favites flexuosa	–	–	–	0.58	–
Favites micropentagonus	0.58	–	–	–	–
Favites sp.	0.04	–	–	–	–
Galaxea fascicularis	–	–	0.33	−0.10	0.73
Goniastrea retiformis	–	–	–	−0.14	–
Goniastrea sp.	–	–	–	1.00	–
Lobophyllia corymbosa	–	–	–	−0.03	–
Montipora efflorescens	–	–	–	1.00	–
Montipora informis	–	–	–	–	1.00
Montipora sp.	–	–	–	0.77	–
Montipora turgescens	–	–	–	1.00	–
Montipora venosa	0.01	–	–	–	–
Platygyra pini	0.40	–	–	–	–
Platygyra sinensis	–	–	–	−0.33	–
Platygyra sp.	−0.11	–	–	–	–
Pocillopora damicornis	0.30	–	–	–	0.31
Porites lobata	–	–	–	–	1.00
Porites lutea	–	–	–	−0.20	−0.22
Porites sp.	–	–	–	–	1.00

XZD, Xiaozhoudao; XDH, Xiaodonghai; WZZ, Wuzhizhou; FJZ, Fenjiezhou; DZD, Dazhoudao.

TABLE 2 Feeding preferences of *Drupella* spp. according to the Ivlev's Electivity Index (E_i) considering the coral genera preyed upon at each station.

Genera	XZD	XDH	WZZ	FJZ	DZD
Acropora	0.09	1.00	0.82	0.77	1.00
Montipora	0.01	–	–	0.85	1.00
Galaxea	–	–	0.33	−0.10	0.73
Echinophyllia	–	–	–	0.58	–
Favites	0.30	–	–	0.58	–
Pocillopora	0.30	–	–	–	0.31
Porites	–	–	–	−0.20	0.31
Goniastrea	–	–	–	0.20	–
Platygyra	0.09	–	–	−0.33	–
Lobophyllia	–	–	–	−0.03	–

XZD, Xiaozhoudao; XDH, Xiaodonghai; WZZ, Wuzhizhou; FJZ, Fenjiezhou; DZD, Dazhoudao.

TABLE 3 Benthic reef substrate variables at each station. mean ± SE.

Variable	XZD	XDH	WZZ	FJZ	DZD	p-value
Average live coral cover	34.00 ± 7.57	0.83 ± 0.60	37.52 ± 6.68	34.00 ± 0.58	27.67 ± 7.54	<0.001
Number of coral species	21 ± 2.2	4 ± 0.9	38 ± 2.5	30 ± 2.3	22 ± 2.1	0.003
Dead coral cover	2.50 ± 0.00	66.50 ± 15.40	43.56 ± 3.09	35.00 ± 0.00	2.50 ± 1.61	<0.001
Rock	59.50 ± 6.51	0.00 ± 0.00	3.00 ± 3.00	4.00 ± 0.00	49.50 ± 5.11	<0.001
Sand	0.67 ± 0.67	6.34 ± 3.28	6.33 ± 4.10	7.00 ± 0.00	12.17 ± 11.43	0.67
Other sessile invertebrate	3.33 ± 2.03	0.00 ± 0.00	9.42 ± 5.89	19.50 ± 0.00	8.17 ± 2.05	0.23
Macroalgae	0.00 ± 0.00	26.33 ± 14.17	0.17 ± 0.17	0.50 ± 0.00	0.00 ± 0.00	0.07

XZD, Xiaozhoudao; XDH, Xiaodonghai; WZZ, Wuzhizhou; FJZ, Fenjiezhou; DZD, Dazhoudao.

Relationship between feeding behavior and benthic variables

The benthic variables were different among the sample stations (SIMPEROF, global π = 0.59, p = 0.001). The Draftsman plots indicated that the number of coral species, other sessile invertebrate and macroalgae were all highly correlated with live coral cover ($|r|$ >0.85, Table S3), and so these variables were excluded from the DISTLM analysis. Additionally, as the dead coral cover was highly correlated with rock (r = −0.95, Table S3), the rock was kept in the analysis based on the forward factor selection process.

The DISTLM analysis indicated that the three benthic variables, including live coral cover, rock, and sand, had a strong relationship with the electivity index of the coral prey at the research stations, although the marginal test showed no statistical significance (p >0.05). The dbRDA included vectors corresponding to these three variables on two axes that explained 91.6% of the fitted variation and 62.4% of the total variation (Figure 4). When considering the variables alone and ignoring all other variables, sand contributed to explaining the highest percentual variance, accounting for 21.03% of the variability in the coral prey communities, followed by rock, accounting for 13.51%, and live coral cover, accounting for 8.79%. The samples corresponding to the relatively high live coral cover stations were distributed along the dbRDA1 axis, while the samples of the different types of stations were dispersed along the dbRDA2 axis.

Comparative analysis of food value of coral prey

PCA analyses revealed that the coral prey species fell into four significantly different groups (Figure 5). The first group comprised the genus *Montipora*, characterized by high Chl-a content and delivering high-polyp density, tissue biomass, and a low *Symbiodinium* density. The second group, comprising the genera *Acropora*, *Pocillopora*, and *Porites*, fell out together along axes of high *Symbiodinium* density, low Chl-a content, and

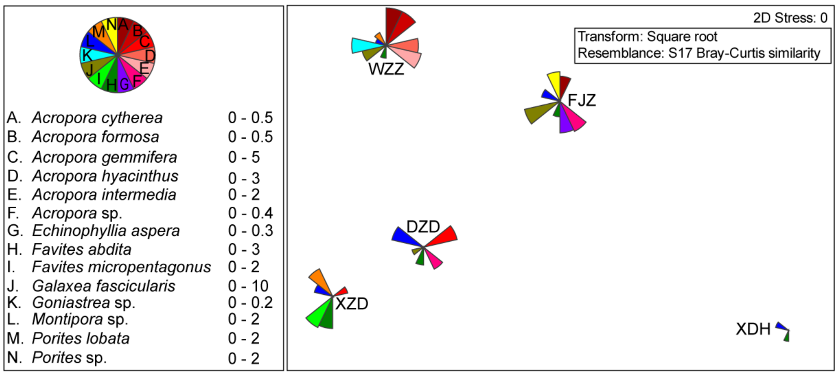

FIGURE 3
Non-parametric multi-dimensional scaling (nMDS) ordinations visualized the similarities and dissimilarities in coral community composition (living coral cover served as the abundance) between stations, with a bubble plot showing the live cover of the coral species preferred by *Drupella* spp. (Ei >0.5 at any station) in each sample station (XZD, Xiaozhoudao; XDH, Xiaodonghai; WZZ, Wuzhizhou; FJZ, Fenjiezhou; and DZD, Dazhoudao).

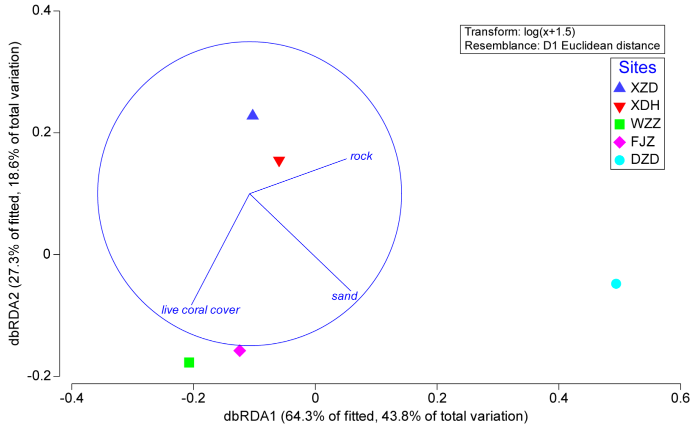

FIGURE 4
Distance-based redundancy analysis (dbRDA) of the Iviev's electivity index (E$_i$) considering the coral prey for each station shows vector overlays of coral species preyed included in the best model by DISTLM analysis (XZD, Xiaozhoudao; XDH, Xiaodonghai; WZZ, Wuzhizhou; FJZ, Fenjiezhou; DZD, Dazhoudao).

delivering high-polyp density. The third group, comprising the genera *Favites*, *Galaxea*, and *Platygyra*, was correlated with high-tissue thickness, low-polyp density, and delivered high-lipid content and *Symbiodinium* density. The fourth group comprised the genera *Goniastrea* and *Lobophyllia*, characterized by high-lipid content, protein content, and tissue biomass, and delivered high-tissue thickness, high Chl-a content, and low-polyp density.

Discussion

In recent years, the overabundance of corallivores has become an increasing threat to coral reef ecosystems across the Indo-Pacific Ocean. In the South China Sea, especially in the near-shore coral reef area, more and more aggregations of *Drupella* spp. have been observed, which would become a potential roadblock to the regional efforts to recover and restore the degraded coral communities in China. This study revealed the spatial differences in density and prey selection of the corallivorous snail *Drupella* spp. in the southeastern Hainan Island, South China Sea. Prey preferences of *Drupella* spp. vary in different stations according to the abundance and availability of coral prey. Corals of the family Acroporidae were preferred positively by *Drupella* spp. among all research stations, and their favored coral preys are of meaty, nutrition-packed, and vegetarian characteristics. Benthic variables, including live coral cover, rock, and sand, had a strong relationship with the coral prey communities among the research stations.

In this study, the overall mean density of *Drupella* spp. was lower than that in previous studies (Ayling and Ayling, 1987; Turner, 1994a; Cumming, 1999; Cumming, 2009b; Schoepf et al., 2010; Moerland et al., 2016), but higher than that in a recent study (Saponari et al., 2021). The corallivores did not outbreak because the mean density in each study site (0.09–1.78 ind m^{-2}) never exceeded the outbreak threshold of >3 ind m^{-2} defined by (Cumming 2009a; Cumming, 2009b). However, the mean density exceeded the level of 0.62 ind m^{-2} suggested by Bessey et al. (2018) that the snails could outbreak on their preferred coral species if the density exceeded this level. In particular, we found there was a maximum of 38 individuals of a single coral species, *Acropora hyacinthus* at DZD. Thus, the high current density of the snails remained potentially destructive to the coral communities in the study regions.

The heterogeneity in the density of *Drupella* spp. recorded at different sites may have been responsible for the anthropogenic activities, such as over-fishing or boating traffic (Ayling and Ayling, 1987; Turner, 1994a), especially the coral collapse in XDH. Additionally, the snail density was found to be higher in the stations with relatively high coral cover than that in the stations with low coral cover across all sites surveyed, such as in FJZ and DZD, independently of the number of coral species. This finding was consistent with the theory of optimal foraging, which assumed that predators fed in such a way as to trade-off between the alternative available prey abundances (Cumming, 2009a; Keesing, 2021). However, we found that the coral cover was relatively high in XZD but with lower snail density. Hence, these between-site variations in the densities of *Drupella* were apparently not just dependent on the differences in the live coral cover at each station. Specifically, our statistical results indicated that the live coral cover only contributed to explaining the percentual variance of 8.79% for the electivity index of the

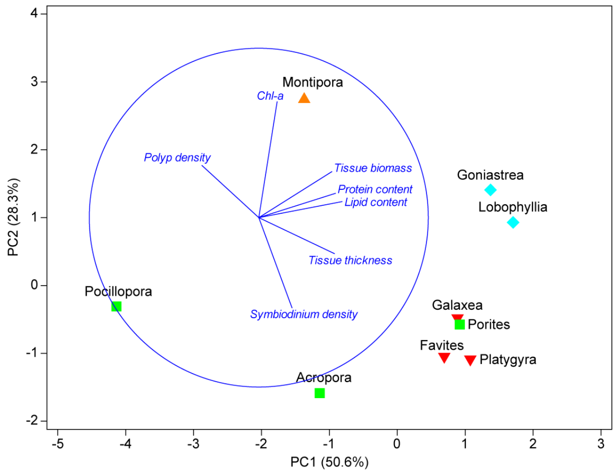

FIGURE 5
Principal components analysis (PCA) plot of multivariate analysis of coral genera nutritional value of prey data: lipid content, protein content, tissue biomass, *Symbiodinium* density, Chl-a content, tissue thickness, and polyp density. PCA analyses are based on the data obtained from the Coral Trait Database and published studies. The missing values were filled using a linear regression. The genus *Echinophyllia* was excluded in these analyses because the data were not available. The triangle, upside-down triangle, square, and diamond symbols indicate the four groups of significant different coral genera based on the SIMPEROF test.

coral prey, which highlights that the coral cover would not always be the main factor. Additionally, the different abundance of their preferred coral species (*Acropora* and *Montipora*) in each station may have been responsible (Morton and Blackmore, 2009). Although they are more mobile, the encounter probability with their preferred prey is probably an additional explanation. Thus, factors other than the live coral cover are probably important in controlling the density of *Drupella* in different reef regions.

For instance, the highest proportion of the coral taxa we found in each research station may be involved in the impact factors. For instance, the highest proportion of the genera *Favites* resulted in positive feeding in XZD, although they are the massive growth form of corals. Prior studies reported that the coral growth forms and intraspecific attraction probably played additional roles in the food selection of *Drupella* spp. (McClanahan, 1997; Schoepf et al., 2010). Corals with branching growth forms were always used as food and shelter (Ayling and Ayling, 1987; Hamman, 2018), especially for the juvenile snail *Drupella* spp. (McClanahan, 1997; Schoepf et al., 2010; Hamman, 2018).

Our study showed there were significant differences in the coral community composition among the research stations. The different *Drupella* densities in each site were probably correlated to the distribution pattern of the coral assemblage (Schoepf et al., 2010). Moreover, variation among coral assemblages has also been linked to the snail relative density because the abundance and distribution of their preferred coral prey were different in each sample station. Specifically, the low abundance of their preferred prey (*Acropora* and *Montipora*) at XZD was probably responsible for the low density of *Drupella*. Previous studies revealed that a decrease in the abundance of preferred coral species might result in a higher density of snails in the reefs (Schoepf et al., 2010). Nonetheless, *Acropora* abundance does not always explain the distribution pattern of *Drupella* (Turner, 1994b), for the snails could aggregate on the remaining corals if the coral population decreased (Hoeksema et al., 2013; Saponari et al., 2021).

Results from our analysis of spatially explicit data of 30 prey species demonstrated that the corallivorous snail displayed dietary plasticity, consistent with the previous findings that they were able to switch to their less preferred corals in the areas where their preferred prey became scarce (Turner, 1994b; Shafir et al., 2008; Schoepf et al., 2010; Hoeksema et al., 2013; Tsang and Ang, 2015; Saponari et al., 2021). In this study, we found coral species of the family Acroporidae were preyed on positively where the abundance of them was relatively high, such as at WZZ, FJZ, and DZD. However, the snails were confined to their less favorite prey. For instance, they had to prey on *Favites* spp. and *Platygyra* spp. when the coral species of Acroporidae were less available at XZD. Similarly, previous observations revealed that *Drupella* were restricted to preying on massive or encrusting corals where branching corals were not available (Mcclanahan, 1994; Cumming and McCorry, 1998; Morton et al., 2002; Hoeksema et al., 2013; Moerland et al., 2016). Moreover, as found in our study, the snails were found expanding their prey range from branching corals (*Acropora* and *Pocillopora*) to a few massive corals (*Porites*, *Favites*, *Galaxea*, etc.) in the Maldives (Bruckner et al., 2017; Saponari et al., 2021) according to the availability of their preferred prey.

Interestingly, previous studies found that some coral species that were not preferentially preyed upon by *Drupella*, such as corals of the genus *Porites* (Morton et al., 2002; Hamman, 2018), while they had a positive tendency to be preyed on in the station DZD in this investigation. These results showed that the complex change of coral community composition in this study area influenced the predation preference of the snail *Drupella*. Additionally, during the survey period, we also found the snails preferred aggregating near the freshly damaged tissues of the corals, which supports evidence from previous observations (Morton et al., 2002; Bright et al., 2015; Bruckner et al., 2017; Hamman, 2018). Kita et al. (2005) reported that the chemicals in the mucus released by damaged coral tissue showed potent feeding-attractant activity toward *D. cornus*.

Besides the influence factors to the prey preferences of the snail *Drupella* spp. proposed by previous studies above, other researches indicated that coral growth forms, such as branching growth form, could strongly influence their feeding preferences (Turner, 1994a; Cumming and McCorry, 1998; Cumming, 1999; Schoepf et al., 2010; Saponari et al., 2021). In this research, we found that benthic variables, including live coral cover, rock, and sand, had a strong relationship with the electivity index of the coral prey at the research stations. This indicated that the substrata condition played an important role in determining the prey preference of *Drupella* spp. This finding is consistent with the reports that the snails showed different reef habitat preferences (Turner, 1994a; Cumming, 1999), such as a high cover of rubble and dead coral (Moerland et al., 2016). However, the correlation was not statistically significant in the present study. This was presumably due to the insufficient sample collection and/or some remaining unclear drivers, although various aspects had been discussed in previous studies, such as coral communities (Morton and Blackmore, 2009; Schoepf et al., 2010; Saponari et al., 2021); depth (Schoepf et al., 2010; Saponari et al., 2021); reef status (Mcclanahan, 1994; Morton et al., 2002). Furthermore, prey selection by *Drupella* spp. could not only be considered in the multivariable analysis because coral species tested were insufficient. Additionally, environmental stressors, including elevated seawater temperature, reduced salinity, mechanical damage, and coral diseases, were also correlated with the feeding preference of *Drupella* (Morton et al., 2002; Al-Horani et al., 2011; Nicolet et al., 2013; Tsang and Ang, 2019).

The comparative analysis suggested that the preferred coral genera were composed of the theoretically favorable traits of high nutritional value, such as high protein content, lipid content, tissue biomass, and thickness. (Keesing, 2021; Keesing, 1990) reported that the nutritional value of coral prey was an important determinant in the evolution of the prey preferences of crown-of-thorns starfish. Our results here demonstrate that the favored coral preys of *Drupella* spp. were among those with high nutritional value, e.g., high protein content, lipid content, tissue biomass, and thickness. In particular, their preferred corals (*Acropora* and *Montipora*) contained high Chl-a content, *Symbiodinium* density, polyp density, and intermediate tissue nutritional value. These indicated that, to a certain extent, the corallivorous snails were smart and their preferred coral prey were full of nutritional value with the features of being meaty, energy-enriching, and vegetarian. However, the location of energy reserves in the coral tissue varied from species to species. For instance, the lipid was typically deposited in the basal half to one-third of the polyp column in hard corals (Stimson, 1987). This would explain why the corals with massive growth form, such as *Porites* spp., had resulted in a random prey choice, because the lipid reserved in polyps penetrating further down into the skeleton (Keesing, 2021). This suggests that linking feeding preference to food nutritional value for *Drupella* spp. feeding on numerous coral species in such a complex environment as coral reef requires more than an assessment of the absolute nutritional content of food.

Conclusions

Overall, our surveys revealed that the abundance of corallivorous snails, *Drupella* spp., varied spatially on the reefs throughout southeastern Hainan Island, South China Sea, while the snail density was found generally related to coral cover, independent of the number of coral species. However, the high coral cover was not always responsible for the high density of the snails. *Drupella* spp. showed a positive preference for Acroporidae corals, and random choice resulted for *Porites*, *Galaxea*, *Platygyra*, and *Lobophyllia* corals, when their favored taxa were abundant in situ. The results of our study suggest that the prey preference of *Drupella* spp. exhibits a dietary plasticity according to the abundance and availability of their favored coral prey, as well as the encounter probability between them. Furthermore, benthic types, including live coral cover, rock, and sand, had a strong relationship with the electivity index of the coral prey, reflecting the prey preference of *Drupella* spp. related to the substrata condition. The nutritional value of coral preys was an additional important determinant in their prey preference, while the location of the nutrient deposits in the corals and the complex environmental context should not be ignored.

As the corals in the shallow water suffering increasing influences, further works should focus on larger geographical areas, and expend to the deeper areas of the coral reefs to make a better understanding of the spatial distribution of *Drupella* spp. In addition, the prey preference and the microhabitat use in each life stage should be well studied. With the future research on how to increase the local predators of the corallivorous snails, there will be more benefit to reducing the cost and need for human interventions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors. Data pertaining to this study are available at South China Sea Ocean Data Center, National Earth System Science Data Center, National Science & Technology Infrastructure of China(http://data.scsio.ac.cn/metaData-detail/1534808395246669824)..

Author contributions

XL: Conceptualization, methodology, investigation, data acquisition and curation, formal analysis, and writing-original draft. CL: Investigation, data acquisition and curation, writing-review and editing. YZ: Analytic tools, investigation, data acquisition, and curation. XY: Investigation, data acquisition, and curation. JY: Investigation, data acquisition, and curation. YL: Investigation, data acquisition, and curation. GZ: Methodology, funding, supervision, writing–review and editing. HH: Funding, supervision, writing–review and editing. All authors contributed to the article and approved the submitted version.

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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

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.990113/full#supplementary-material

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