

Diversity and distribution of gastropods in the seaweed-dominated rocky intertidal area of Thikkodi, southwest coast of India

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Original Article

Abstract

Gastropods are a diversified class of the phylum Mollusca, and one of the most represented taxa associated with seaweeds. Studies on the gastropod diversity along the rocky intertidal area are extensive, however, the distribution of gastropods in the seaweed-dominated intertidal area specifically is limited. This study was conducted to know the influence of seaweed abundance on the spatial and seasonal diversity of gastropod species and the zonal preference of individuals of gastropods in littoral, eulittoral and sublittoral areas. The littoral zone showed an abundance of Littoraria undulata and Cellana radiata and the seaweed species viz., Ulva intestinalis, Ulva compressa and Cladophora vagabunda. The eulittoral zone showed higher abundance (263 Ind./m²) and diversity (H'=2.54) of gastropods, mostly comprised of species of Clypeomorus batillariaeformis, Planaxis sulcatus, Turbo intercostalis, Trochus radiatus, Nerita albicilla and seaweed species like Valoniopsis pachynema, Lychaete herpestica, Acrosiphonia orientalis, Chondracanthus acicularis and Gelidium pusillum. The sublittoral zone recorded more species of the family Muricidae and an abundance of Anachis terpsichore from the family Columellidae. The highest biomass of seaweed in the postmonsoon season supports a higher numerical abundance of gastropod individuals during this study. The pre-monsoon season was characterized by higher species number and diversity (H' = 2.79; d =5.11) followed by the monsoon season (H' = 2.77; d =4.73). The abundance of gastropod species is more correlated to a combination of seaweeds, indicating that, structurally complex types, with high biomass of seaweeds are more preferred for assemblages of gastropods than species specificity. Overall, this study revealed that spatial heterogeneity in terms of the abundance of seaweed is one of

the factors for the difference in gastropod species distribution and diversity in this study area.

Keywords: Distribution, diversity, gastropods, macroalgal associations, rocky intertidal, Thikkodi

Introduction

Understanding the community structure and species assemblage pattern based on quantitative description of different species is an important fact of ecology (Andrew and Mapstone, 1987; Underwood and Chapman, 1998). The intertidal zone represents one of the productive environments which support several associated organisms (Imchen and Anil, 2017). Topographic features present on the rocky coast may determine the distribution of diverse assemblages of fauna and flora (Archambault and Bourget, 1996; Underwood et al., 2000). The rocky intertidal seaweed habitats effectively serve as biological habitat structures (Colman, 1940; Jones and Andrew, 1992; Chemello and Milazzo, 2002) and providing suitable living space for abundant and diverse organisms (Viejo, 1999; Jones and Thornber, 2010).

Biogenic habitat provided by seaweeds or macroalgae increases structural complexity, and space availability, which increases the diversity, abundance and coexistence of associated macrofaunal communities (Hayward, 1980; Edgar, 1983; Jones and Andrew, 1992; Liuzzi and Gappa, 2011; Kovalenko, et al., 2012; Jeeva, et al., 2018). Gastropods are a more diversified class of the phylum Mollusca, and one of the most represented taxa associated

with seaweeds and considered important macroalgal grazers (Underwood, 1980; Williams, 1993; Milazzo, *et al.*, 2000; Chemello and Milazzo, 2002). The spatial separation of algal resources between grazers influenced species distribution (Hawkins and Hartnoll, 1983) and grazers benefit from algal resources with the increase of food availability and shelter (Williams, 1993, 1994; Williams *et al.*, 2000).

There are studies on the gastropod distribution along the rocky intertidal area of the Kerala coast (Ravinesh and Bijukumar, 2013; Karnaver *et al.*, 2023); however, the distribution of gastropods in the seaweed-dominated intertidal area and factors controlling the distribution of gastropods are poorly understood. The present study would therefore enhance the knowledge of the distribution of gastropod species in a rocky intertidal area characterised by a different assemblage of seaweed species and also the influence of the seaweed abundance on spatial and seasonal diversity of gastropod species.

Material and methods

The Thikkodi rocky intertidal region (11° 28' 29.64" N, 75° 37' 11.92" E) is located on the Kerala coast, southwest coast of India. This area is characterised by a laterite rocky bottom with the presence of seaweed assemblages. Depending on the tidal range and expanse of the intertidal area, the study area divided into Z1 (littoral zone), Z2 (Eulittoral zone) and Z3 (Sub-littoral zone). The nomenclature of the zones was adopted based on the system recommended by Lewis (1964). Upper part of the littoral zone is placed with artificially laid stones and seasonal abundance of seaweeds, especially in monsoon. Rock pools, abundance of seaweed and elevated bare rock surfaces are present in the eulittoral zone. The sublittoral zone is characterised by high-wave action and presence of dense patches of seaweeds.

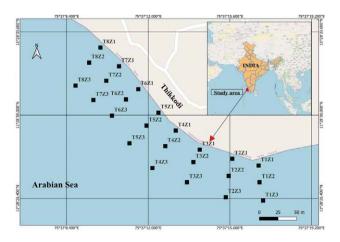


Fig. 1. Study location–Thikkodi rocky intertidal area (T- transect, Z- Zones)

Gastropod samples were collected from October 2020 to September 2022 during the lowest low tide in each month using fixed point quadrats (1 m²) along the transect lines (English et al., 1997) (Fig. 1). Gastropod and seaweed samples were collected from each quadrat. Replicate samples were taken randomly around the quadrat area. The gastropod fauna in the quadrats was enumerated and representative species were collected by handpick method for morphological examination and species identification in the laboratory. The gastropods were not only sampled from the seaweed substratum but also from bare rock areas from the fixed points. Seaweed samples were removed with the help of a scalpel. Collected seaweed species were transferred into polythene bags for estimating wet biomass in the laboratory. In the laboratory, each species of seaweed was segregated, and washed in seawater, and the wet biomass of each seaweed species was estimated using a high-precision electronic balance. The biomass of each species of seaweed per unit area was obtained. Identification was done by using standard taxonomic identification keys for gastropods (Abbot and Dance, 1982; Houbrick, 1985; Rao, 2003) and seaweeds (Rao, 1987; Jha et al., 2009; Palanisamy et al., 2015).

Univariate and multivariate analyses were performed with PRIMER + v.7.0.23 PERMANOVA + add-on (Clarke and Gorley, 2015). Univariate measures such as Margalef's index (d), Shannon-Weaver index (H') and Pielou's evenness (J) were analysed. For multivariate analysis, the abundance data were log-transformed to reduce the influence of the dominant taxa in the samples and to increase the contribution of less common species. Non-metric multidimensional scaling (nMDS) was used for the visual representation of distribution patterns based on the Bray-Curtis similarity matrix. PERMANOVA test was carried out for the abundance of variation of gastropods and seaweeds in which a three-factor model was used with season, zone and year as a fixed factor with 9999 permutations of residuals under a reduced model. Individual species responsible for abundance in each zone were detected through their similarity contribution using the Similarity Percentage (SIMPER) test. BVSTEP in BEST analysis was carried out for correlation between the gastropod and seaweed species.

Results and discussion

Gastropod community composition

A total of 30 species of gastropods representing 18 families were recorded (Fig. 2). Of the 18 families, nine families showed abundance (Fig. 3). The family Cerithiidae recorded the highest abundance (38.4%) mainly due to the abundance of *Clypeomorus batillariaeformis* (50.62 Ind./m²). The family Planaxidae (15.34%) was dominated by the species *Planaxis*



Fig. 2. Gastropod species. A. Cellana radiata; B. Littoraria undulata; C. Littoraria intermedia; D. Planaxis sulcatus; E. Anachis terpsichore; F. Supplanaxis niger; G. Semiricinula tissoti; H. Purpura bufo; I. Arakawania ceylonica; J. Arakawania granulata; K. Indothais blanfordi: L. Siphonaria basseinensis; M. Scutus unguis; N. Trochus radiatus; O-Q. Clypeomorus batillariaeformis; R. Elysia sp, S. Diodora singaporensis; T,t. Turbo intercostalis; U,u. Turbo bruneus; V. Monetaria caputserpentis; W. Mauritia histrio; X,x. Nerita albicilla; Y,y. Nerita chamaeleon; Z,z. Nerita plicata

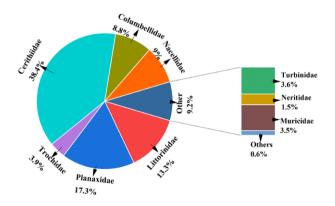


Fig. 3. Bar of Pie-graph indicates the abundance of percentage of each family of the total gastropod sample

sulcatus (22.76 Ind./m²) and Supplanaxis niger (0.064 Ind./m²), and family Littorinidae (13.3%), predominantly had three species viz., Littoraria intermedia (1.33 Ind./m²), Littoraria undulata (14.85 Ind./m²) and Echinolittorina malaccana (1.38 Ind./m²). The family Neritidae (1.5%) comprised of Nerita albicilla (1.65 Ind./m²), Nerita plicata (0.156 Ind./m²), and Nerita chamaeleon (0.11 Ind./m²). Muricidae family encompassed six species viz., Arakawania granulata (1.41 Ind./m²), Arakawania ceylonica (0.98 Ind./m²), Semiricinula tissoti (1.041 Ind./m²), Purpura bufo (1.15 Ind./m²), Reishia clavigera (0.55 Ind./m²) and

Indothais blanfordi (0.025 Ind./m²). The family Nacellidae (9%) comprised Cellana radiata (11.85 Ind./m²), family Turbinidae (3.6%) comprised of Turbo intercostalis (4.71 Ind./m²) and Turbo bruneus (0.064 Ind./m²), family Trochidae (3.9%) comprised of Trochus radiatus (5.1 Ind./m²), and family Columbellidae (8.8%) encompassed Anachis terpsichore (11.61 Ind./m²) and family Chilodontaidae with Euchelus asper (0.55 Ind./m²). Cypraeidae family was represented by Monetaria caputserpentis (0.051 Ind./m²) and Mauritia histrio (0.025 Ind./m²). Five species were recorded in Heterobranchia, viz., Sebadoris fragilis, Siphonaria basseinensis, Elysia sp., Placida sp., Caloria militaris while the family Fissurellidae was represented by Diodora singaporensis and Scutus unguis which were rarely found.

Distribution and abundance of gastropods

Species abundance variations were analysed using the PERMANOVA test (Table 1) which showed that a significant difference in the abundance of gastropods in zonal (ZN) (Pseudo-F=56.61; P=0.0002), seasonal (SE) (Pseudo-F=4.91; P=0.0068) and Se vs. Zo (P=0.019, Pseudo-F=3.404) factors. There are no yearwise variations detected. The nMDS plot indicated the lowest 2D stress value of 0.077 (Fig. 4) for the spatial distribution of gastropods. This study has shown clear spatial variability in the abundance of gastropod species and assemblages of seaweed species present in each zone (SIMPER test-Table 2). Each zonal abundance of the species may be the preference for a suitable habitat that provides more refuge, physiological needs, and biological interactions (Kastendiek, 1982; Benedetti-Cecchi et al., 2000; Veras et al., 2013). The littoral zone showed abundance of L. undulata (32.71%) and C. radiata (29.9%) and the seaweed species viz., U. intestinalis, U. compressa and C. vagabunda. Littoraria sp. and Cellana sp. graze on ephemeral green algae such as Ulva spp., Enteromorpha spp., Cladophora spp. (Rao and Sundaram, 1972; Lubchenco,

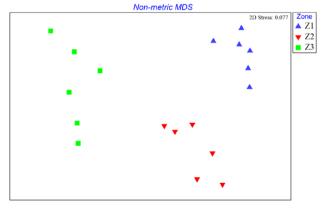


Fig. 4. nMDS showing the gastropod distribution pattern in three zones (Z1-Littoral zone, Z2-Eulittoral zone, Z3-Sublittoral zone)

Table 1. PERMANOVA test results of gastropod abundance (Se, season; Zo, zone; Ye, year; df, degrees of freedom; SS, sum of squares; MS, mean sum of squares). Significant values are highlighted in bold (p < 0.05)

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Se	2	2502.6	1251.3	4.91	0.0068	9966
Zo	2	28822	14411	56.61	0.0002	9954
Ye	1	312.06	312.06	1.22	0.34	9956
Se vs. Zo	4	3466.1	866.53	3.404	0.019	9945
Se vs. Ye	2	511.07	255.53	1.0039	0.47	9952
Zo vs. Ye	2	518.46	259.23	1.018	0.46	9943
Res	4	1018.2	254.54			
Total	17	37150				

1978; Bertness, 1984) and also preferred bare rock surfaces (Carlson *et al.*, 2006). Lim and Lee (2009) and Pandey and Thiruchitrambalam (2018) investigated that, most littorinids have specific zone preferences and mostly occur in the upper intertidal area.

The eulittoral zone predominantly had *C. batillariaeformis* (31.11%), *P. sulcatus* (22.25%), *T. intercostalis* (10.74%) and *T. radiatus* (10.1%) and seaweed species like *Valoniopsis* pachynema, *Lychaete herpestica, Acrosiphonia orientalis, Chondracanthus acicularis* and *Gelidium pusillum.* Structural heterogeneity was more prevalent in the eulittoral zone in this study area. Substratum heterogeneity and physical

Table 2. Results of the SIMPER test showing the gastropod and seaweed species that contribute more to the similarity in three zones (Average abundance of the species (Av. Abund.), standard deviation of similarity (Sim/SD), percentage contribution to similarity (Contrib %), percentage of cumulated contribution to similarity (Cum.%-70% cut-off)

Zone (Av. sim.)	Gastropod species	Av. Sim	Sim/SD	Contrib %
	Littoraria undulata	25.17	7.99	32.71
Littoral zone-Z1	Cellana radiata	23.01	11.18	29.9
	Planaxis sulcatus	8.17	7.03	10.62
	Clypeomorus batillariaeformis	23.01	7.56	31.11
Culitarial anno 70	Planaxis sulcatus	16.45	4.53	22.25
Eulittoral zone-Z2	Turbo intercostalis	7.95	6.17	10.74
	Trochus radiatus	7.47	6.65	10.1
	Anachis terpsichore	11.93	1.52	23.43
0. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1.	Arakawania ceylonica	9.76	3.21	19.17
Sublittoral zone-Z3	Semiricinula tissoti	8.35	2.99	16.38
	Arakawania granulata	7.97	2.36	15.64
	Seaweed species			
	Cladophora vagabunda	14.57	4.53	24.75
150	Ulva intestinalis	12.75	1.66	21.67
Littoral zone-Z1	Valoniopsis pachynema	8.82	3.21	14.98
	Ulva compressa	7.92	2.12	13.46
	Lychaete herpestica	11.81	5.73	18.56
	Valoniopsis pachynema	11.52	2.47	18.11
Eulittoral zone-Z2	Acrosiphonia orientalis	10.47	12.16	16.46
	Gelidium pusillum	9.34	3.96	14.69
	Chondracanthus acicularis	7.27	1.42	11.44
	Caulerpa chemnitzia	6.7	2.54	9.68
	Gelidium pusillum	6.46	4.11	9.32
	Gracilaria corticata	6.31	2.8	9.11
	Chondracanthus acicularis	5.59	2.85	8.07
Sublittoral zone-Z3	Centroceras clavulatum	5.5	2.17	7.94
	Acanthophora spicifera	5.3	2.19	7.65
	Valoniopsis pachynema	5.19	3.2	7.5
	Ceratodictyon variabile	4.62	6.54	6.67
	Lychaete herpestica	4.28	2.23	6.19

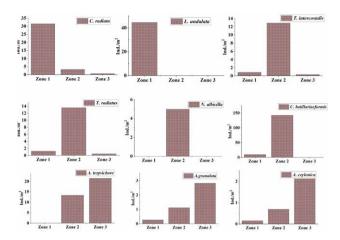


Fig. 5. Graphical representations showing numerical abundance of most abundant gastropod species in the Z1 (Littoral zone), Z2 (Eulittoral zone), and Z3 (Sublittoral zone)

attributes of habitat were the most important factors determining community structure (Lapointe and Bourget, 1999; Benedetti-Cecchi, 2001) numerical abundance and diversity of gastropods (Beck, 1998; Pandey et al., 2018). The presence of rock pools and the abundance of many seaweed species may be the factors for the highest abundance of species like C. batillariaeformis, T. intercostalis, T. radiatus and N. albicilla in the eulittoral zone. The population of Cerithidae family was mostly concentrated in the middle littoral region and tidepool which is also characterised by the presence of macroalgal species (Gohil and Kundu, 2013; Trivedi and Vachhrajani, 2013; Gohel et al., 2016; Baxi et al., 2017). Generally, members of the family Turbinidae, Trochidae, and Neritidae are herbivores that dominate at locations with higher macroalgae (Miloslavich et al., 2013; Pandey et al., 2018). In addition to these species, P. sulcatus, microphagous herbivorous species which require elevated rock surfaces with no longer submergences are prevalent (Mckillup and Mckillup, 1993; Samakraman et al., 2010).

In the sub-littoral zone, the highest biomass of *Caulerpa chemnitzia*, *Acanthophora spicifera* and *Gracilaria corticata* were observed where the gastropod *A. terpsichore* (23.43%) of the family Columbellidae was present. This zone recorded more species of the family Muricidae and *A. ceylonica* (19.17%), *S. tissoti* (16.38%) and *A. granulata* (15.64%) contributed more in similarity. *A. terpsichore* was recorded from the sublittoral region as the most numerous species, on the west coast of Ceylon, which was characterised by a rich growth of macroalgae (Arudpragasam, 1970). Species of Muricid mainly occurred in the rock holes throughout the study period, but, *A. terpsichore* was mostly associated with structurally complex type seaweed species *viz., C. chemnitzia*, and *A. spicifera*, *V. pachynema*, *L. herpestica*, *A. orientalis* and *Padina* spp. than rock holes and also showed seasonal

abundance mainly in pre-monsoon season on this coast. Generally, the family Muricidae is characterised in the lower intertidal rocky area (Pandey and Thiruchitrambalam, 2018); however, these were found in all zones in this coast, but, abundancy was detected in the upper part of the sublittoral zone during this study. Numerical abundance of most abundant gastropod species in the Z1 (Littoral zone), Z2 (Eulittoral zone), and Z3 (Sublittoral zone) are represented in Fig. 5.

Diversity and association of gastropods with seaweed species

The species diversity of gastropods differed between zonal levels (Table 3A). The highest average numerical abundance (263 Ind./m²), diversity (H'=2.54±0.63) and species richness (d=4.56±1.08) of gastropod species were recorded in the eulittoral zone. The littoral zone recorded the highest evenness (J'=0.62±0.08) and the average numerical abundance was 99 Ind./m². The sub-littoral zone recorded the lowest average numerical abundance (33 Ind./m²) and also the lowest diversity $(H'=1.93\pm0.4, d=4.44\pm0.2)$. This study found that the highest biomass of filamentous type macroalgae such as V. pachynema, A. orientalis, L. herpestica and A. orientalis present in the eulittoral zone enhances the high abundance and diversity of gastropods. Sub-littoral regions were characterized by a lower abundance of gastropod individuals even though a high biomass of macroalgae was present. It may be due to high wave action on organisms, which can limit the abundance of organisms by detachment from the substrate (Lubchenco and Menge, 1978).

The highest abundance of gastropods was found in the post-monsoon season (176±12.73 Ind. /m²) followed by pre-monsoon (129 \pm 9.82 Ind./m²) and monsoon season (90±8.62 Ind./m²) (Table 3 B). In the case of species number and diversity, pre-monsoon season (H' =2.79; d=5.11) was characterized by higher species number and diversity followed by monsoon season (H' = 2.77; d = 4.73). Most common gastropod species showed higher abundance in the post-monsoon season (*Planaxis sulcatus* (24.76 Ind./m²), Nerita albicilla (1.72 Ind./m²), Turbo intercostalis (4.94 Ind./m²), Trochus radiatus (4.34 Ind./m²), Clypeomorus batillariaeformis (45.76 Ind./m²), Cellana radiata (12.86 Ind./m²). Littoraria undulata showed higher abundance in the post-monsoon season (22.84 Ind./m²), followed by the pre-monsoon season (11.95 Ind./m²) and this species was present only in the littoral zone in all seasons. From post-monsoon onwards, Anachis terpsichore abundance (3.36 Ind./m²) gradually increased and the highest abundance was observed in the pre-monsoon season (27.31 Ind./m²) mainly in the sublittoral zone. Muricid species such as A. granulata (2.51 Ind./m²), A. ceylonica

Table 3. Gastropod diversity indices with standard deviation in different zones (A) and seasonal (B). Margalet's index (d), Shannon-Weaver index (H'), and Pielou's evenness (J)

A.	Zones	d	J'	H'(log2)
	Z1	3.28±0.32	0.62±0.08	2.49±0.39
	Z2	4.56±1.08	0.54±0.11	2.54±0.63
	Z3	4.44±0.2	0.47±0.14	1.93±0.14
B.	Seasons	d	J'	H'(log2)
	PRM	5.11±0.51	0.61±0.02	2.79±0.19
	MON	4.73±0.28	0.64±0.06	2.77±0.31
	PSM	3.86±1.32	0.601±0.18	2.63±0.17

(1.803 Ind./m²) and Semiricinula tissoti (1.47 Ind./m²) showed higher abundance in the post-monsoon season. From the intertidal area of the Indian coast, the diversity of gastropods was higher during pre-monsoon and lowest in post-monsoon season (Samakraman et al., 2009; Baxi et al., 2017; Pandey et al., 2018), but a total abundance of gastropod individuals was recorded to be higher in winter or post-monsoon season (Pandev et al., 2018), Benedetti-Cecchi (2001) opined that the physical attributes of habitat play an important role in determining the gastropod community assemblages than physicochemical parameters. The highest abundance of seaweed was detected in the post-monsoon (279±11.46 g/m²) season, followed by pre-monsoon (270±12.3 g/m²) and monsoon (193±9.47 g/m²) season. This study revealed that the highest biomass of seaweed in the post-monsoon season supports a higher numerical abundance of gastropod individuals (Fig. 6). During this study, most gastropod species were present in all seasons, but in pre-monsoon and monsoon seasons, species numbers increased compared to post-monsoon seasons, and so did the diversity. Sanchez-Moyano et al. (2001) observed that the greatest biomass of vegetation often had the lowest diversity or species richness, and the vegetative cycle of algae also influenced associated invertebrate macrofaunal communities. This study observed that species number increased in the early growth season of seaweed in the pre-monsoon season and the maximum

abundance of individuals was in the post-monsoon season, at the time of highest biomass of seaweed in the habitat.

BVSTEP analysis between gastropod species abundance and seaweed species biomass detected that only combinations of different species of seaweeds are more correlated (Table 4), A. terspsichore showed the highest correlation (r=0.681) with seaweed species such as C. chemnitzia, V. pachynema, A. spicifera and P. tetrastomatica. U. intestinalis and U. compressa were found to be more correlated with L. undulata (r=0.497) than C. radiata (0.324). C. batillariaeformis was more correlated with a combination of A. orientalis, V. pachynema, C. sertularioides and P. tetrastomatica (r=0.489). The lowest correlation was detected in P. sulactus (r=0.197) with U. compressa, A. orientalis and V. pachynema. The lowest correlation coefficient with seaweed reveals that this species harms seaweed assemblages. By analysing these results, it is found that no single species of seaweed are preferred by gastropods and instead, they prefer more in structurally complex types with high biomass of macroalgal zone, more than species specificity of macroalgae (Stoner and Lewis, 1985; Edgar, 1991; Russo, 1997). Macroalgal architectural pattern, such as filamentous, higher number of branches

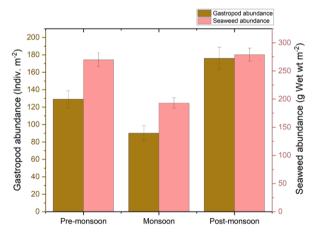


Fig. 6. Bar plot showing seasonal variation in total abundance of gastropod individuals and total biomass of seaweed

Table 4. BVSTEP results: Correlation between gastropod and seaweed species

Species	Spearman correlations (r)	Combination of variables
L. undulata	0.497	Ulva intestinalis, Ulva compressa, Cladophora vagabunda
P. sulcatus	0.197	Ulva compressa, Gelidium pusillum, Valoniopsis pachynema
C. batillariaeformis	0.489	Lychaete herpestica, Valoniopsis pachynema, Acrosiphonia orientalis, Caulerpa sertularioides
A. terspsichore	0.681	Caulerpa chemnitzia, Padina tetrastromatica, Valoniopsis pachynema, Acrosiphonia orientalis
T. intercostalis	0.294	Valoniopsis pachynema, Lychaete herpestica
C. radiata	0.324	Ulva intestinalis, Claadophora vagabunda
T. radiatus	0.369	Valoniopsis pachynema, Gelidium pusillum, Acrosiphonia orientalis

increases the structural complexity of the habitat which provides more functional space, and refuges which support higher molluscan abundance and diversity (Russo, 1990; Beck, 1998; Chemello and Milazzo, 2002; Gan *et al.*, 2019).

Conclusion

Variations in the assemblage structure of seaweed in each zone and seasonal variability in this area are decisive factors for the distribution and diversity of gastropod species. This study would also be helpful to compare the distribution of species in other similar locations and enhance the scope for future studies on their functional roles in ecology in terms of zones and habitat.

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Author contributions

Conceptualization: PF, KV, PKA; Methodology: PF, KV; Data collection: PF; Data analysis: PF, PRJ; Writing original draft: PF; Writing review and editing: KV, PKA; Supervision: KV

Data availability

The data are available and can be requested from the corresponding author.

Conflict of interests

The authors declare that they have no conflict of financial or non-financial interests that could have influenced the outcome or interpretation of the results.

Ethical statement

No ethical approval is required as the study does not include activities that require ethical approval or involve protected organisms/ human subjects/ collection of sensitive samples/ protected environments.

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