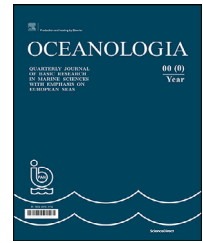


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ORIGINAL RESEARCH ARTICLE

Does topography of rocky intertidal habitat affect aggregation of cerithiid gastropods and co-occurring macroinvertebrates?

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Abstract Species aggregation has important implications for population survivorship and ecological functioning in many habitats, including rocky intertidal shores, which have been valuable to research for understanding ecological patterns and process. Intertidal gastropods of the family Cerithiidae often form extensive aggregations for which the driving mechanism may be positive thigmotaxis, i.e. movement occurring until an obstructing surface is contacted, then cessation of movement. However, it is unknown if thigmotaxis may occur by cerithiids contacting and aggregating around uneven surfaces of the rock topography, or by contacting other conspecific individuals. We quantified aggregation patterns in invertebrate assemblages and topographic complexity at intertidal rock platforms in NW India with extensive cerithiid populations. The cerithiids *Clypeomorus moniliferus* and *Cerithium caeruleum* were the most common species. Distribution analysis confirmed significant over-dispersion indicative of aggregation (densities were often around zero but occasionally reached up to 680 dm⁻²). Multivariate correlation analyses showed that topographic complexity contributes to overall species assemblage variability, but there was no evidence that topographic complexity correlates with cerithiid abundances or was likely to affect their aggregation. Thus the thigmotaxis producing cerithiid aggregation is probably associated with individuals contacting each other rather

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than any feature of the rock surface such as crevices or raised areas. Overall, while some components of species assemblages were associated with complex topography, regarding the abundant cerithiids, potential population benefits from aggregation (e.g. reduced desiccation and temperature) may be expected on rocky shores with any level of topographic complexity. © 2022 Institute of Oceanology of the Polish Academy of Sciences. Production and hosting by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Aggregation or spatial patchiness is one of the most important population features to evaluate for understanding processes controlling species distribution (He et al. 2000) and consequent wider implications (e.g. setting conservation priorities for species of concern or quantifying the fertilization and reproductive capability of broadcast spawners; e.g. Button, 2008; Green and Ostling, 2003). Aggregation may be related to biotic factors such as predation defence (Ray and Stoner, 1994) and food supply (Lauzon-Guay and Scheibling, 2009; Lapointe and Sainte-Marie, 1992; Schmitt, 1987) or to environmental factors such as habitat complexity (Stafford and Davies, 2005) and environmental harshness (Chappon et al., 2013; Rojas et al., 2013). Aggregations can have important ecological implications such as increased population survivorship and altered interactions with co-occurring species (Stafford and Davies, 2005; Stoll and Prati, 2001). There can also be implications related to economic use of species as resources (Hallier and Gaertner, 2008).

Invertebrates on rocky shores including limpets (Aguilera and Navarrete, 2011; Coleman, 2010; Moisez, et al. 2020), gastropods (Chapman and Underwood, 1996; Underwood, 2004) and chitons (Aguilera and Navarrete, 2011; Grayson and Chapman, 2004; Montecinos et al., 2020) are often observed to aggregate or occur in over-dispersed distributions. Past research has shown that habitat complexity is a main driver of aggregation for invertebrates in intertidal rocky habitats. Difficulty of moving through areas of high topographic complexity of the rock substratum may reduce population turn-over (Underwood and Chapman, 1989) and cause higher densities compared to habitat patches of less complex topography (Chapman and Underwood, 1994). Alternatively, a complex rocky intertidal topography may involve crevices and other features where susceptible species aggregate to avoid harsh environmental conditions (Montecinos et al., 2020; Stafford and Davies, 2005) or predation (Garrity and Levings, 1981). Although if predators themselves use crevices, then any prey aggregation may involve higher abundances outside crevices (Fairweather, 1988). More recently there has been interest in increasing the scope of our knowledge about intertidal species aggregation to include other less studied taxa, e.g. research on economically important aggregating gastropods in China (Yu et al., 2020) and on aggregation of poorly studied taxa from cryptic intertidal habitats done by Grayson and Chapman (2004). Stafford et al. (2008) did computer simulations of intertidal gastropod aggregation behaviour in connection

with availability of crevices and trail following. Crevice abundance appeared important in determining aggregation patterns. However for broadcast spawning species aggregation behaviour also develops on flat rock. These simulations highlighted the potential complexity of influences from topographic features toward affecting aggregation, which could be followed up with observational or experimental testing.

Rocky intertidal gastropods such as cerithiids and littorinids often have aggregated distributions (Chapman and Underwood, 1996; Denadai et al., 2004; Moulton, 1962; Rohde and Sandland, 1975). Cerithiid aggregations may be formed during movement, involving individuals moving until contact occurs with some obstacle and then cessation of movement (Moulton, 1962). This has been described as positive thigmotaxis, i.e. the tendency for individuals to move into pressure such as from a solid surface. Surfaces causing thigmotaxis and aggregation might be features of the rock associated with uneven topography (Moulton, 1962). Alternatively, it is possible that bodies/shells of other gastropod individuals may be the surfaces most commonly involved in thigmotaxis, in which case aggregation may occur irrespective of topographical features. In addition, aggregation formation appears to vary among cerithiids, an example of apparent lack of aggregation being found for the low density *Cerithium nodulosum* populations (2 individuals per 100 m²) studied by Yamaguchi (1977); this can be compared to the *Clypeomorus moniliferum* populations studied by Moulton (1962) which had closely positioned clusters containing hundreds to thousands of individuals. Cerithiids are a useful taxon for gaining insight about intertidal aggregation processes because of the wide extent of their distribution globally across temperate (Garilli et al., 2018) and tropical shores (Denadai et al., 2004), and due to the apparent consistency and distinctiveness of the aggregation patterns that have so far been described (e.g. Moulton, 1962). This hints at the possibility of related research programmes on these observations being able to reveal mechanistic ecological understanding with high spatiotemporal consistency (Underwood et al., 2000). Cerithiids can be considered as a model research taxon from which research findings can be applied to other aggregating intertidal species, some of which are economically important (abalone – Button, 2008; whelks – Yu et al., 2020). The potential ecological importance of cerithiids themselves (Nicolaidou and Nott, 1999) also highlights the usefulness of research to understand main processes determining distributions of their populations and functions.

Here we aimed to test hypotheses about patterns of over-dispersion of intertidal macroinvertebrate distributions on the Kathiawar Peninsula of Gujarat State in NW

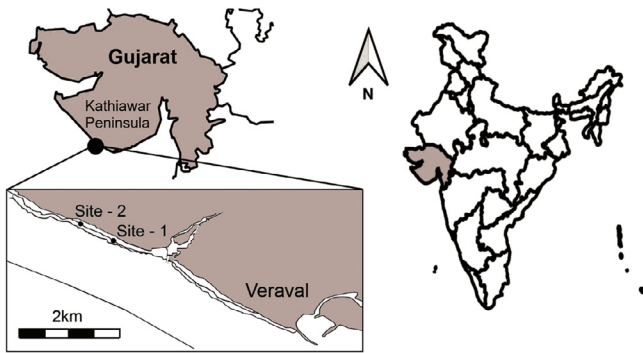


Figure 1 Map showing the coastal sampling sites near the municipality of Veraval in the state of Gujarat in NW India.

India, using an observational study (Underwood et al., 2000). The Kathiawar Peninsula has extensive intertidal rock platforms that harbour diverse plant (Ishakani et al., 2016) and animal (Bhadja et al., 2014) assemblages. The intertidal biota of this region has been quantified in relation to different locations and seasons (Misra and Kundu, 2005) but few studies have revealed specific physical habitat features that may affect species distribution patchiness.

Cerithiid gastropods are particularly widespread on NW Indian rocky shores, often with extremely patchy distributions. This applies to large-scale distributions, with mean densities per m^2 found to vary between 30–279 among different sites and seasons (Thivakaran and Sawale, 2016) and preliminary observations suggested strong patchiness may also be common at smaller scales (here cerithiids were often observed in clusters within areas of about $0.1 m^2$ where most individuals were in contact with each other). Our specific aim was to quantify intertidal invertebrate distributions, focusing on cerithiids, as well as features of their habitat. This study tested two main hypotheses: 1) The distribution of cerithiids within rock-platforms is over-dispersed (confirming significant aggregation patterns) and 2) similar to studies on gastropod aggregation as mentioned by Chapman and Underwood (1994) and Meager et al. (2011), cerithiid abundances will positively correlate with rock topographic complexity. In addition to tests focusing on cerithiids, this correlation was also tested of rock topography on the whole invertebrate assemblage structure.

2. Material and methods

Measurements of macroinvertebrate populations and habitat complexity were taken during low tides at two sites near Veraval (i.e. $20^{\circ}55'01.15''N$, $70^{\circ}20'35.29''E$ and $(20^{\circ}55'29.36''N$, $70^{\circ}19'46.28''E)$ on the Kathiawar Peninsula (Figure 1) in January 2020. These were selected as random sites, with biotic and abiotic structure appearing similar between them. The Veraval shore has a gently sloping rock platform at the mid tidal zone below a sand beach at the high zone. A steep drop-off into deep subtidal waters occurs at the seaward end of the low intertidal zone. The nearest settlement is the Veraval municipality approximately 1–2km from the sampling sites. There are extensive

algae present, which includes foliose algae but most notably non-geniculate coralline algal mats that had a mean cover of 31% when measured during nearby algal quadrat surveys. The sampling was done during winter, with mean temperature of the intertidal rock surface at low tide being $25.18^{\circ}C$ (S.E. = 0.66).

At each site, topographic complexity of the rock substratum was measured along twenty randomly placed 2 m transects at each site (40 transects total). Each transect was separated from other transects by approximately 2–10 metres. The method for measuring topography was using a steel chain draped across the undulating rock surface, which can involve a single measurement taken per quadrat (Aguilera et al., 2014) or multiple measurements (Beck, 1998). The length of each chain link section was 2.6 cm, allowing the chain to provide a topographic profile of features such as crevices and boulders that have previously been shown as important for affecting aggregation of intertidal species of similar body dimension to these cerithiids (Snyder-Conn, 1979). We laid one chain length along each transect which had four 20×20 cm quadrats placed along the transect at evenly spaced intervals for sampling densities of all macroinvertebrates, allowing the biotic data to be correlated to the linear topographic measurements that ran through the middle of each quadrat. Complexity of the rock surface did not appear to differ according to any specific spatial axis (e.g. the vertical profile from low to high tide level, compared to the alongshore horizontal profile), so topographic measurement from a single spatial axis was considered sufficient for estimating the general topographic habitat profile within a quadrat.

The first hypothesis was tested using one sample Kolmogorov-Smirnov goodness-of-fit tests, separately for each site. This method was previously used by Grayson and Chapman (2004) for investigating intertidal mollusc aggregation patterns by testing if populations have over-dispersed distributions among discreet patches of rocky habitat, but in our study the over-dispersion was tested among quadrats on a continuous intertidal rock platform. These analyses were done on the most widespread cerithiid species (*Clypeomorus moniliferus* and *Cerithium caeruleum*) and tested if any patterns of over-dispersion in observed distributions among quadrats caused significant differences to the Poisson distributions expected if cerithiids were distributed randomly.

The second hypothesis was tested using permutational analysis of covariance (ANCOVA) to test the correlation between cerithiid density (averaged from the four quadrats included in each transect) and rock surface topography for the transect. Site was included as a categorical random factor. The analysis was done in PRIMER 6 and used the resemblance measure of Euclidean distance and Type III Sums of Squares. Homogeneity of variances was tested with PERMDISP using medians, equivalent to Levene's Test (Anderson et al., 2008). All PRIMER analyses used 9999 permutations.

Lastly, the total invertebrate assemblage (molluscs, arthropods, annelids and cnidarians) was analysed using the Distance Based Linear Modelling (DistLM) function in PRIMER, correlating multivariate assemblage structure (biotic data) with the ratio values characterising topographic complexity (environmental data). Data were combined from both sites. Biotic data were fourth-root transformed to re-

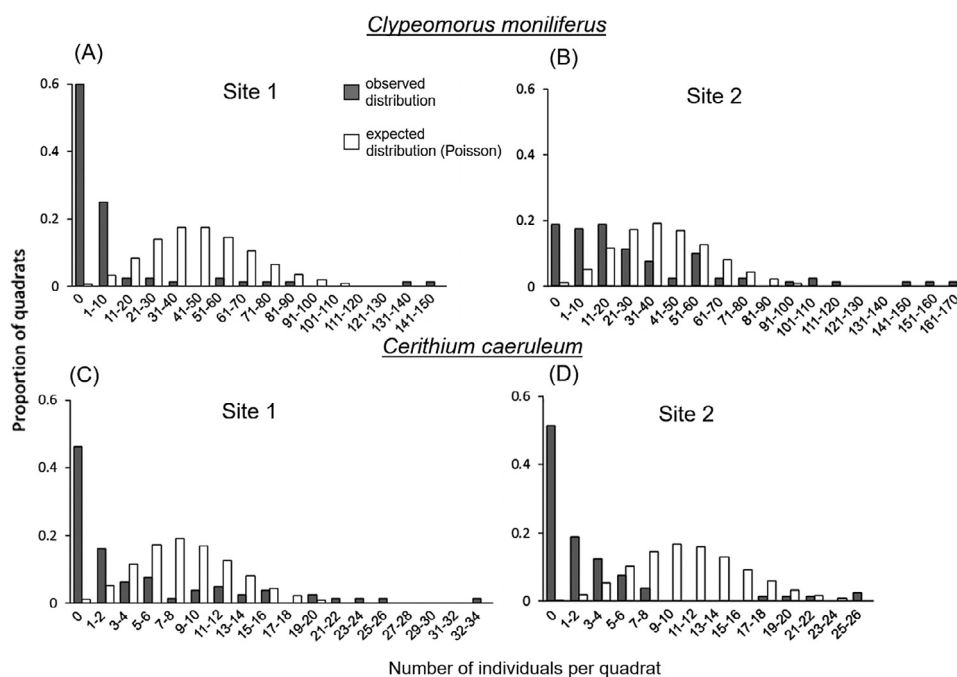


Figure 2 Frequency distributions showing proportions of quadrats (20 × 20 cm) having different abundances of the cerithiid gastropod species *Clypeomorus moniliferus* (A, B) and *Cerithium caeruleum* (C, D) sampled at two sites on the rocky intertidal coast of Veraval. Grey bars show the measured frequency distributions of the actual populations; white bars show the calculated Poisson distributions expected if the populations were distributed randomly. In all cases the actual and Poisson distributions differed significantly (one-sample Kolmogorov-Smirnov goodness-of-fit tests).

duce the influence of abundant taxa. These data were plotted using Principle Coordinates (PCO) with vectors added to visualise which sample groups were associated with which different taxa and values of the topography variable.

3. Results

A total of 24 macroinvertebrate taxa were observed, mostly gastropod molluscs (Table 1). Two species in the family Cerithiidae were observed in large abundances (*Clypeomorus moniliferus* with mean density per quadrat of 21.01 (S.E. = 3.58) and *Cerithium caeruleum* with 3.71 (0.76)) and two others more rarely (*Cerithium zonatum* 0.04 (0.03) and *Rhinoclavis sinensis* 0.01 (0.01)). Analyses were done on the large populations of *C. moniliferus* and *C. caeruleum*. For both species at both sites, observed frequency distributions among transects differed to the distributions expected if cerithiids were distributed randomly (Table 2). They were often sparsely distributed in or absent from the majority of quadrats, while smaller proportions had densities up to 680 dm⁻² for *C. moniliferus* (Figure 2a,b) and 136 dm⁻² for *C. caeruleum* (Figure 2c,d), confirming significantly over-dispersed distributions indicative of aggregation. However, in one case (*C. caeruleum* at site 2), the distribution expected with random (Poisson) distribution had similar proportions of samples with large densities compared to the empirical data (Figure 2d), so in this case the significant difference in frequency distributions may be largely attributable to the large proportion of vacant/low-density quadrat samples.

There was highly variable topographic complexity on the sampled rock platforms, indicated by measurements of the ratio of the chain length (that followed the contours of the rock surface) to the linear length of the transect (2 m); values ranged from 0.717 to 0.995. The ANCOVA revealed no correlations between cerithiid abundances and topographic complexity (Table 3). The only significant effect was from the random site factor for *C. moniliferus* (Table 3).

The multivariate assemblage structure was significantly correlated with measures of topographic complexity (DistLM – Pseudo-F = 3.128, P = 0.015). However, there was an R² value of only 0.076 so topographic complexity explained relatively minor amounts of the total variation. The vectors on the PCO plot (Figure 3) showed that hermit crabs and *Siphonaria* spp. limpets were most strongly associated with the samples from rock surfaces with more complex/uneven topography.

4. Discussion

Aggregated distributions on the scale of metres are common for invertebrates on rocky shores (Aguilera and Navarrete, 2011; Chapman and Underwood, 1996; Coleman, 2010; Grayson and Chapman, 2004; Moisez et al., 2020; Montecinos et al., 2020). Even so, the high levels of such patchiness for varied species on the Veraval shore was striking. This suggests that the processes causing patchiness on other shores are acting strongly here, or other processes are involved. For some intertidal gastropods, patchiness may be caused by aggregation in areas of abundant food (Lauzon-

Table 1 List of total numbers of macrofaunal taxa found in January 2020 during the sampling at two sites on the intertidal rock platforms at Veraval.

Phylum	Class	Order	Family	Species/common name	Authority	Site 1	Site 2		
Mollusca	Gastropoda	Caenogastropoda	Cerithiidae	<i>Clypeomorus moniliferus</i>	Kiener, 1841	831	2531		
				<i>Cerithium caeruleum</i>	G. B. Sowerby II, 1855	224	369		
				<i>Cerithium zonatum</i>	W. Wood, 1828	0	6		
				<i>Rhinoclavis sinensis</i>	Gmelin, 1791	0	2		
			Neogastropoda	Muricidae	<i>Murex brunneus</i>	Link, 1807	1	0	
					<i>Purpura panama</i>	Röding, 1798	1	1	
				Conidae	<i>Conus cumingii</i>	Reeve, 1848	0	1	
					<i>Conus figulinus</i>	Linnaeus, 1758	0	1	
				Melongenidae	<i>Tylothais savignyi</i>	Deshayes, 1844	2	1	
				Cycloneritida	Neritidae	<i>Nerita albicilla</i>	Linnaeus, 1758	2	0
		Systemmatophora	Onchidiidae	<i>Paronia verruculata</i>	Cuvier, 1830	1	1		
				Patellogastropoda	Nacellidae	<i>Cellana karachiensis</i>	Winckworth, 1930	3	0
		Arthropoda	Malacostraca	Trochida	Turbinidae	<i>Lunella coronata</i>	Gmelin, 1791	13	70
						Sacoglossa	Limapontiidae	<i>Placida</i> sp.	–
				Siphonariida	Siphonariidae	<i>Siphonaria</i> spp.	–	21	42
						Nudibranchia	Plakobranchidae	<i>Elysia</i> sp.	–
				Chitonida	Chitonidae	<i>Rhyssoplax peregrina</i>	Thiele, 1909	2	2
						Stomatopoda	Squillidae	<i>Gonodactylaceus</i> sp.	–
				Decapoda	Pilumnidae	<i>Pilumnus vespertilio</i>	Fabricius, 1793	2	0
						Plagusiidae	<i>Plagusia squamosa</i>	Herbst, 1790	0
–	Unidentified hermit crabs						–	143	155
Annelida	Polychaeta			Sabellida	Sabellidae	<i>Sabella pavonina</i>	Savigny, 1822	0	6
Cnidaria	Anthozoa	Actiniaria	Actiniidae	<i>Aulactinia veratra</i>	Drayton in Dana, 1846	1	0		
				<i>Gyractis sesere</i>	Haddon & Shackleton, 1893	0	3		

Table 2 Statistical details from the one-sample Kolmogorov-Smirnov goodness-of-fit tests done on two cerithiid gastropod species at two sites on the Veraval coast. Gastropod distributions among quadrats were compared to Poisson distributions expected if distributions are random, with significant values representing population over-dispersion.

Species	Site	Max. deviation D	Kolmogorov-Smirnov test statistic ks	P
<i>Clypeomorus moniliferus</i>	1	0.80	5.06	<0.001
<i>Cerithium caeruleum</i>	2	0.38	2.37	<0.001
<i>Cerithium caeruleum</i>	1	0.75	4.74	<0.001
<i>Cerithium caeruleum</i>	2	0.56	3.56	<0.001

Table 3 ANCOVA on abundances of two intertidal gastropods testing effects of topographic habitat complexity (continuous variable) and random site (categorical variable). PERMDISP tests showed that variances were homogenous.

Species	Source	DF	MS	F	P
<i>Clypeomorus moniliferus</i>	Habitat complexity covariate	1	46.44	0.11	>0.5
	Site	1	4294.30	10.32	<0.001
	Residual	37	416.20		
<i>Cerithium caeruleum</i>	Habitat complexity covariate	1	0.51	0.00	>0.75
	Site	1	31.24	1.32	>0.25
	Residual	37	23.60		

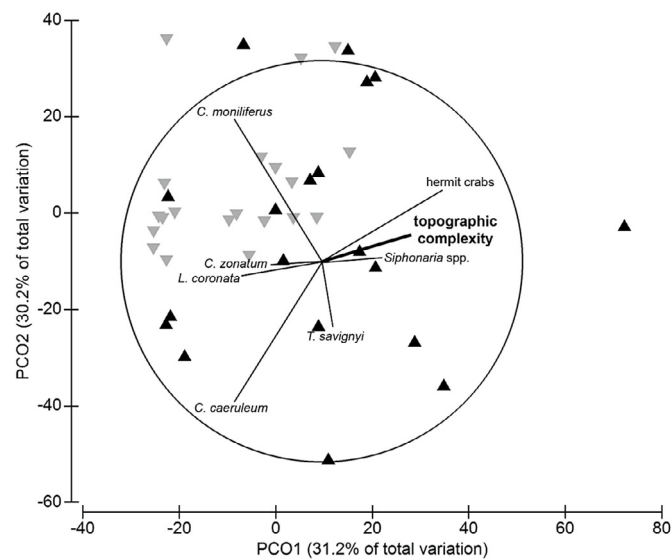


Figure 3 PCO ordination showing the structure of macroinvertebrate assemblages in quadrat samples of intertidal rock platforms at two sites near Veraval (Site 1 has black symbols, Site 2 grey). Vectors are included showing the macroinvertebrate taxa with strongest correlations to sample points (Pearson correlation $R^2 > 0.25$) and the sampling points associated with the measured environmental variable (topographic complexity, highlighted in bold); the vector length represents the strength of the correlation.

Guay and Scheibling, 2009). The cerithiids here have a highly generalised diet including microalgae and detritus that can be taken from surfaces such as on rocks, mud, seaweeds, or seagrasses (Ayal and Safriel, 1982). Here we did not quantify these potential food sources but their generalised nature may be considered to result in a relatively even spread over rock platforms such as at Veraval, so we considered that food supply may not be a feature of priority to test for explaining this small-scale clustering. There was evidence that habitat complexity, in the form of unevenness of the rock topography, was to a limited extent structuring the invertebrate assemblage as a whole. Based

on the current results, however, it may be ruled out that such habitat complexity is involved in the strong patterns of cerithiid aggregation at the scale of complexity we measured, although further studies may consider testing if complexity of the rock surface at different scales may still affect cerithiid aggregation.

Highly uneven topography may involve the presence of beneficial crevices and other shelters that produce some tendency for processes resulting in aggregation (e.g. Chapman and Underwood, 1994). However, gastropods may still acquire such shelter using the presence of conspecifics. For example, although crevices and pits may protect from

temperature/desiccation (Stafford and Davies, 2005) or predation (Garrity and Levings, 1981), similar protection may also occur for individuals within dense aggregations (Ray and Stoner, 1994; Rojas et al., 2013) even on flat rock. In the case of cerithiid aggregations, the latter situation may be occurring.

Observations of intertidal cerithiid behaviour in other regions have shown that while feeding at high tide they are not aggregated, and that cluster formation occurs shortly before low tide. Clustering possibly occurs via initiation of the thigmotactic response while moving (Moulton, 1962), although it has been unclear whether thigmotaxis is directed to features of the rock substratum or to surrounding conspecifics. Our evidence suggests this situation may likewise be occurring for *Clypeomorus moniliferus* and *Cerithium caeruleum* in our study location, and that features of the rock substratum are not involved. Thus, regardless of variability in topographic complexity, aggregations likely develop in response to the presence of other gastropods. Individuals of *Austrolittorina unifasciata*, a similar aggregating intertidal gastropod studied by Chapman (1995, 1998), follow each other's trails, and chemotaxis is a potential mechanism to allow gastropod individuals to contact each other during the aggregation forming process. Other features of *A. unifasciata* do not, however, relate to the cerithiids studied here, such as the association of *A. unifasciata* with complex rock topography (Chapman and Underwood, 1994). Informal observations of cerithiids done by Moulton (1962) suggested a process of desiccation and temperature stress reduction may occur within cerithiid aggregations, but the study by Stafford et al. (2012) should also be considered that discussed the difficulties of confirming any such process.

Although there was no evidence that cerithiids were affected by habitat topography, the multivariate analysis indicated such an effect may occur for hermit crabs and limpets of the genus *Siphonaria*. This is similar to results from Loke et al. (2019) who found that a related limpet in Singapore, *Siphonaria atra*, is also associated with uneven intertidal topography. They may be acquiring predation, temperature or desiccation protection by using features of uneven rocky topography. Snyder-Conn (1979) found that hermit crabs can have aggregation patterns similar to cerithiids (i.e. dispersed distributions during high tide immersion followed by aggregation at low tide emersion; Moulton, 1962). However, hermit crab aggregation was clearly controlled by topographic features such as crevices and boulders (Snyder-Conn, 1979). The lack of evidence for such topographic control in the cerithiids we studied highlights the importance of testing correlations or effects of substratum features to understand intertidal invertebrate aggregation, as explanations clearly cannot be extrapolated from one taxon to another, even if the biotic patterns have close similarity.

Shelter seeking aggregation behaviours may be used by macroinvertebrate prey on the Veraval coast due to large abundances of intertidal crab and whelk predators (Bhadja et al., 2014) and the potential for extreme regional summer temperatures (Azhar et al., 2014). Also, while topographic complexity appears largely ineffectual, other environmental factors unexplored in this study may be contributing to gastropods aggregating in certain areas. For cerithiids, there may be implications from aggregation for survivorship from harsh environmental condi-

tions or predators, but also for processes such as parasitism (Cannon, 1979). In addition, for some cerithiids, factors affecting their populations may in turn have consequences for the wider ecological system, e.g. via changes to biochemical cycling (Nicolaidou and Nott, 1999). These results can guide further research on factors affecting cerithiid aggregation. Our results indicate plausibility of aggregation being affected not by topography, but more likely by the alternative explanation of the presence of conspecifics. This could be tested experimentally, with aggregation levels measured following manipulation of densities of conspecific cerithiids or artificial mimics of cerithiids. Overall, the current study along with any further related observational or experimental research will inform our understanding of causes for and consequences of aggregation behaviour in intertidal invertebrates.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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