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Patterns of rockpool molluscs in differing shore exposures

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Abstract

Rockpools are understudied systems of extreme importance due to their proven vulnerability to climate change. Rockpool molluscs play essential ecological roles therein, directly by acting both as prey and predator and, indirectly by influencing the topography via grazing. However, the environmental factors driving their rockpool occupation remain largely unknown. Our study is one of the few to focus on rockpool molluscs community patterns, particularly at a large scale between shores of differing exposure to wave action, being the first focused assessment of rockpool molluscs in Portugal. Overall, 32 intertidal rock pools on four rocky shores were studied during the summer spring tide of 2015. We used multivariate analysis to evaluate the potential impact of sheltered versus exposed wave action, physical pool structure (length, width, and depth), and relationships within the pool community on the abundance and diversity of molluscs. Wave exposure significantly influenced mollusc abundance and diversity. Among the 37 different taxa identified, there was a greater abundance of grazing gastropods (62.2%), followed by bivalves (27.0%) and chitons (10.8%). We suggest that mollusc taxa may have preferences for particular rock pool habitats depending on the type of algae present rather than pool size. We also suggest that species-specific mollusc presence in rockpool can be related to their shell size, aperture, and foot size due to corresponding variation in musculature needed to hold the snail to the substrate in hydrodynamic conditions. Further investigation would benefit from disentangling the potential role of algal pool coverage as a predator refuge for molluscs.

Introduction

Intertidal communities are found at the boundary between sea and land and are influenced by tidal flooding and consequent dynamic periods of emersion and immersion (Coutinho et al. 2016; Legrand et al. 2018). During low tides, seawater can get retained in eroded patchy depressions of rock, i.e. rockpools, representing mesocosms of marine life (Legrand et al. 2018). Compared to the surroundings, the environment inside these rock pools is substantially less harsh due to the lower amplitude of physicochemical fluctuations (temperature, salinity, pH, and dissolved O2), offering refuge, feeding areas, and nurseries for several marine species (Underwood and Jernakoff 1984; Dias et al. 2014; Vinagre et al. 2015; Mendonça et al. 2018). The study of rockpools is of extreme importance due to their proven vulnerability to climate change, namely global warming, sea level rise, and overall anthropogenic activities that can lead to an abrupt biodiversity loss in these coastal areas (Fairchild et al. 2018; González-Murcia et al. 2020).

Whereas intertidal rocky shore platforms have been well studied, intertidal rock pools therein have received relatively less attention, particularly on their community dynamics (Martins et al. 2007; Mendonça et al. 2018). However, there has been growing interest in determining the biotic (e.g. competition, predation, recruitment) and abiotic (e.g. tidal isolation, desiccation, salinity) factors structuring their communities (Metaxas and Scheibling 1993, Arauújo et al. 2006, Brendonck et al. 2015, Bezerra et al. 2017). Within these communities, the mollusc group is particularly understudied with only a

few examples in literature (e.g. Underwood 1976, Breves and Moraes 2014, Souza and Matthews-Cascon 2019) and hence, the target group of our work.

Rockpool molluscs play essential ecological roles therein including acting both as prey and predator, indirectly influencing the topography via grazing and, shaping the habitat resulting in a complex benthos community, which in turn attracts other intertidal organisms to the area (Martins et al. 2007; Gartner et al. 2013; Souza and Matthews-Cascon 2019). Marine molluscs are also currently threatened by future ocean acidification conditions as it is predicted that they will produce thinner shells of lower structural integrity (Fitzer et al. 2018), thus highlighting the importance of collecting data about this taxon.

Almost no environmental factors are known to affect the habitat selection of molluscs in intertidal rock pools. Previous studies (Underwood and Skilleter 1996; Marsh et al. 1978; Carvalho et al. 2021) proved that pool size does not affect species richness or abundance within rock pools, namely in molluscan assemblages (Souza and Matthews-Cascon 2019), but this is still a matter of debate as other authors reported differing results (Martins et al. 2007). Other studies on molluscs in rock pools have evaluated grazing intensity (Noel et al. 2009), nutrient and sediment effects (Atalah and Crowe 2010), and trophic relationships (Masterson et al. 2008, Breves and Moraes 2014). Recently, Sousa and Matthews-Cascon, (2019) showed that variation of molluscan assemblages between pools within the same site is not due to different pool sizes but rather due to the association between these organisms and the substrate of the pool. Hence, little is still known in the literature regarding the factors that drive their diversity and distribution in these habitats.

Our study is one of the few existing to focus on rockpool molluscs community patterns, particularly at a large scale between shores of differing exposure to wave action. This last factor has been shown to be significantly important for other pool taxa such as crustaceans (e.g. Carvalho et al. 2021). Our study also provides the first focused assessment of rockpool molluscs in Portugal, with previous studies being limited to fish (e.g. Compaire et al. 2022) and amphipods (Carvalho et al. 2021), hence allowing to set a database baseline for comparison with future research. We tested the hypothesis that molluscan diversity and abundance vary between shores of differing wave action (sheltered and exposed). We also assessed the relationship between the overall rockpool community composition and the presence of molluscs and evaluated whether physical rockpool structure (size, depth, and width) influences the abundance and diversity patterns of molluscs.

Material And Methods

Sampling locations framework

Rockpool community data was collected in 2015 summer tides as this season typically corresponds to a peak in biodiversity and species abundance found in intertidal rock pools (Underwood and Jernakoff 1984; Moore and Seed 1986). Two sheltered and two exposed shores were chosen on the Portuguese west coast and where eight intertidal rock pools were sampled per shore: Sheltered shores (*Paimogo* –

39°17'11.4"N 9°20'23.7"W and *Peralta* 39°14'28.9"N 9°20'36.8"W) and Exposed shores (*Cabo Raso* – 38°42'38.2"N 9°29'09"W and *Raio Verde* – 39°17'11.4"N 9°20'23"W).

Pool size was standardized as much as possible to enable full biological sampling within the low-tide time frame. Overall, 32 pools were sampled, and their physical features were assessed, whereby the average length was 2.73 ± 0.20 , average width 1.54 ± 0.18 and average depth 1.28 ± 0.97 .

Biological Sampling

Most pool biota was identified *in situ*, with ocasional laboratory validation for smaller taxon where specimens were preserved in 70% alcohol and later identified in the laboratory with a stereomicroscope. Given the complexity of rockpool communities, a combined visual, collection and laboratory sampling approach was used to secure a more complete assessment: *in situ* visual percentage cover and counts of colony-like organisms easily identified in the field (e.g. algae, anemones, barnacles); hand-net collection, in situ identification and counting of all mobile animals such as fish, crabs, snails, and amphipods, and; three replicated 5 cm2 quadrate scrapings for laboratory identification and quantification of remaining biota such as small snails and algae dwellers.

Data Analysis

All data was analysed with the PRIMER statistical software given its multivariate nature. The PERMANOVA (9999 permutations) was used to test the hypothesis of wave exposure as a significant factor in mollusc rockpool presence and abundance (based on the sum of animals in the scrapped quadrates and hand collections). Dissimilarities found with PERMANOVA were visually organised via a multidimensional ordination plot (MDS). The taxa most contributing to shore exposure differences were identified using the SIMPER analysis. Further data exploration between exposures was made using a PCO ordination analysis to assess potential correlations between the pool's entire community and the mollusc presence. Also, any potential relation between the pool physical features (depth, length, and width) and the abundance of molluscs was examined using the BEST analysis.

Results

There were significant differences between the mollusc abundance between pools of exposed and sheltered shores (P-value = 0.01) and also between different locations within the same wave action exposure (P-value = 0.01). These were visually evident from the MDS ordination clustering patterns (Fig. 1). Also, rock pools from both locations within exposed wave action were more similar regarding molluscan assemblages than rock pools from both locations within sheltered wave action (Fig. 1).

The principal component ordination (PCO) identified the molluscan taxa most crucial in differentiating the rock pools from shores of different wave exposure and locations (Fig. 2). The horizontal vectors represent the molluscs *Crisilla ugesae* (snail), *Tricolia pullus* (snail), *Steromphala umbilicalis* (snail), *Mytilus galloprovincialis* (bivalve) (Fig. 2) and the algae *Bifurcaria* sp. and *Ulva* sp. (Fig. 3), those explaining most of the variability between exposed and sheltered shores. Cabo Raso (exposed location)

had the highest average coverage of *Ulva* sp. (algae) whereas Peralta (sheltered location) had the highest average coverage of *Bifurcaria* sp. (algae). The BEST analysis showed a negligible relationship (R = 0.3) between pool physical features (length, width, and depth) and the abundance of molluscs.

Among the 37 different taxa identified, there was a greater abundance of grazing gastropods (62.2%), followed by bivalves (27.0%) and chitons (10.8%). Raio Verde (exposed location) showed the highest diversity of taxa with 28 different molluscan taxa, followed by Peralta and Cabo Raso, which showed a total of 25 and 24 different taxa, respectively. Paimogo (sheltered location) showed the lowest taxa diversity with only 21 in a total of 37 taxa.

The SIMPER analysis identified the average dissimilarity between locations, which ranged between 28.0% and 39.9% indicating a reasonable similarity of approximately 60% between locations.

The SIMPER analysis also provided the mean abundance of the molluscan taxa most contributing to differences between shores of differing exposure. The most abundant taxa found were *Musculus costulatus* (bivalve), *Mytilus galloprovincialis* (bivalve), and *Omalogyra atomus* (snail). Raio Verde showed the higher mean molluscan abundance of all four locations. *M. costulatus*, *M. galloprovincialis*, *Lepidochitona cinerea* (chiton), *Aplysia punctata* (slug), and *Steromphala umbilicalis* (snail) showed higher mean abundances on exposed shores (Fig. 4). On the other hand, *Tritia reticulata* (snail), *Barleeia* sp. (snail), *Crisilla ugesae* (snail), *Tricolia pullus* (snail), *Patella ulyssiponensis* (snail) and *Acanthochitona crinita* (chiton) showed higher mean abundances in sheltered shores (Fig. 4). *O. atomus* showed similar average abundance on both shores exposures.

The SIMPER analysis also identified the molluscan taxa (based on abundance) most contributing to differences between shores of differing exposure. The species that most contributed to the separation between exposed and sheltered locations were: *M. costulatus*, *M. galloprovincialis*, *Barleeia* sp., and *C. ugesae*. *M. costulatus* was responsible for the separation between the shores Raio Verde and Paimogo, Raio Verde and Peralta, and Raio Verde and Cabo Raso with percentages of contribution of 12.9%, 12.6%, and 11.2%, respectively (Fig. 5), and showed higher mean abundance in Raio Verde. *C. ugesae* was responsible for the separation between the shores Cabo Raso and Peralta, and between Cabo Raso and Paimogo with contribution percentages of 9.5% and 9.9%, respectively, and showed higher mean abundance in both sheltered locations. *Barleeia* sp. had the major contribution in separating the location Peralta from Paimogo, with a contribution percentage of 10.4% (Fig. 5) and showing a higher mean abundance in Peralta.

Discussion

Molluscan abundance and species richness on shores of different wave exposure

The richness and diversity of particular taxa varied widely between replicate pools, as did their abundance. This feature may be characteristic of patchy marine habitats (Underwood and Skilleter 1996). Moreover, locations within sheltered shores were much more similar between themselves than locations within exposed shores, as found also by Carvalho et al. (2021) on amphipod communities. This result denotes higher variation in exposed conditions gradients, making it essential for future studies to clarify the underlying causes of this variation.

Differences in taxa richness were identified between locations of different wave-action exposure. Raio Verde (exposed location) rockpools showed the highest mollusc taxa richness. This matches Underwood and Skilleter (1996) findings, which showed that molluscan species richness may be higher in wave-exposed locations. However, other studies showed that reduced wave action may increase molluscan species diversity (Rahman and Barkati 2012; D'Souza et al. 2022). We suggest that exposed location type seems to be favorable for molluscs, possibly due to higher hydrodynamism allowing different molluscan larvae to reach these pools, as shown by Spotorno-Oliveira et al. (2015).

The functional group bivalve was more characteristic of exposed locations whereas the functional group snail showed higher mean abundance in sheltered habitats. The snails *Tricolia pullus* and *Crisilla ugesae* had higher average abundance on sheltered wave action shores. However, little is known regarding the latter species distribution due to previous studies being limited to Olivier et al. (2019). This is a microgastropod typically habiting shallow coastal waters (Olivier et al. 2019) possibly taking advantage of sheltered rock pools for refuge or as a feeding ground. The gastropod *T. pullus* is also a small sea snail often found feeding around red seaweeds (Duffus 1969), such as *Corallina* sp..

The species *Mytilus galloprovincialis* (bivalve) and *Steromphala umbilicalis* (snail) displayed higher mean abundance in exposed locations. The latter has usually higher dimensions than the snail species most abundant in sheltered habitats so, we suggest that size may play an important factor in exposed conditions as larger animals are expected to have stronger attachment capacity, hence minimized vulnerability to dislodgement. For instance, limpets showed a proportionally larger foot on wave-exposed shores, suggesting that stronger attachment is an important mechanism to deal with wave action dislodgement (Vieira and Bueno 2019). Snail shell design can also be important, albeit beyond the scope of our study, as previous studies have stated that shorter and broader shells would be more advantageous in wave-exposed locations, allowing less turbulence of water flow over the snail shell and hence reducing the risk of wave dislodgement (Frid and Fordham 2012). Moreover, exposed locations seem to be favorable for filter-feeding bivalves such as *Musculus costulatus* and *M. galloprovincialis* probably by allowing increased food supply associated with increased water movement (Branch et al. 2008) and relatively increased availability of fixation spots when compared to the large algae cover typically found in sheltered conditions.

Algal rock pool coverage and physical features

The PCO analysis showed that it is possible that wave action accounted for the differences in algal coverage between shores and that molluscan patterns are correlated with the rockpool algal coverage.

One of the pool features most contributing to the differences between wave-exposed and sheltered pools was the increased presence of the green algae *Ulva* sp. on wave-exposed shores, especially in Cabo Raso. This suggests that green fleshy algae are probably more resistant to wave action than red or brown algae for instance, as found by van Tamelen (1996). However, contrary to what we would have expected, this is not the location with higher species richness, although rockpool molluscs are likely to benefit from *Ulva* sp. fronds as shelter from predation pressure by both in-house residents such as blenniiformids and some crabs, and by high-tide occasional predators such as subtidal fish and other larger crab species (Wakefield and Murray 1998; Kemppainen et al. 2005; Silva et al. 2010). Bivalves such as *M. costulatus* and *M. galloprovincialis* are usually associated with filamentous substrates (such as the macroalgae *Ulva* sp.) or with small substrate depressions (Hunt and Scheibling 1996) in sites with relatively increased availability of fixation spots, such as exposed habitats due to its lower algae cover compared to sheltered conditions.

Tuya et al. (2008) stated that molluscs living on algae with wider fronds, such as *Ulva* sp., are possibly more affected by wave action due to the higher surface area exposed to the water flow compared to smaller algae. However, the highest abundance of *Ulva* sp. was found in exposed locations, which exhibited the greatest taxa richness. This fact suggests that both wave action and great *Ulva* sp. algal coverage may have accounted for the high taxa richness observed in these locations.

Other algae taxa contributing to the separation of wave-exposed and sheltered pools was the increased presence of *Bifurcaria* sp. and *Corallina* sp. on sheltered shores. Coralline algae are poor competitors for space and very resistant to physical disturbances, including the mechanical impact of waves, dominating rocky habitats exposed to higher abiotic stress (Bertocci et al. 2005). Nonetheless, we found higher coverage of *Corallina* sp. in sheltered locations. It has been shown that grazing microgastropods (snails) have a preference to live on Coralline algae (Olabarria et al. 2002; Spotorno-Oliveira et al. 2015) enhancing their establishment and persistence (Johnson and Paine 2017) and, therefore, justifying the higher abundance of snails found on sheltered habitats comparatively to exposed ones. Another possible explanation, albeit less liable, could be that the considerably high diversity of herbivorous snails may have led to the scarcity of erect fleshy algae like *Ulva* sp. and higher concentrations of *Bifurcaria* sp. and *Corallina* sp. on sheltered locations.

We found that physical pool features (size, depth, and width) do not influence the abundance and diversity patterns of molluscs, corroborating the work by Sousa and Matthews-Cascon, (2019) and contrary to what some previous studies stated (Martins et al. 2007; Annusa et al. 2012). Mollusc taxa may have preferences for particular rock pool habitats depending on the type of algae present rather than the size, depth, or width of the pool. We hypothesize that larger and more diverse environments are not as important for molluscs as the refuge given by the algae cover which acts as their substrate for refuge and feeding.

Conclusion

Our study showed that intertidal rockpool molluscs are significantly affected by hydrodynamism, hence filling an important gap in the knowledge of the driving factors of molluscan distribution in intertidal rock pools. We also pinpointed algal coverage as an important pool feature influencing molluscan abundance. These data add baseline information to our understanding of rock pool systems and can be applied to monitoring programmes that evaluate ecological changes brought on by anthropogenic and natural disturbances. We suggest future work towards focusing on the role of specific algae pool coverage as a refuge from predation and dislodgement for rockpool molluscs. We also suggest that species-specific mollusc presence in rockpool can be related to their shell size, aperture and foot size due to corresponding variation in musculature needed to hold the snail to the substrate in hydrodynamic conditions.

Declarations

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.

Ethics approval

No ethical approval was required for this study.

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MDS ordination plot of Mollusca abundance per sampled location and wave action exposure. Grey vertical line signals exposure clear separation. CR - Cabo Raso, RV - Raio Verde, PE – Peralta, PA – Paimogo.



Principal component ordination (PCO) representing the Mollusca taxa that are most associated with the molluscan distribution across shores of different wave action exposure. CR - Cabo Raso, RV - Raio Verde, PE – Peralta, PA – Paimogo.



Principal component ordination (PCO) representing the algae taxa most associated with the differing molluscan distribution across shores of different wave action exposure. (Most contributing taxa for exposure differences are shown in bold). CR - Cabo Raso, RV - Raio Verde, PE – Peralta, PA – Paimogo.



Average abundance (±SE) of each Mollusca taxa at each shore. CR (Cabo Raso) and RV (Raio Verde) correspond to shores of high wave exposure; PE (Peralta) + PA (Paimogo) correspond to sheltered shores of low wave exposure. Only the taxa with a cumulative contribution percentage of 50% are presented.