



# Patterns of rock pool molluscs in differing shore exposures

Inês Gonçalves<sup>1,3</sup> · Catarina Vinagre<sup>2,3</sup> · Ana Silva<sup>4,5</sup>

Received: 12 December 2022 / Accepted: 2 May 2023 / Published online: 13 May 2023  
© The Author(s) 2023

## Abstract

Rock pools are understudied systems of extreme importance due to their proven vulnerability to climate change. Rock pool molluscs play essential ecological roles therein, directly by acting both as prey and predator and, indirectly by influencing the macroalgal canopy/vegetation topography via grazing. However, the environmental factors driving their rock pool occupation remain largely unknown. Our study is one of the few to focus on community patterns in rock pool molluscs, particularly at a large scale between shores of differing exposure to wave action, being the first focused assessment of rock pool 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. The majority of the 37 different taxa identified were 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 rock pools 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 refuge for molluscs.

**Keywords** Intertidal · Exposed · Sheltered · Wave-action · Richness · Structure

## 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. rock pools, 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 O<sub>2</sub>), 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 rock pools 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.

---

Responsible Editor: P. Kraufvelin .

✉ Ana Silva  
ana.c.f.silva@tecnico.ulisboa.pt

<sup>1</sup> Faculdade de Ciências e Tecnologia, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

<sup>2</sup> MARE, Marine and Environmental Sciences Centre, Faculty of Sciences, University of Lisbon, Campo Grande, 1749-016 Lisbon, Portugal

<sup>3</sup> Centre of Marine Sciences, CCMAR, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

<sup>4</sup> CERIS, Instituto Superior Técnico, Universidade de Lisboa, Av. Rovisco Pais 1, 1049-001 Lisbon, Portugal

<sup>5</sup> Departamento de Engenharia e Ciências Nucleares (DECN), Instituto Superior Técnico, Universidade de Lisboa, Bobadela, Portugal

tidal isolation, desiccation, salinity) factors structuring these communities (Metaxas and Scheibling 1993; Araújo 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), which this study tries to partly remediate.

Rock pool molluscs play essential ecological roles therein including acting both as prey and predator, indirectly influencing the vegetation/macroalgal canopy 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 (Marsh et al. 1978; Underwood and Skilleter 1996; 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 (Wai and Williams 2006; 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, the literature remain unclear regarding the factors that drive their diversity and distribution in these habitats.

Climate change will trigger changes in coastal sea level and wave patterns, which in turn are important factors predicted to shift coastal species distribution and structure (Westerbom et al. 2019). Albeit several studies have focused on climate-related warming effects on intertidal species physiology and distribution (e.g. Vinagre et al. 2019; Hemraj et al. 2020), few have evaluated the potential role of crucial wave patterns on intertidal organisms. Our study is one of the few existing to focus on community patterns in rock pool molluscs, 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 rock pool molluscs in Portugal, with previous studies being limited to fish (e.g. Compaire et al. 2016) 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 rock pool community composition and the presence of molluscs and evaluated whether physical rock pool structure (size, depth, and width) influences the abundance and diversity patterns of molluscs.

## Material and methods

### Sampling locations framework

Rock pool community data were 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). 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*—38°42'29.8"N 9°29'7.6"W). Levels of shore exposure were confirmed using measures of mean flow conditions, using the dissolution of gypsum (CaSO<sub>4</sub>) blocks as described in detail in (Silva et al. 2009). Sets of twelve discs were attached to the rock surface ~3 m above Chart Datum (CD) during high tide on two occasions at each location. Blocks on sheltered shores dissolved significantly more slowly (~4 g/h) than on more exposed shores (~6 g/h) ( $P < 0.04$ ), proving a difference in exposure between locations.

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  $2.73 \pm 0.20$  cm, average width  $1.54 \pm 0.18$  cm and average depth  $1.28 \pm 0.97$  cm.

### Biological sampling

Most pool biota was identified in situ, with occasional laboratory validation for smaller taxa where specimens were preserved in 70% alcohol for later identification with a stereomicroscope. Given the complexity of rock pool 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 cm<sup>2</sup> quadrat scrapings for laboratory identification and quantification of remaining biota such as small snails and algae dwellers.

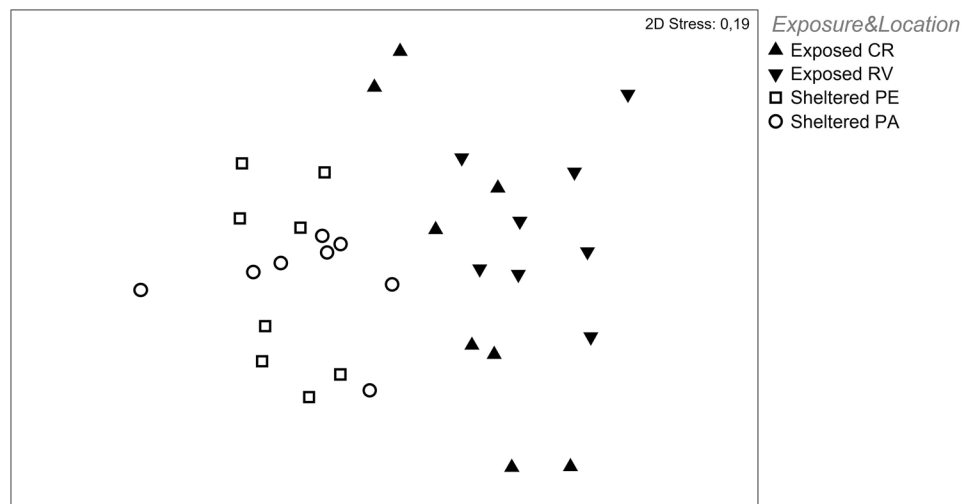
## Data analysis

All data were analysed with the PRIMER statistical software given its multivariate nature (Clarke and Gorley 2006). PERMANOVA (Anderson 2008) was used to test the hypothesis of wave exposure as a significant factor in mollusc rock pool presence and abundance (based on the sum of animals in the scraped 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 visualise 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.

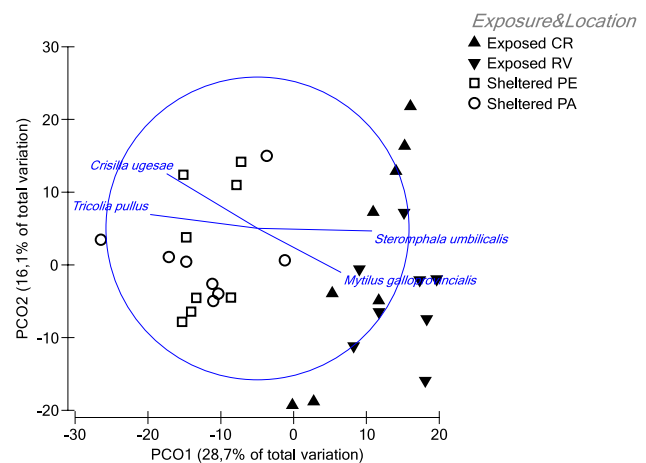
## Results

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).

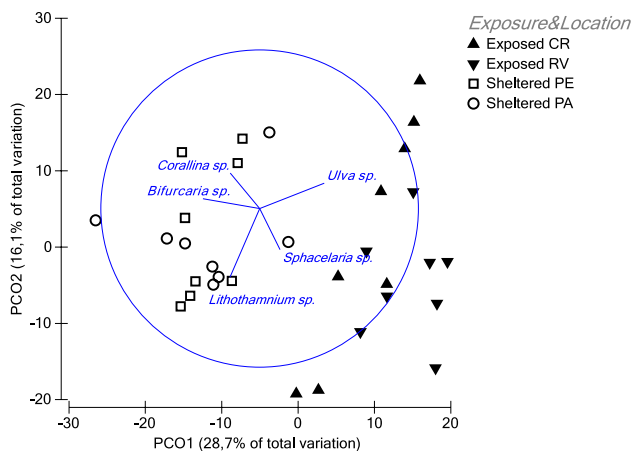
**Fig. 1** MDS ordination plot of Mollusca abundance per sampled location and wave action exposure. CR Cabo Raso, RV Raio Verde, PE Peralta, PA Paimogo



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) and *Tricolia pullus* (snail), which were more associated with sheltered rock pools, as well as *Steromphala umbilicalis* (snail) and *Mytilus galloprovincialis* (bivalve), which were more associated with exposed rock pools (Fig. 2) and the algae *Bifurcaria* sp. (sheltered pools) and *Ulva* sp. (exposed pools) (Fig. 3), as those specific taxa explaining most of the variability according to shore exposure levels. 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



**Fig. 2** 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



**Fig. 3** 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

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 at least 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. *Musculus 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). *Omalogyra atomus* showed similar average abundance on both exposure levels.

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*. *Musculus 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 (Online Resource 1), and showed higher mean abundance in Raio Verde. *Crisilla 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% (Online Resource 1) and showing a higher mean abundance in Peralta.

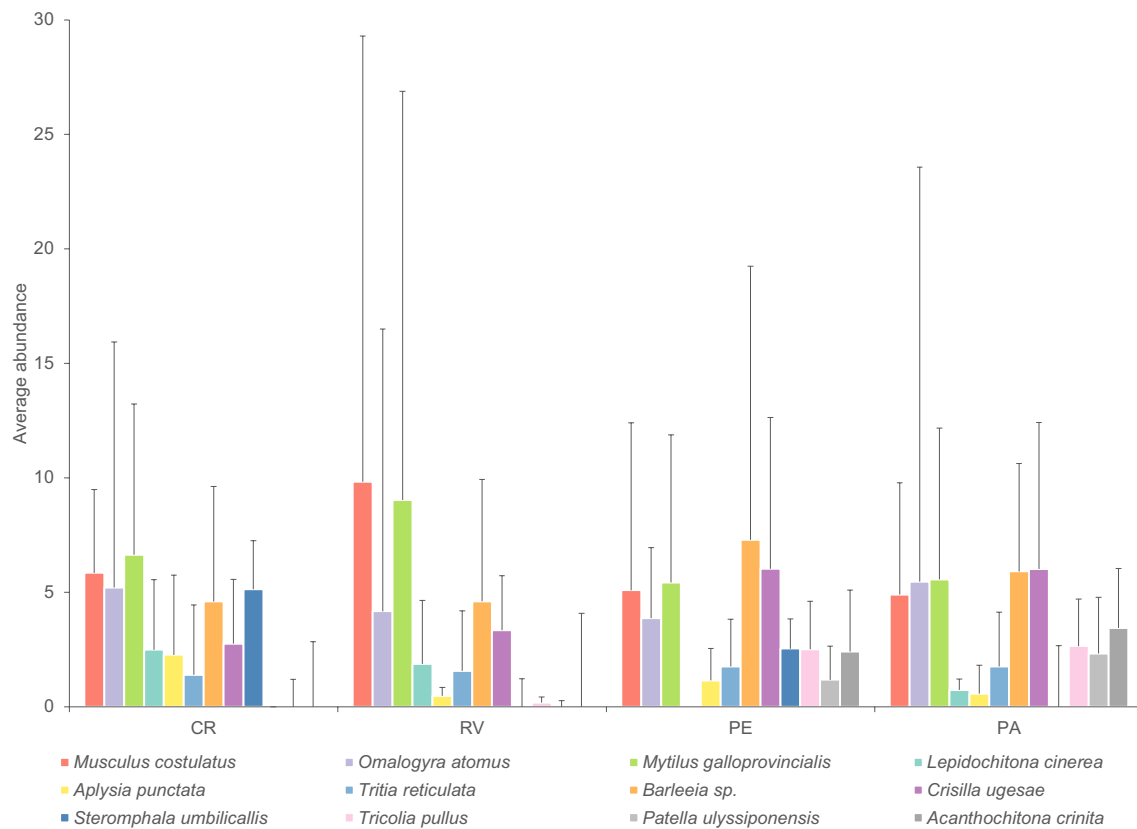
## Discussion

### Molluscan abundance and species richness on shores of different wave exposure

The richness, abundance and diversity of particular taxa varied widely between replicate pools. This feature may be characteristic of patchy marine habitats (Underwood and Skilleter 1996; Veras et al. 2013). 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) rock pools showed the highest mollusc taxa richness. This matches findings by Underwood and Skilleter (1996) that 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 an exposed location type seems to be favorable for molluscs, possibly due to higher hydrodynamic action 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 the one by Oliver et al. (2019). *Crisilla ugesae* is a microgastropod typically habiting shallow coastal waters (Oliver et al. 2019) possibly



**Fig. 4** Average abundance ( $\pm$ 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 shel-

tered shores of low wave exposure. Only the taxa with a cumulative contribution percentage of > 50% are presented

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 that were 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 capacities and a lower 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 1994). 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 rock pool 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 rock pool molluscs are likely to benefit from *Ulva sp.* fronds as shelter from predation pressure by both in-house residents such as blenniiform fish 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 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. Coral-line 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. 2012). 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 2016) and, therefore, justifying the higher abundance of snails found on sheltered habitats comparatively to exposed ones. Another possible explanation 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; Anusa 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 also serves as a food item.

## Conclusion

Our study showed that intertidal rock pool 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 rock pool molluscs. We also suggest that species-specific mollusc presence in rock pool 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 under different hydrodynamic conditions.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-023-04223-2>.

**Acknowledgements** The authors thank everybody who assisted with the field and laboratory work, in particular Carolina Madeira. This study had the support of the Portuguese Fundação para a Ciência e a Tecnologia (FCT) through the project WarmingWebs PTDC/MAR-EST/2141/2012, the grant SFRH/BD/109618/2015 awarded to V. Mendonça, a FCT researcher contract to C. Vinagre; and through the strategic projects UIDB/04292/2020 and UIDB/04326/2020. The authors are grateful for the Foundation for Science and Technology's support through funding UIDB/04625/2020 from the research unit CERIS.

**Author contributions** The author IG contributed to data analysis and manuscript conceptualisation and writing. The author CV contributed to data collection and analysis and manuscript writing. The author AS contributed to data analysis and manuscript conceptualisation and writing.

**Funding** Open access funding provided by FCTIFCCN (b-on). This work was supported by Fundação para a Ciência e a Tecnologia, grant numbers UIDB/04625/2020 and SFRH/BD/109618/2015.

**Data availability** The datasets generated during and/or analysed during the current study are available at <https://doi.org/10.25829/iDiv.283-3-756>.

## Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

**Ethics approval** No ethical approval was required for this study.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Anderson M (2008) Permanova+ for primer: Guide to software and statistical methods. Primer-E Limited.
- Anusa A, Ndagurwa HGT, Magadza CHD (2012) The influence of pool size on species diversity and water chemistry in temporary rock pools on Domboshawa Mountain, northern Zimbabwe. *Afr J Aquat Sci* 37:89–99. <https://doi.org/10.2989/16085914.2012.666378>
- Araújo R, Sousa-Pinto I, Bárbara I, Quintino V (2006) Macroalgal communities of intertidal rock pools in the northwest coast of Portugal. *Acta Oecol* 30:192–202. <https://doi.org/10.1016/j.actao.2006.04.002>
- Atalah J, Crowe TP (2010) Combined effects of nutrient enrichment, sedimentation and grazer loss on rock pool assemblages. *J Exp Mar Biol Ecol* 388:51–57. <https://doi.org/10.1016/j.jembe.2010.03.005>
- Bertocci I, Araújo R, Incera M, Arenas F, Pereira R, Abreu H, Larsen K, Sousa-Pinto I (2012) Comunidades bentónicas de charcas rocosas del norte de Portugal: variabilidad estacional y entre charcas. *Sci Mar* 76:781–789. <https://doi.org/10.3989/scimar.03669.21A>
- Bezerra LAV, Padial AA, Mariano FB, Garcez DS, Sánchez-Botero JI (2017) Fish diversity in tidepools: assembling effects of environmental heterogeneity. *Environ Biol Fishes* 100:551–563. <https://doi.org/10.1007/s10641-017-0584-3>
- Branch GM, Odendaal F, Robinson TB (2008) Long-term monitoring of the arrival, expansion and effects of the alien mussel *Mytilus galloprovincialis* relative to wave action. *Mar Ecol Prog Ser* 370:171–183. <https://doi.org/10.3354/meps07626>
- Brendonck L, Jocqué M, Tuytens K, Timms BV, Vanschoenwinkel B (2015) Hydrological stability drives both local and regional diversity patterns in rock pool metacommunities. *Oikos* 124:741–749. <https://doi.org/10.1111/oik.01710>
- Breves A, Moraes FC (2014) Rock pool malacofauna from a marine protected area in Rio de Janeiro (Brazil). *Strombus* 21:1–9
- Carvalho J, Mendonça V, Vinagre C, Silva A (2021) Environmental factors impacting the abundance and distribution of amphipods in intertidal rock pools. *J Sea Res*. <https://doi.org/10.1016/j.seares.2021.102035>
- Clarke K, Gorley R (2006) Primer v6: User Manual/Tutorial.
- Compaire JC, Cabrera R, Gómez-Cama C, Soríguer MC (2016) Trophic relationships, feeding habits and seasonal dietary changes in an intertidal rockpool fish assemblage in the Gulf of Cadiz (NE Atlantic). *J Mar Syst* 158:165–172. <https://doi.org/10.1016/j.jmarsys.2016.02.006>
- Coutinho R, Yaginuma LE, Siviero F, dos Santos JCQP, López MS, Cristofaletti RA, Berchez F, Ghilardi-Lopes NP, Ferreira CEL, Gonçalves JEA, Masi BP, Correia MD, Sovierzoski HH, Skinner LF, Zalmon IR (2016) Studies on benthic communities of rocky shores on the Brazilian coast and climate change monitoring: Status of knowledge and challenges. *Braz J Oceanogr* 64:27–36. <https://doi.org/10.1590/S1679-875920161015064sp2>
- D'Souza SL, D'Souza N, Shenoy KB (2022) Molluscan diversity of coastal Karnataka, India and role of physicochemical parameters on their diversity. *J Coast Conserv*. <https://doi.org/10.1007/s11852-021-00849-w>
- Dias M, Silva A, Cabral HN, Vinagre C (2014) Diet of marine fish larvae and juveniles that use rocky intertidal pools at the Portuguese coast. *J Appl Ichthyol* 30:970–977. <https://doi.org/10.1111/jai.12450>
- Duffus JH (1969) Associations of Marine Mollusca and Benthic Algae in the Canary Island of Lanzarote. *J Molluscan Stud*. <https://doi.org/10.1093/oxfordjournals.mollus.a065047>
- Fairchild TP, Fowler MS, Pahl S, Griffin JN (2018) Multiple dimensions of biodiversity drive human interest in tide pool communities. *Sci Rep*. <https://doi.org/10.1038/s41598-018-33155-x>
- Fitzer SC, Torres Gabarda S, Daly L, Hughes B, Dove M, O'Connor W, Potts J, Scanes P, Byrne M (2018) Coastal acidification impacts on shell mineral structure of bivalve mollusks. *Ecol Evol* 8:8973–8984. <https://doi.org/10.1002/ece3.4416>
- Frid CLJ, Fordham E (1994) The morphology of the sub-littoral gastropod *Gibbula cineraria* (L.) along a gradient of wave action. *Ophelia* 40:135–146. <https://doi.org/10.1080/00785326.1994.10430580>
- Gartner A, Tuya F, Lavery PS, McMahon K (2013) Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *J Exp Mar Biol Ecol* 439:143–151. <https://doi.org/10.1016/j.jembe.2012.11.009>
- González-Murcia S, Erdmann S, Alvarado-Larios R (2020) Is this rock pool suitable habitat? Fish diversity in intertidal rock pools of El Zonte, El Salvador. *Rev Mex Biodivers*. <https://doi.org/10.22201/IB.20078706E.2020.91.3099>
- Hemraj DA, Posnett NC, Minuti JJ, Firth LB, Russell BD (2020) Survived but not safe: marine heatwave hinders metabolism in two gastropod survivors. *Mar Environ Res*. <https://doi.org/10.1016/j.marenvres.2020.105117>
- Hunt HL, Scheibling RE (1996) Physical and biological factors influencing mussel (*Mytilus trossulus*, *M. edulis*) settlement on a wave-exposed rocky shore. *Mar Ecol Prog Ser* 142:135–145. <https://doi.org/10.3354/meps142135>
- Johnson LE, Paine RT (2016) Consistency in a marine algal-grazer interaction over multiple scales. *J Phycol* 52:942–950. <https://doi.org/10.1111/jpy.12475>
- Kemppainen P, Van Nes S, Ceder C, Johannesson K (2005) Refuge function of marine algae complicates selection in an intertidal snail. *Oecologia* 143:402–411. <https://doi.org/10.1007/s00442-004-1819-5>
- Legrand E, Riera P, Pouliquen L, Bohner O, Cariou T, Martin S (2018) Ecological characterization of intertidal rockpools: Seasonal and diurnal monitoring of physico-chemical parameters. *Reg Stud Mar Sci* 17:1–10. <https://doi.org/10.1016/j.rsma.2017.11.003>
- Marsh B, Crowe TM, Siegfried WR (1978) Species richness and abundance of clinid fish (Teleostei; Clinidae) in intertidal rock pools. *Zool Afr* 13:283–291. <https://doi.org/10.1080/00445096.1978.11447629>
- Martins GM, Hawkins SJ, Thompson RC, Jenkins SR (2007) Community structure and functioning in intertidal rock pools: effects of pool size and shore height at different successional stages. *Mar Ecol Prog Ser* 329:43–55. <https://doi.org/10.3354/meps329043>
- Masterson P, Arenas FA, Thompson RC, Jenkins SR (2008) Interaction of top down and bottom up factors in intertidal rockpools: effects on early successional macroalgal community composition, abundance and productivity. *J Exp Mar Biol Ecol* 363:12–20. <https://doi.org/10.1016/j.jembe.2008.06.001>
- Mendonça V, Madeira C, Dias M, Vermande F, Archambault P, Disanayake A, Canning-Clode J, Flores AAV, Silva A, Vinagre C (2018) What's in a tide pool? Just as much food web network complexity as in large open ecosystems. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0200066>
- Metaxas A, Scheibling RE (1993) Community structure and organization of tidepools. *Mar Ecol Prog Ser* 98:187–198. <https://doi.org/10.3354/meps098187>
- Noël LMLJ, Hawkins SJ, Jenkins SR, Thompson RC (2009) Grazing dynamics in intertidal rockpools: connectivity of microhabitats. *J Exp Mar Biol Ecol* 370:9–17. <https://doi.org/10.1016/j.jembe.2008.11.005>
- Olabarria C, Underwood AJ, Chapman MG (2002) Appropriate experimental design to evaluate preferences for microhabitat: an example of preferences by species of microgastropods. *Oecologia* 132:159–166. <https://doi.org/10.1007/s00442-002-0940-6>

- Oliver JD, Rolán E, Templado J (2019) The littoral species of the genus *Crisilla* Monterosato, 1917 (Caenogastropoda, Rissoidae) in Azores, Madeira, Selvagens and Canary Islands with notes on West African taxa and the description of four new species. *Sociedad Española De Malacología* 37:23–80
- Rahman S, Barkati S (2012) Spatial and temporal variations in the species composition and abundance of benthic molluscs along 4 rocky shores of Karachi. *Turkish J Zool* 36:291–306. <https://doi.org/10.3906/zoo-1004-26>
- Silva ACF, Brazão S, Hawkins SJ, Thompson RC, Boaventura DM (2009) Abundance, population structure and claw morphology of the semi-terrestrial crab *Pachygrapsus marmoratus* (Fabricius, 1787) on shores of differing wave exposure. *Mar Biol* 156:2591–2599. <https://doi.org/10.1007/s00227-009-1283-1>
- Silva ACF, Hawkins SJ, Boaventura DM, Brewster E, Thompson RC (2010) Use of the intertidal zone by mobile predators: influence of wave exposure, tidal phase and elevation on abundance and diet. *Mar Ecol Prog Ser* 406:197–210. <https://doi.org/10.3354/meps08543>
- Souza SMAR, Matthews-Cascon H (2019) Molluscan assemblages in rock pools on sandstone reefs: local and between pools variability. *J Shellfish Res* 38:201–208. <https://doi.org/10.2983/035.038.0119>
- Spotorno-Oliveira P, Figueiredo MAO, Tâmega FTS (2015) Coralline algae enhance the settlement of the vermetid gastropod *Dendropoma irregulare* (d'Orbigny, 1842) in the southwestern Atlantic. *J Exp Mar Biol Ecol* 471:137–145. <https://doi.org/10.1016/j.jembe.2015.05.021>
- Tuya F, Wernberg T, Thomsen MS (2008) The spatial arrangement of reefs alters the ecological patterns of fauna between interspersed algal habitats. *Estuar Coast Shelf Sci* 78:774–782. <https://doi.org/10.1016/j.ecss.2008.02.017>
- Underwood AJ (1976) Analysis of patterns of dispersion of intertidal prosobranch gastropods in relation to macroalgae and rock-pools. *Oecologia* 25:145–154. <https://doi.org/10.1007/bf00368850>
- Underwood AJ, Jernakoff P (1984) The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in new south wales. *J Exp Mar Biol Ecol* 15:71–96. [https://doi.org/10.1016/0022-0981\(84\)90024-8](https://doi.org/10.1016/0022-0981(84)90024-8)
- Underwood AJ, Skilleter GA (1996) Effects of patch-size on the structure of assemblages in rock pools. *J Exp Mar Biol Ecol* 197:63–90. [https://doi.org/10.1016/0022-0981\(95\)00145-X](https://doi.org/10.1016/0022-0981(95)00145-X)
- van Tamelen PG (1996) Algal zonation in tidepools: experimental evaluation of the roles of physical disturbance, herbivory and competition. *J Exp Mar Biol Ecol* 201:197–231. [https://doi.org/10.1016/0022-0981\(95\)00182-4](https://doi.org/10.1016/0022-0981(95)00182-4)
- Veras DRA, Martins IX, Matthews-Cascon H, Monte H (2013) Mollusks: how are they arranged in the rocky intertidal zone? *Iheringia Ser Zool* 103:97–103. <https://doi.org/10.1590/s0073-47212013000200003>
- Vieira EA, Bueno M (2019) Small spatial scale effects of wave action exposure on morphological traits of the limpet *Lottia subrugosa*. *J Mar Biol Assoc UK* 99:1309–1315. <https://doi.org/10.1017/S0025315419000195>
- Vinagre C, Mendonça V, Narciso L, Madeira C (2015) Food web of the intertidal rocky shore of the west Portuguese coast—Determined by stable isotope analysis. *Mar Environ Res* 110:53–60. <https://doi.org/10.1016/j.marenvres.2015.07.016>
- Vinagre C, Dias M, Cereja R, Abreu-Afonso F, Flores AAV, Mendonça V (2019) Upper thermal limits and warming safety margins of coastal marine species—Indicator baseline for future reference. *Ecol Indic* 102:644–649. <https://doi.org/10.1016/j.ecolind.2019.03.030>
- Wai T-C, Williams GA (2006) Monitoring spatio-temporal variation in molluscan grazing pressure in seasonal, tropical rock pools. *Mar Biol* 149:1139–1147. <https://doi.org/10.1007/s00227-006-0291-7>
- Wakefield RL, Murray SN (1998) Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). *Mar Biol* 130:631–642. <https://doi.org/10.1007/s002270050285>
- Westerbom M, Kraufvelin P, Erlandsson J, Korpinen S, Mustonen O, Díaz E (2019) Wave stress and biotic facilitation drive community composition in a marginal hard-bottom ecosystem. *Ecosphere*. <https://doi.org/10.1002/ecs2.2883>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.