Rev. Mus. Argentino Cienc. Nat., n.s.
26(2): 185-193, 2024
ISSN 1514-5158 (impresa)
ISSN 1853-0400 (en línea)

Use of microhabitat features for egg capsule deposition by a marine limpet

Andres AVERBUJ[1] & Juan P. LIVORE[2*]

[1]Laboratorio de Reproducción y Biología Integrativa de Invertebrados Marinos (LARBIM), Instituto de Biología de Organismos Marinos (IBIOMAR), Centro Científico Tecnológico (CCT CONICET-CENPAT). Bvd. Brown 2915, U9120ACV Puerto Madryn. Chubut, Argentina. [2]Grupo de Ecología Bentónica (GEBen), Instituto de Biología de Organismos Marinos (IBIOMAR), Centro Científico Tecnológico (CCT CONICET-CENPAT). Bvd. Brown 2915, U9120ACV Puerto Madryn. Chubut, Argentina.

Abstract. Patagonian intertidal habitats are one of the world's most extreme environments for marine organisms. These have different life-history strategies to reduce the stress that they are exposed to and survive within these habitats. In this study, we search for the presence of a common grazer along the different intertidal levels, then, identify areas used for egg capsule deposition, and investigate the microhabitat features associated with them. To achieve these goals, we described biotic and abiotic microhabitat characteristics, as well as their relationship with egg capsules. We found that individuals were present from the high intertidal level to the fringe area between the mid and low levels, but not beyond this point. Egg masses were only observed within this fringe level and were closely associated with sessile organisms present in that area, such as sponges, algae, and barnacles. We propose that limpet reproductive output may be enhanced by favourable microhabitats that are related to biotic features that would protect egg masses from desiccation and potential predation.

Keywords. Pulmonate limpet, marine gastropod, desiccation stress, spawning site, Patagonia

Resumen. **Uso de las características del microhabitat para la oviposición por parte de una lapa marina.** Los ambientes intermareales patagónicos están entre los más extremos del mundo para organismos marinos. Estos tienen diferentes estrategias asociadas a sus historias de vida para reducir el estrés al que están expuestos y sobrevivir en esos hábitats. En este estudio investigamos la presencia de un ramoneador común en los distintos niveles del intermareal, luego identificamos áreas usadas para la oviposición de masas ovígeras, e investigamos los microhabitats asociados a ellas. Para ello, describimos las características bióticas y abióticas de los microhábitats y sus relaciones con las ovicápsulas. Los individuos se encontraron desde el intermareal alto hasta la transición entre el nivel medio y bajo, pero no más allá de ese punto. Las masas ovígeras sólo se encontraron en esa zona de transición y siempre fuertemente asociadas a organismos sésiles, como esponjas, algas y cirripedios. Proponemos que el desempeño reproductivo de esta especie de lapa marina puede ser favorecido a través de microhábitats favorables relacionados a factores bióticos que protegería a las masas ovígeras de la desecación y potenciales depredadores.

Palabras clave. Lapa pulmonada, gasterópodo marino, stress por desecación, sitio de oviposición, Patagonia

INTRODUCTION

Living in intertidal habitats is challenging for invertebrate species that have to deal with desiccation, UV-radiation, extreme temperatures, predation, and competition for food or space (Rawlings, 1994, 1999; Moran, 1999; Przeslawski, 2004; Przeslawski & Davis, 2007; Cubillos *et al.*, 2022). Within these habitats, resources can be limited, thus, leading to different life-history strategies among species and ontogenetically within a species (Werner & Gilliam, 1984; Marshall & Keough, 1994). Lower intertidal levels usually present more humidity and food availability. Yet, competition for resources (*e.g.*, food and space) due to higher individual densities is greater in such habitats, and exposure to predators may be more intense compared to higher levels of the intertidal (Vermeij, 1972; Gosselin & Chia, 1995). The capability to move and selectively use microhabitats to avoid stress differs throughout life history and is particularly low or null during intracapsular developmental stages (Gosselin, 1997; Moran, 1999; Przeslawski & Davis, 2007; Chaparro *et al.*, 2018).

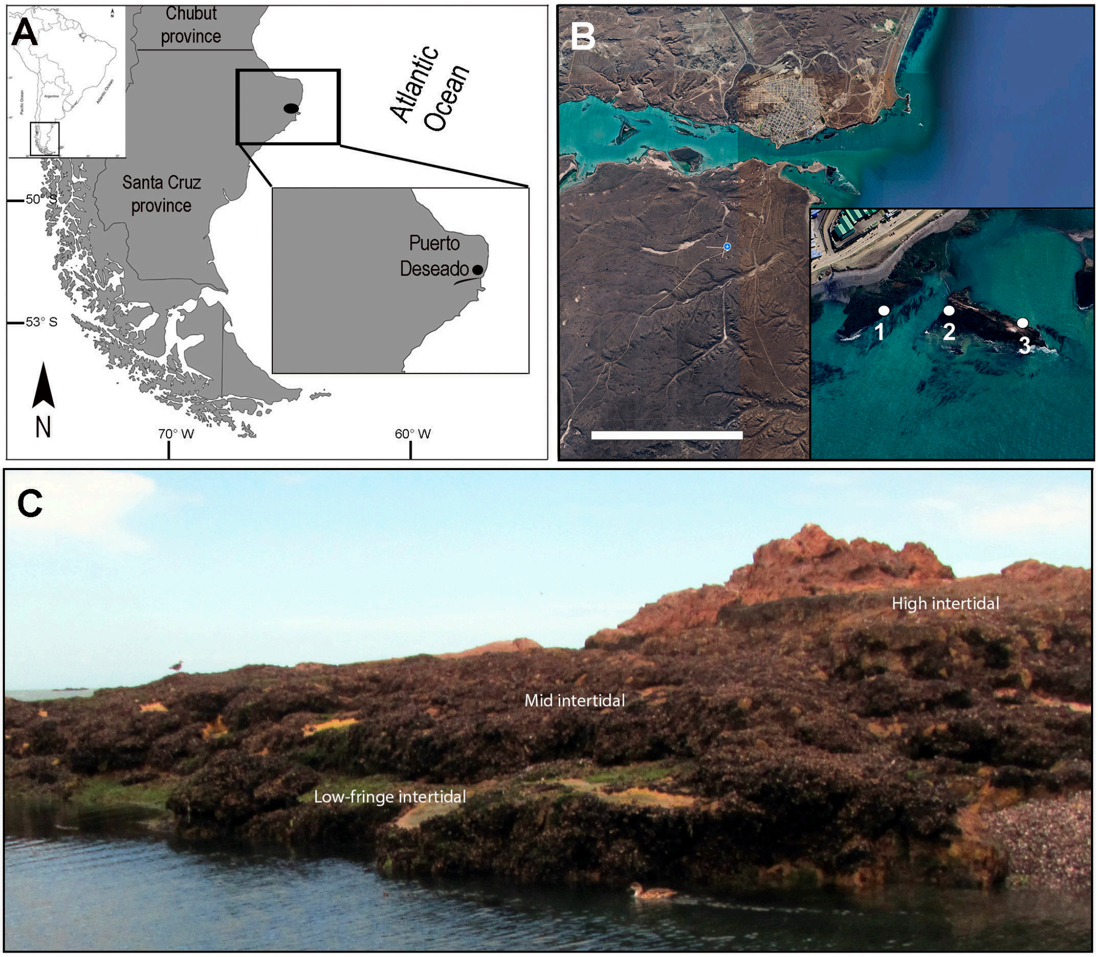

Fig. 1. Graphical description of the studied area showing: (A) map of the study area showing the location of Puerto Deseado; (B) the detailed location of the sites; (C) the vertical biological zonation highlighting the high intertidal (HI) dominated by bare rock and barnacles, the mid intertidal (MI) dominated by the mussels *Perumytilus purpuratus* (Lamarck, 1819), and the low-fringe intertidal (LFI) dominated by algae. Scale bar= 5 km (B).

An important aspect of successful life histories is their reproductive strategy. *Siphonaria lateralis* Gould, 1846 is a siphonariid limpet that is hermaphrodite with internal fertilization and is distributed from Puerto Deseado, in Santa Cruz province, Argentina, to the Beagle Channel and South Georgia Island (Creese, 1980; Hodgson, 1999). Eggs are laid in egg capsules, embedded in a gelatinous matrix that is generally attached to hard substratum. Their egg masses include extraembryonic nutrients to achieve direct development, with offspring hatching as crawling juveniles (Zabala *et al.*, 2020). Many gastropod species attach their egg capsules to substrates using different strategies that would increase the survival rates of offspring (Pastorino & Penchaszadeh, 2002; Averbuj & Penchaszadeh, 2016; Zabala *et al.*, 2018, 2024). These strategies that reduce environmental or biological stress, such as desiccation, UV-radiation, and predation, include the selection of favourable microhabitats for egg capsule deposition (Rawlings, 1996; 1999; Przeslawski, 2004; Przeslawski & Davis, 2007). Other gastropod species deposit their egg capsules influenced by certain physical environmental features such as crevices or rough floor depressions which may confer them advantages against desiccation and predation pressure (Gosselin & Chia, 1995; Kano & Fukumori, 2010).

Patagonian rocky intertidal shores are considered to be among the harshest environments for intertidal organisms to survive in (Bertness *et al.*, 2006). Strong dry winds, low rainfall, extremely low air humidity, and large tidal ampli-

Fig. 2. Egg masses (EM) on the rocky floor associated with barnacles and macroalgae. Scale bar= 1 cm.

tudes determine a strong and consistent biological zonation along Atlantic Patagonian rocky shores. The high intertidal is dominated by bare rock and the presence of an invasive barnacle (*Balanus glandula,* Darwin, 1854), the mid intertidal is almost entirely covered by dense mats of scorched mussels, *Perumytilus purpuratus* (Lamarck, 1819), and the low intertidal is predominantly covered by macroalgae with an important presence of *Corallina officinalis* Linnaeus, 1758 (Bertness *et al.*, 2006; Livore *et al.*, 2021). Desiccation is the main environmental stressor on these coasts and the increase in extreme weather events, such as heat waves that are predicted due to the changing climate conditions only exacerbates this scenario (Mendez *et al.*, 2020). In this context, species that are behaviourally or physiologically resilient may have an advantage over others. Intraspecific resource partitioning, such as vertical size segregation on rocky intertidal habitats, has been described for pulmonate limpets in Patagonia (Livore *et al.*, 2018) and may be a beneficial strategy for certain species.

In this study, we aimed to identify and characterize areas used by *S. lateralis* for reproduction and investigate, within these areas, the microhabitats used for egg capsule deposition and their relationship with biotic and abiotic features.

MATERIAL AND METHODS

We sampled three sites separated by > 200 m on the rocky intertidal of Puerto Deseado (Santa Cruz Province), in southern Patagonia (47°45′05″ S, 65°54′04″ W; Fig. 1A–B) in mid-November 2017. A typical Atlantic Patagonian vertical biological zonation pattern was observed at all sites. A visual inspection of all levels revealed that *Siphonaria lateralis* was absent from the low intertidal, hence, effort was focused on the fringe area between the low and mid intertidal (LFI), where they were first observed, as well as in the mid and high intertidal (MI and HI, respectively) (Fig. 1C).

Random 25 x 25 cm quadrats (n = 10 level^{-1} site^{-1}, N = 90) were inspected in the field to quantify *S. lateralis* capsules and individuals at all levels upwards the LFI. Within each quadrat, the total number of *S. lateralis* egg capsules and

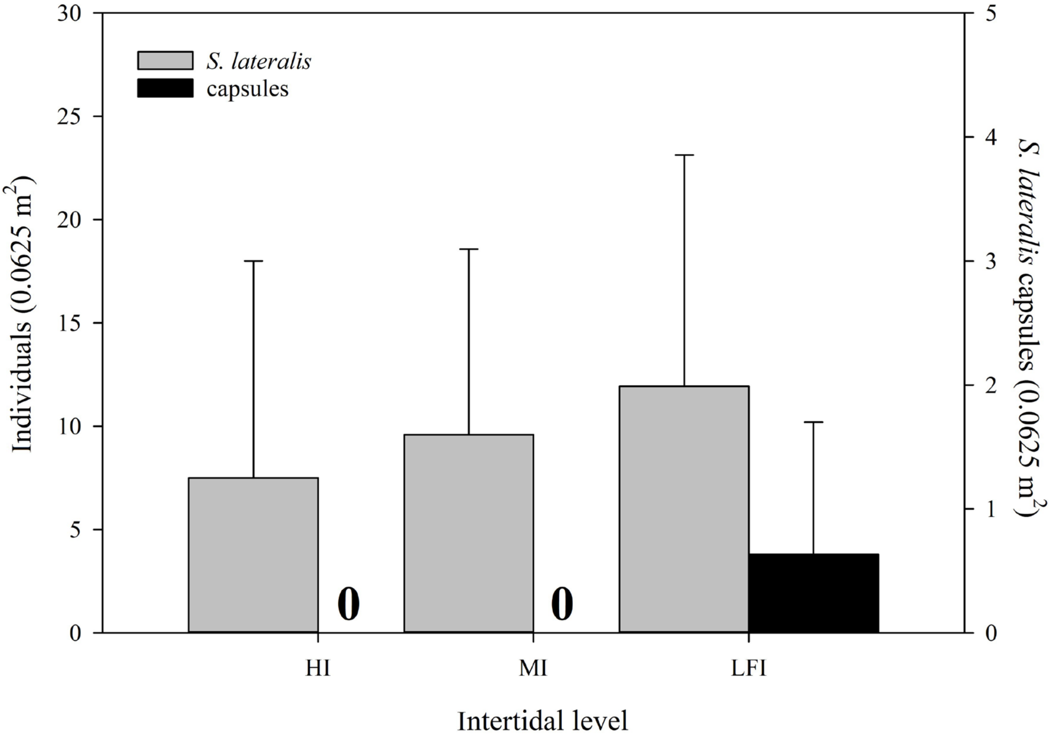

Fig. 3. Mean (± SD) *Siphonaria lateralis* individuals and egg capsules per quadrat (0.0625 m2) on three levels of the rocky intertidal shores (HI: high, MI: middle, and LFI: low fringe) at Puerto Deseado, Patagonia, Argentina"

individuals were counted. Capsules were only observed in the LFI. Thus, a targeted search for capsules was performed to describe biotic and abiotic features associated with them. The substrate type on which capsules were observed was recorded individually within five categories, namely, floor (a flat horizontal surface), crevice (cracks < 2 cm wide and < 3 cm deep), plinth (the meeting of a horizontal and vertical surface not taller than a few cm), cave (semi-spherical intrusions in the rock with a horizontal floor, between 2–5 cm from the opening) and *S. lateralis* shell (live individual). When capsules were in contact with biotic elements, this was also recorded into the following categories: algae, sponges, barnacles, and mytilids. This procedure was repeated until 100 capsules were found and each capsule's substrate and biotic elements had been recorded (N = 100).

Similarity matrices based on the Bray-Curtis measure were generated for the analyses, which used 999 permutations of residuals under a reduced model (Anderson & Gorley, 2015). SIMPER analysis was used to determine which biotic association contributed more to differences among substrates. DistlM analyses were performed on pooled data to identify and visualize which biotic associations to capsules (variables: algae, sponges, *Balanus*, mytilids, and *S. lateralis*) contributed most to the observed differences among substrate types (factors: floor, plinth, and cave).

RESULTS

Capsules were more frequently found on the horizontal floor (56), followed by plinths (25), caves (16), crevices (2), and the shell of other *S. lateralis* individuals (1) (Fig. 2; Table 1a). A single capsule was also observed on the shell of a live *S. lateralis* individual. *Siphonaria lateralis* individuals were continuously present from the HI level to the fringe area between the mid and low-intertidal (LFI); however, capsules were only present in the LFI (Fig. 3). Individual presence (% quadrats with *S. lateralis)* at all sites within each level ranged: HI = 30–70%; MI = 70–100%, and LFI = 80–100% of quadrats. There was no relationship between the abundance of *S. lateralis* individuals and the number of capsules within

Table 1. (a) Percentage of capsules with simultaneous associations (0–4) per substrate type; b) number of capsules associated with biotic features in each type of substrate.

a)		**Biotic associations**					**capsules**
		0	**1**	**2**	**3**	**4**	**Total**
Substrate	**Floor**	1	18	25	8	4	56
	Plynth	3	11	8	3	0	25
	Crevice	0	1	1	0	0	2
	Cave	6	5	4	1	0	16
	S. lateralis	0	1	0	0	0	1

b)		**Biotic associations**					
		Algae	***Balanus***	**Mytilidae**	**Sponge**	***S. lateralis***	**Free**
Substrate	**Floor**	40	43	4	13	7	1
	Plynth	5	5	4	18	1	3
	Crevice	0	1	0	2	0	0
	Cave	2	3	3	3	2	6
	S. lateralis	0	0	0	0	1	0

each plot ($R^2 = 0.078$). Most capsules were associated (in contact) with at least one biotic element. Only 10 of the observed capsules were free (not in contact with biotic features), most of which were found within caves (Table 1a). Of the sampled capsules, 42 were associated with only one biotic factor, whilst 48 were associated with at least 2 biotic factors (46 involved algae and *Balanus* sp.) (Table 1b). The SIMPER results show that the biotic associations that explain similarity among capsules were different for each substrate type (Table 2). Capsules with the floor as substrate were associated with algae and barnacles, whilst those laid on plynths were associated with sponges and algae, and, finally, capsules in caves were mainly explained by no associations (*i.e.*, free) followed by mytilids, sponges, and barnacles (Table 2). DistlM analysis confirmed these results and visualized these patterns of association (Fig. 4).

DISCUSSION

This study describes the relationship between *Siphonaria lateralis* egg capsule deployment and some ecological features on the environmentally stressful Atlantic Patagonian rocky shores. Although *S. lateralis* individuals were observed on all levels above the low intertidal, it was only in the fringe area between the low and mid intertidal levels, dominated by algae, that egg capsules were observed. Furthermore, detailed insights into the microhabitat where egg capsules were found showed a direct relationship between them and some biotic features that were described and analysed, to our knowledge, for the first time for siphonarid species.

The differential use of intertidal levels by two ecomorphs of the pulmonate limpet *Siphonaria lessonii* on Patagonian coasts has previously been described. The different shell shapes from the high and middle intertidal were related to variations in water loss and recovery rates from heat stress, which contrast between these intertidal levels (Livore *et al.*, 2018). Here, we show how *S. lateralis* also differentially uses intertidal levels by occupying the high, middle, and low fringe intertidal, but specifically only uses the low fringe for egg capsule deposition. This behaviour likely confers ecological advantages to the species by allowing it to utilize several habitats and their resources, which would reduce competition (Branch, 1984).

Microhabitat selection for egg mass deposition by gastropod species can be variable within and among species. Species of varied and unrelated taxa with different capsule types (structure, composition, and morphology), including Anaspidea, Basommatophora, Neogastropoda, Neritopsidea, Notaspide, and Nudibranchia, share the behavioural adaptation of depositing egg masses in protected microhabitats, such as

Table 2. Results of SIMPER analysis for each substrate type showing which biotic association to egg capsule contributed more to similarity among samples. Abbreviations: Av. Abund, average abundance; Av. Sim, average similarity; Contrib%, percentage contribution; Cum %, cumulative percentage contribution.

Substrate	Biotic associaton	Av. Abund	Av. Sim	Contrib%	Cum %
Floor					Average similarity: 49.46
	Algae	0.71	25.92	52.40	52.40
	Balanus	0.71	19.57	39.57	91.96
Plynth					Average similarity: 39.89
	Sponges	0.72	35.47	88.91	88.91
	Algae	0.20	2.01	39.57	93.95
Cave					Average similarity: 19.03
	Free	0.38	12.50	65.69	65.69
	Mytilids	0.19	1.94	10.22	75.91
	Sponges	0.19	1.94	10.22	86.13
	Balanus	0.19	1.53	8.03	94.16

beneath boulders (Przeslawski & Davis, 2007). In a study from Australian rocky shores, Benkendorff & Davis (2004) showed that most gastropod species exhibited this behaviour where encapsulated embryos are sheltered from extreme environmental conditions, even in summer months. On Atlantic Patagonian rocky shores, other gastropod species spawn their capsules on rocks, sometimes within tidal pools, mussel beds, crevices, or under boulders or kelps (Pastorino & Penchaszadeh, 2002; Cumplido *et al.*, 2010). However, studies on microhabitat selection for these species are not available. *Siphonaria lateralis* egg masses were found to have specific relationships between substrate morphology and biotic features. Flat floor, inherently the most exposed substrate, was the most commonly used followed by plinths and caves. Concurrently, egg masses laid on flat floors had the most simultaneous biotic associations, reducing exposure and potentially providing more favourable conditions, such as humidity. Egg mass deposition was strongly related to sponges, algae, and barnacles, which are known to mitigate desiccation stress (Buschmann, 1990; Kemppainen *et al.*, 2005). On the contrary, isolated egg masses (with no biotic associations) were rare although free substrate was available. These masses were predominantly, but not exclusively, laid within caves which imply some level of intrinsic protection.

Egg masses need the low desiccation stress conditions found in low intertidal levels to obtain higher embryonic survival rates (Przeslawski, 2005). These low intertidal levels usually represent higher predatory risk environments for encapsulated _non-mobile_ embryos, yet there is no information for predation on *S. lateralis* capsules. Thus, some species have evolved spawning behaviours that minimize those risks by selectively using particular microhabitats for egg masses deposition, such as living individuals of the same or other species that offer hard substrates to attach the capsules, depressions in the rock, crevices, or areas beneath boulders in shallow tidal pools (Przeslawski & Davis, 2007; Kano & Fukumori, 2010). However, once juveniles hatch, exposure to predation by crabs, snails, sea stars, and polychaetes, among others, is likely much higher in the lower intertidal levels, where these predators are abundant (Yamada & Boulding, 1996, and citations therein). On the HI for example, the risk of predation by invertebrates such as sea stars is low as these predators are extremely vulnerable to desiccation and thus physiologically limited to the lower intertidal levels (Arribas *et al.*, 2017). As *S. lateralis* has a direct embryonic development within the egg capsule and emerges as a crawling hatchling, a vertical migration towards the higher intertidal levels where predation risks are lower, would be beneficial. An avoidance strategy by migrating towards habitats with high desiccation pressure may be an ecological refuge from predation that would increase survival and is a possible expla-

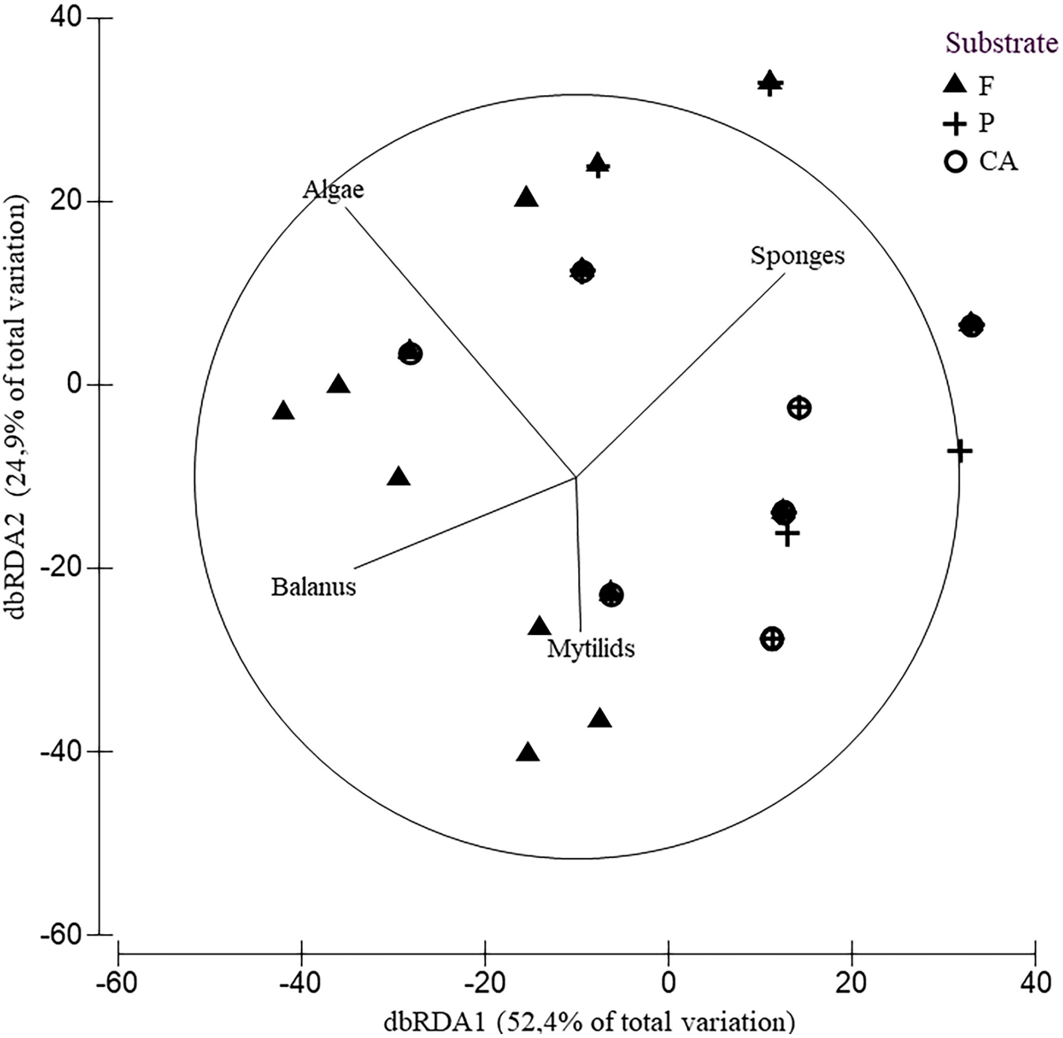

Fig. 4. DistlM analysis of *S. lateralis* capsules laid on the open floor (F), plynths (P), and caves (CA). Vectors represent biotic features that were correlated with plot axes.

nation for the presence of *S. lateralis* individuals within the higher intertidal levels, although this is yet to be tested.

CONCLUSIONS

We have shown the differential use of the intertidal rocky shore by a marine herbivore. We also describe the positive interspecific interaction limpets (deposition of egg masses) and sessile organisms that would ameliorate conditions against desiccation and potential predation. This appears particularly relevant in a species with an extended intracapsular developmental period of approximately four spring-summer months (Zabala *et al.*, 2020). These findings open the way for future experiments on the potential ecological refuge from predation through occupying different levels of the intertidal shore, desiccation tolerance, and effects of environmental stressors on embryonic development, among many other topics. The ontogenetic differences in resource use may be a process through which this marine herbivore survives the extreme conditions of Atlantic Patagonian intertidal shores.

ACKNOWLEDGEMENTS

Our sincere gratitude goes to Pablo Penchaszadeh, who motivated this study and, most importantly, inspired our careers in marine research. Thanks to Soledad Zabala for helping with the map preparation and to Marcelo Santo (Histological service from CCT CENPAT) for histological assistance. We are grateful to Centro de Investigaciones de Puerto Deseado of the Universidad Nacional de la Patagonia Austral for kindly offering their facilities. The authors are members of CONICET. This work was partially funded by “Fondo para la Investigación Científica y Tecnológica” (PICTs Nº 2023-540 (AA), 2018-04386 (AA) and PIP 1966. We would like to thank two anonymous reviewers who improved the MS through insightful suggestions.

REFERENCES

Anderson, M.J. & R.N. Gorley. 2015. Getting started with PRIMER v7. *PRIMER-e: plymouth, plymouth marine laboratory* 20(1).

Arribas, L.P., C. Bagur, M.G. Palomo & G Bigatti. 2017. Population biology of the sea star *Anasterias minuta* (Forcipulatida: Asteriidae) threatened by anthropogenic activities in rocky intertidal shores of San Matías Gulf, Patagonia, Argentina. *Revista de Biología Tropical* 65(S1): 73–84.

Averbuj, A. & P.E. Penchaszadeh, 2016. Reproductive biology in the South Western Atlantic genus *Buccinanops* (Nassariidae): the case of *Buccinanops paytensis Molluscan Research* 35(2): 75–83.

Benkendorff, K. & A.R. Davis. 2004. Gastropod egg mass deposition on a temperate, wave-exposed coastline in New South Wales, Australia: implications for intertidal conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14(3): 263–280.

Bertness, M.D., C.M. Crain, B.R. Silliman., M.C. Bazterrica, M.V. Reyna, F. Hildago & J.K. Farina. 2006. The community structure of Western Atlantic Patagonian rocky shores. *Ecological Monographs* 76(3): 439−460.

Branch, G.M. 1984. Competition between marine organisms: ecological and evolutionary implications. *Oceanography and Marine Biology Annual Review* 22: 429−593.

Buschmann, A.H. 1990. Intertidal macroalgae as refuge and food for Amphipoda in central Chile. *Aquatic Botany* 36(3): 237−245.

Chaparro, O., L.P. Salas-Yanquin, A. Matos, J.A. Bűchner-Miranda, M. Gray, V. Cubillos & J. Pechenik. 2018. Pre-hatching development in the intertidal zone negatively affects juvenile survival and physiology in the muricid gastropod *Acanthina monodon*. *Marine Biology* 165: 1−8.

Creese, R. 1980. Reproductive cycles and fecundities of two species of *Siphonaria* (mollusca: Pulmonata) in south-eastern Australia. *Marine and Freshwater Research* 31(1): 37–47.

Cubillos, V.M., L.P Salas-Yanquin, J.A. Büchner-Miranda, F. Ramírez, M.S. Zabala, A. Averbuj, F. Márquez, H.N. Jaramillo & O. Chaparro. 2022. Uv-r mitigation strategies in encapsulated embryos of the intertidal gastropod *Acanthina monodon*: A way to compensate for lack of parental care. *Marine Environmental Research* 180: 105711.

Cumplido, M., A. Averbuj & G. Bigatti. 2010. Reproductive seasonality and oviposition induction in *Trophon geversianus* (Gastropoda: Muricidae) from Golfo Nuevo, Argentina. *Journal of Shellfish Research* 29(2): 1–6.

Darwin, C. 1854. *A monograph on the subclass Cirripedia: with figures of all species*. Vol. 2. Ray Society, London.

Gosselin, L.A. 1997. An ecological transition during juvenile life in a marine snail. *Marine Ecology Progress Series* 157:185–194. Gould, A.A. 1846. Descriptions of new shells, collected by the United States Exploring Expedition. *Proceedings of the Boston Society of Natural History* 2: 141–145.

Gosselin, L.A. & F.S. Chia. 1995. Distribution and dispersal of early juvenile snails: Effectiveness of intertidal microhabitats as refuges and food sources. *Marine Ecology Progress Series* 128: 213–223.

Gould, A.A. 1846. Descriptions of new shells, collected by the United States Exploring Expedition. Proceedings of the Boston Society of Natural History 2: 141–145.

Hodgson, A.N. 2002. The biology of siphonariid limpets (gastropoda: Pulmonata). In: A. Hodgson (ed.), *Oceanography and Marine Biology, An Annual Review,* pp. 253–322, CRC Press, South Africa.

Kano, Y. & H. Fukumori. 2010. Predation on hardest molluscan eggs by confamilial snails (Neritidae) and its potential significance in egg-laying site selection. *Journal of Molluscan Studies* 76(4): 360–366.

Kemppainen, P., S.V. Nes, C. Ceder & K. Johannesson. 2005. Refuge function of marine algae complicates selection in an intertidal snail. *Oecologia* 143: 402–411.

Lamarck, J.B.P. 1819. *Histoire naturelle des animaux sans vértebrés*, Tome 6, Pt 1. Verdieve, Paris, 343 pp.

Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata [10th revised edition], 824 pp.

Livore, J.P., M.M. Mendez, G. Bigatti & F. Marquez. 2018. Habitat-modulated shell shape and spatial segregation in a Patagonian false limpet (*Siphonaria lessonii*). *Marine Ecology Progress Series* 606: 55–63.

Livore, J.P., M.M. Mendez, P. Miloslavich, G. Rilov & G. Bigatti. 2021. Biodiversity monitoring in rocky shores: Challenges of devising a globally applicable and cost-effective protocol. *Ocean & Coastal Management* 205: 105548.

Marshall, P.A. & M.J. Keough. 1994. Asymmetry in intraspecific competition in the limpet *Cellana tramoserica* (Sowerby). *Journal of Experimental Marine Biology and Ecology* 177(1): 121–138.

Mendez, M.M., J.P. Livore, G. Bigatti & E. Montes. 2020. Integrating in situ and satellite-based observations to unravel a mass mortality event of mussel beds in Patagonia, Argentina. AGU Fall Meeting 2020: B060–0011.

Moran, A.L. 1999. Size and performance of juvenile marine invertebrates potential contrasts between intertidal and subtidal benthic habitats. *American Zoologist* 39(2): 304–312.

Pastorino, G. & P.E. Penchaszadeh. 2002. Spawn of the Patagonian gastropod *Pareuthria plumbea* (Philippi, 1844) (Buccinidae). *The Nautilus* 116(3): 105-108.

Przeslawski, R. 2004. A review of the effects of environmental stress on embryonic development within intertidal gastropod egg masses. *Molluscan Research* 24(1): 43–63.

Przeslawski, R. 2005. Combined effects of solar radiation and desiccation on the mortality and development of encapsulated embryos of rocky shore gastropods. *Marine Ecology Progress Series* 298: 169–177.

Przeslawski, R. & A.R. Davis. 2007. Does spawning behavior minimize exposure to environmental stressors for encapsulated gastropod embryos on rocky shores? *Marine Biology* 152: 991–1002.

Rawlings, T.A. 1994. Effect of elevated predation risk on the metabolic rate and spawning intensity of a rocky shore marine gastropod. *Journal of Experimental Marine Biology and Ecology* 181(1): 67–79.

Rawlings, T.A. 1996. Shields against ultraviolet radiation: an additional protective role for the egg capsules of benthic marine gastropods. *Marine Ecology Progress Series* 136: 81-95.

Rawlings, T.A. 1999. Adaptations to physical stresses in the intertidal zone: The egg capsules of neogastropod molluscs. *American Zoologist* 39(2): 230–243.

Vermeij, G.J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology* 53(4): 693–700.

Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15: 393–425.

Yamada, S.B. & E.G. Boulding. 1996. The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *Journal of Experimental Marine Biology and Ecology* 204(1): 59–83.

Zabala, S., A. Averbuj, P.E. Penchaszadeh & G. Bigatti. 2018. Early development of the limpet Siphonaria lessonii Blainville, 1827 in populations affected by different physical stressors. *Marine Biology Research* 14(2): 148–157.

Zabala, M.S., A. Averbuj, G. Bigatti & P.E. Penchaszadeh. 2020. Embryonic development of the false limpet *Siphonaria lateralis* from Atlantic Patagonia. *Invertebrate Biology* 139(1): e12276.

Zabala, S., V. Teso, P.E. Penchaszadeh & A. Averbuj. 2024. Spawn and development of the olivid gastropod *Olivancillaria carcellesi* from north Patagonia, Argentina. *Invertebrate Biology* 143(1): e12420.

Doi: 10.22179/REVMACN.26.880

Recibido: 5-08-2024
Aceptado: 30-09-2024