Contents lists available at ScienceDirect

Regional Studies in Marine Science

Faunal turnover between meso- and infralittoral algal turf assemblages: A case study in a highly biodiverse Marine Protected Area of the northern Alboran Sea (W Mediterranean)

Ernesto Ruiz Villaespesa [a,b,*], Javier Urra [c], Carmen Salas [b], Serge Gofas [b]

[a] *Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avenida Fuente Nueva, s/n, 18071 Granada, Spain*
[b] *Departamento de Biología Animal, Facultad de Ciencias, Universidad de Málaga, 29071 Málaga, Spain*
[c] *Centro Oceanográfico de Málaga, Instituto Español de Oceanografía, Puerto pesquero s/n, 29640 Fuengirola, Málaga, Spain*

ARTICLE INFO

ABSTRACT

The molluscan fauna inhabiting the algal turfs of mesolittoral rocky outcrops, dominated by the coralline alga *Ellisolandia elongata*, has been quantitatively analysed in a Marine Protected Area of Málaga, southern Spain (W Mediterranean). A total of 2520 mollusc specimens belonging to 46 species were identified. This taxocenosis was compared to that previously studied from the infralittoral level, where the alga *Halopteris scoparia* was prevailing and 4084 specimens belonging to 66 species of Mollusca were found. The species *Pisinna glabrata, Skeneopsis planorbis, Nodulus spiralis* and *Tricolia miniata* dominated the mesolittoral stage. The occurrence of congeneric species pairs (*Tricolia miniata/Tricolia pullus, Nodulus spiralis/Nodulus contortus*) which achieve high abundance in one of the levels and are scarce or absent in the other was striking. Therefore, the coralline algal turf in the lower part of the intertidal zone is not just an extension of the "Photophilous Algae" community but a benthic community of its own.

© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

The intertidal zone is a harsh environment which undergoes seasonal and daily extreme variations in environmental factors (Raffaelli and Hawkins, 1996). At low tide, long periods of exposure to air may trigger high temperatures and rapid evaporation in summer, whereas in other seasons rain may induce drastic variations in salinity. With the high tide, exposure to wave action is a challenge for mobile animals, benefiting sessile organisms. Most of the intertidal zone corresponds to the mesolittoral level, comprised between the prevalent levels of high and low tide (Pérès and Picard, 1964; Pérès, 1982), an area constantly swept by the swaying of the waves that represents the most temporally and spatially variable of all marine habitats.

The infralittoral zone is comprised between the normal low-water level and the depth at which the incident light does not allow the survival of the photophilic algae and seagrasses (Pérès and Picard, 1964). On rocky shores, it is the zone of greater algal growth, sometimes presented as analogues of terrestrial forests.

Permanent immersion makes the environment more stable and this will be reflected in its fauna composition, with a high degree of spatial structuring and high specific diversity (Ros et al., 1989).

In the Mediterranean, the tides are generally small and the mesolittoral level is narrow (Ros et al., 1989). The mesolittoral algal belt are mainly constituted by small red algae, with a changing species composition along the year in relation to environmental variables (Templado et al., 2012). In areas where the mesolittoral rocks form an extensive platform, pools with infralittoral conditions may be found as enclaves (Pérès, 1982).

Many of the organisms in the mesolittoral and infralittoral fringes live associated with algae, which provide their food source as well as a fundamental protection for their development, both against biotic factors (possible predators) and abiotic factors (environmental stress) (Ros et al., 1989). Furthermore, the retention of sediment by algae allows the development of a more complex habitat (Urra et al., 2013) in which three subsystems can be defined: (1) the algal community itself, which functions as engineering species of the ecosystem; (2) the species associated with the algal fronds; and (3) the species associated with the underlying substrate (Fernández et al., 1988; Urra et al., 2013). The underlying substrate, where a quantity of sediment is usually retained, appears to be a more stable microhabitat since it does not usually present large seasonal or annual changes (Urra et al., 2013). In addition, the fauna associated with the

---

* Corresponding author at: Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avenida Fuente Nueva, s/n, 18071 Granada, Spain.
E-mail addresses: rvillaespesa@ugr.es (E. Ruiz Villaespesa), javier.urra@ieo.csic.es (J. Urra), casanova@uma.es (C. Salas), sgofas@uma.es (S. Gofas).

Fig. 1. The rocky shore at Calahonda photographed in February 2017 at low hater of spring tide. The algal turf on the emerged part was sampled in this study. The submerged part is infralittoral characterized by the presence of the brown algae *Halopteris scoparia* (dark tufts).

algal fronds could vary depending on the structural differences between algae, mainly morphology (Chemello and Milazzo, 2002; Urra et al., 2013), but also composition (e.g., calcium carbonate in coralline algae) or metabolites (e.g., caulerpine in algae of the genus *Caulerpa*) (Waters et al., 1996; Catra et al., 2019). In the mesolittoral, exposed at low tide, the refuge from desiccation constituted by algae becomes even more important than in the infralittoral (Brown and Taylor, 1999).

Molluscan communities are important in these habitats where they find refuge and food. They are valuable indicators of biodiversity due to their abundance (representing approximately a quarter of total marine species), diversification and widespread distribution, along with the abundant existing information regarding their biology, ecology and taxonomy (Gladstone, 2002; Smith, 2005).

This study is part of a comprehensive assessment of the biota in the Special Area of Conservation of Calahonda, on the littoral of Málaga (NW Alboran Sea). We focus on the composition of the molluscan taxocenosis associated with algae in the mesolittoral and we compare it to that previously found at the algal cover from the infralittoral level by Urra et al. (2013) to know vertical zonation in this area.

2. Material and methods

2.1. Study area

The study was carried out at the Special Area of Conservation (SAC) of Calahonda, between Calahonda (36°28′N, 04°44′W) and Punta de Calaburras (36°30′N, 04°38′W), in the western part of the province of Málaga. This area comprises extensive metamorphic rocky outcrops, whereas elsewhere in the littoral of Málaga over 90% of the shores are beaches of coarse sand or gravel, or artificial substrates. In the SAC of Calahonda, during the low tide, there are many pools between the rocks (Fig. 1) and an algal mat is visible below the fringe of *Chthamalus*.

2.2. Sampling procedures

To recovery the maximum number of specimens in each area, two methodologies were applied in order to optimize collection, taking into account the characteristics of each area: scraping completely a quadrat in the intertidal zone, and the airlift pump in permanently submerged bottoms.

The mesolittoral samples were collected at 36°29.225′N, 04°42.705′W on February 28, 2017, coincident with a near-100 tide coefficient, at low tide, where a continuous algal turf was present. Four 25 × 25 cm square frames were randomly distributed on the bedrock surfaces, discarding loose boulders, because the formers are stable and reflect more accurately the characteristic diversity at these levels (Hawkins and Jones, 1992); these areas also feature a more or less flat surface to facilitate a thorough scraping. The algae and the retained sediment were collected by entirely scraping the square delimited by the grid (Bellan-Santini, 1965). The algae were kept in a freezer at −20 °C for later identification and the remaining fraction was sieved on 3, 2, 1 and 0.5 mm meshes and preserved in 70% ethanol (Urra et al., 2013).

In order to compare the taxocenosis of molluscs associated with the mesolittoral algal turf collected in the present study with that present in infralittoral algae, we used the data obtained in the same area by Urra et al. (2013), at 36°29.316′N, 04°42.066′W. Samples of the infralittoral algal turf were collected on replicated 50 × 50 cm quadrats, first collecting the algal fronds and then sampling the underlying surface with an airlift pump (Urra et al., 2013). Four seasonal sets of samples at two sites were considered by Urra et al. (2013) of which we used here the set collected in winter (January 2008). The sieving (down to 0.5 mm) was the same as in the present study.

The samples were collected in different years but, albeit there can be some interannual variation, this has been reported elsewhere as not affecting markedly the species richness and composition (Augustin et al., 1997; Nicolaidou et al., 2006; Ciércoles et al., 2016).

For both sets of samples, molluscs were sorted and identified at the species level following Gofas et al. (2011) and counted. The

scientific names of each species were checked against the nomenclature of the "World Register of Marine Species (WoRMS)" (WoRMS, 2022).

2.3. Data analysis

After the identification of the species obtained in each sample, an area-species curve was performed in order to determine if the minimum sampling area was reached according to Cain and Castro (1959), assuming that the minimum area has been reached when an increase of 10% of the area corresponds less than 10% increase in the number of species.

The characterization of each species takes into account: (1) the abundance (N); (2) the frequency index (%F: percentage of samples in which the species is present); and (3) the dominance index (%D: percentage of individuals of one particular species with respect to the total). The characterization of the taxocenosis was obtained according to: (1) the species richness (S); (2) diversity as indicated by the Shannon–Wiener index (H′ log 2), which incorporates both the species richness and the relative abundance of each species, thereby accounting for the composition and structure of the communities in a quantitative mode (Krebs, 1989); and (3) evenness index (J) that determines the degree of distribution of individuals among the identified taxa, where values close to 1 show a most equitable distribution (Pielou, 1969). These ecological indices were calculated using the software PRIMER (v.6) from the Plymouth Marine Laboratory, UK.

A data matrix was created in a spreadsheet for all species found in this study (mesolittoral samples), and in the Calahonda winter samples of Urra et al. (2013) (infralittoral samples). All abundance values were converted to density values (individuals/m^2) in order to standardize the data from both studies. We applied PRIMER (v.6) software (Clarke and Warwick, 1994) for the analysis of affinity between samples. The data were transformed by applying the fourth root (executed by default in PRIMER v.6), which reduces the effect of the most abundant species on the similarity of two samples, allowing the least abundant to contribute to a greater extent to the estimate of the similarity. This previous step is important, since we use the Bray and Curtis Dissimilarity Index (Bray and Curtis, 1957), which is very sensitive to extreme abundance values when there is a high dominance of a species. From the transformed data, the Bray and Curtis index was calculated and a semi-matrix was obtained with the resulting values.

A dendrogram and MDS (Non-Metric Multidimensional Scaling) were also applied to the semi-matrix based on the similarity obtained with the Bray and Curtis index. Dendrogram nodes are distributed according to an axis indicating percentage of similarity between samples. In MDS, the distance between the points (samples) that are represented graphically would be proportional to the similarity between the samples. In addition to the graphic representation, a stress coefficient was shown (Kruskal and Wish, 1978) that measures the discrepancies between the resulting distances. A value of 0.1 would correspond to a very reliable interpretation of the graphical representation, while values above 0.3 suggest an almost arbitrary arrangement (Clarke and Warwick, 1994).

A SIMPER (SIMilarity PERcentage) analysis was done in order to know the contribution of the species in the similarity/dissimilarity within and between the groups of samples (meso- and infralittoral, defined a-priori). The ANOSIM test, through a R$_{ANOSIM}$ value which varies between 1 and −1, was applied to check if the differences between groups were significant (R$_{ANOSIM}$ value approaching 1 or −1) or not (R$_{ANOSIM}$ value near 0).

3. Results

3.1. Habitat characterization

The most representative alga in all mesolittoral samples was *Ellisolandia elongata* (J. Ellis & Solander) K.R. Hind & G.W. Saunders, 2013 (formerly known as *Corallina elongata*). This coralline alga covers the mesolittoral rocks creating a few centimetres thick layer where sediment is retained producing a compact mat, which provides a humid environment for the fauna. Other algae that were found in a much lower percentage are *Chondracanthus acicularis* (Roth) Fredericq in Hommersand, Guiry, Fredericq & Leister 1993 and *Jania rubens* (Linnaeus) J.V. Lamouroux 1812.

The photophilous algal assemblage in the infralittoral was dominated by the brown alga *Halopteris scoparia* (Linnaeus) Sauvageau, 1904, which is one of the most abundant and common algae species in southern Spain, but the calcareous red algae *Jania rubens* (Linnaeus) J.V. Lamouroux, 1816 and *Ellisolandia elongata* were also present.

3.2. Characterization of the taxocenosis of molluscs

A total of 2520 individuals belonging to 46 species of the phylum Mollusca were collected in the mesolittoral samples. Of these, 34 species (2260 individuals) were Gastropoda, 11 species (258 individuals) were Bivalvia class and 1 species (2 individuals) was Polyplacophora. The winter samples of Urra et al. (2013) used for comparison to the infralittoral contained 4084 specimens belonging to 66 species of Mollusca of which 44 (3524 individuals) were Gastropoda, 20 species (456 individuals) were Bivalvia and 2 species (8 individuals) were Polyplacophora (see Table 1).

The most dominant species in the mesolittoral algal turf were: *Pisinna glabrata* (27.02%), *Skeneopsis planorbis* (17.08%), *Nodulus spiralis* (15.89%), *Tricolia miniata* (14.22%), *Rissoa similis* (5.55%), *Cardita calyculata* (4.99%) and *Bittium reticulatum* (2.02%) (Fig. 2). On the other hand, the species with 100% frequency were *Bittium reticulatum*, *Gibberula miliaria*, *Haminoea* sp., *Musculus costulatus*, *Mytilaster minimus*, *Nodulus contortus*, *Nodulus spiralis*, *Pisinna glabrata*, *Rissoa similis*, *Skeneopsis planorbis* and *Tricolia miniata*.

The values of Shannon-Wiener diversity index (H′) in mesolittoral samples ranged between 2.5 and 3.5 among the replicates and the pooled samples. The evenness index (J) values ranged between 0.54 and 0.72 among replicates and the pooled samples (Table 2).

In the winter samples of Urra et al. (2013), the dominant species were: *Rissoa guerinii* (27.51%), *Bittium reticulatum* (14.14%), *Rissoa similis* (12.47%), *Musculus costulatus* (8.91%), *Nodulus contortus* (5.01%) and *Tricolia pullus* (3.90%) (Fig. 2). The most frequent species (% F = 100) were: *Rissoa guerinii*, *Bittium reticulatum*, *Musculus costulatus*, *Tricolia pullus*, *Pusillina philippi*, *Gibberula philippii*, *Gibberula miliaria*, *Tritia incrassata* and *Chauvetia mamillata*.

The species richness (Table 2) in the infralittoral was higher than in the mesolittoral level. However, the diversity and evenness indices are rather similar in both zones, with slightly higher values in the infralittoral taxocenosis.

3.3. Differences between the mesolittoral and infralittoral molluscan taxocenosis

The analysis of affinity shows that mesolittoral samples (IM) form a group completely separated from the aggregation of infralittoral samples (IF) (Fig. 3) with a similarity of only 27% between the two clusters. The ANOSIM test yields the maximum possible value: R$_{ANOSIM}$ = 1; $p < 0.05$, indicating a highly significant grouping.
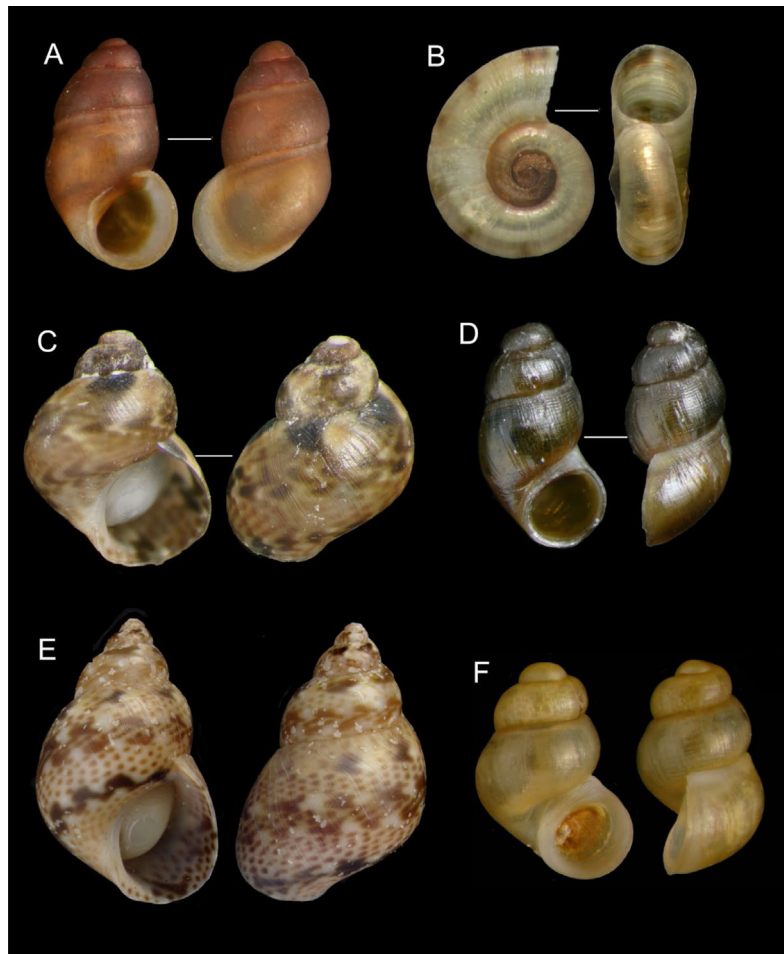
Fig. 2. Dominant species of molluscs in the mesolittoral algal turf of SAC Calahonda (A-D), and vicariant species in the infralittoral level (E-F). A: *Pisinna glabrata* (1.2 mm); B: *Skeneopsis planorbis* (1.2 mm); C: *Tricolia miniata* (3.2 mm); D: *Nodulus spiralis* (1.25 mm); E: *Tricolia pullus* (5.9 mm); F: *Nodulus contortus* (1.2 mm).

The SIMPER analysis recognized the above mentioned dominant and constant species as mostly responsible for the within-group similarity and indicated as most contributing to dissimilarity the following: *Tricolia miniata* (5.21%), *Skeneopsis planorbis* (4.80%), *Pisinna glabrata* (4.42%), *Nodulus spiralis* (4.39%), occurring only in the mesolittoral; and *Rissoa guerinii* (4.72%) and *Tricolia pullus* (2.84%), both restricted to the infralittoral.

4. Discussion

Ellisolandia elongata (known until 2013 as *Corallina elongata*) is a calcareous alga that is usually found in areas of strong wave action, forming a turf on rocky substrata of the mesolittoral and shallow infralittoral (Ballesteros, 1982). The first studies on the fauna associated with the algal turf in which *Corallina* spp. dominated were carried out in the Azores by Chapman (1955), where a great abundance of small molluscs was recorded. These were followed by others such as those by Azevedo and Manuel (1992) and Ávila et al. (2005), in which this algal turf is presented as a place where small animals find excellent protection against wave action, high temperatures and desiccation. This is why we found the greatest abundance and the greatest number of species in the smallest fractions (0.5–1 mm).

In the study carried out by Urra et al. (2013) in the infralittoral level of Calahonda, *E. elongata* was described as abundant, but well behind *Halopteris scoparia* (Linnaeus) Sauvageau. In the mesolittoral, *E. elongata* occupies the main role as habitat-structuring species in the absence of the latter. The dominance

of this alga in the most exposed areas is even more because it is able to resist the waves thanks to its calcareous nature (Sierra and Fernández, 1984).

The gastropod *Pisinna glabrata* has been the most dominant species in our study. This species was also the most abundant in a study on the fauna associated with *E. elongata* that was carried out in the mesolittoral of the Azores islands (Ávila et al., 2005), where together with *Skeneopsis planorbis* (the second dominant species in our sampling) and *Lasaea adansoni*, characterized the malacological associations of algae. However, in that study, only 19 species of molluscs were found, far fewer than those found here. This could be due, apart from differences in sampling techniques, to the geographical location of our sampling area at a point of confluence of Mediterranean and Atlantic fauna (Gofas et al., 2011) where the oceanographic characteristics (Sarhan et al., 2000; García-Raso et al., 2010) could favour the development of an outstanding biodiversity (Urra et al., 2013).

Juveniles of *Cardita calyculata*, a bivalve that lives in the fissures of the rocks of this same level, were abundant in the mesolittoral. The juveniles of this brooding species could take advantage of the protection of this microhabitat that is used by this species as a "nursery". These phenomena have already been described for other species such as, for example, the mussel *Mytilus galloprovincialis*, which establishes its recruiting place in infralittoral algae, being the intertidal rocks its final place of residence (Urra et al., 2013).

Comparing the species richness of the Calahonda mesolittoral (45 species) with that obtained for the infralittoral (66 species),

Table 1
List of the molluscan species found in both mesolittoral and infralittoral samples at the SAC Calahonda. IF1 to IF5, number of specimens in each of the winter replicas of infralittoral samples from Urra et al. (2013); IM1 to IM4, number of specimens in each replica of mesolittoral samples from this study. Dominance (% D) and Frequency (% F) were calculated from these numbers. Species present across the two levels are highlighted in grey.

SPECIES	IF1	IF2	IF3	IF4	IF5	IM1	IM2	IM3	IM4
Class Polyplacophora									
Acanthochitona crinita (Pennant, 1777)							1	1	
Acanthochitona fascicularis (Linnaeus, 1767)		4							
Lepidochitona cinerea (Linnaeus, 1767)		4							
Class Gastropoda, subclass Vetigastropoda									
Gibbula racketti (Payraudeau, 1826)	4								
Calliostoma laugieri Payraudeau, 1826				20	4				
Tricolia miniata (Monterosato, 1884)						51	161	60	87
Tricolia pullus (Linnaeus, 1758)	52	56	16	16	36				
Class Gastropoda, subclass Caenogastropoda									
Alvania montagui (Payraudeau, 1826)	36	56	8	28					
Alvania rudis (Philippi, 1844)	8	4				1			
Alvania scabra (Philippi, 1844)						2		2	
Alvania sculptilis (Monterosato, 1877)						1			
Bittium reticulatum (da Costa, 1778)	156	172	156	24	40	14	11	20	6
Caecum auriculatum de Folin, 1868	4								
Cerithiopsis jeffreysi Watson, 1885				4					
Cerithiopsis minima (Brusina, 1865)	4		16						
Cerithiopsis nana Cecalupo & Robba, 2010	12								
Cerithiopsis tubercularis (Montagu, 1803)	12		12	4	4			1	
Chauvetia mamillata (Risso, 1826)	16	12	4	8	20		4		
Columbella rustica (Linnaeus, 1758)	8	4					1	3	1
Conus mediterraneus Hwass in Bruguière, 1792	4						3	3	3
Crisilla semistriata (Montagu, 1808)				4	4				
Crisilla tenera (Philippi, 1844)		4							
Eatonina fulgida (Adams J., 1797)			4		8				
Gibberula miliaria (Linnaeus, 1758)	16	16	12	16	4	1	6	5	5
Gibberula philippii (Monterosato, 1878)	40	40	12	4	4				
Manzonia crassa (Kanmacher, 1798)		4							
Melanella polita (Linnaeus, 1758)	4								
Metaxia metaxae (delle Chiaje, 1828)		4							
Mitrella bruggeni van Aartsen, Menkhorst & Gittenberger, 1984				4					
Nodulus contortus (Jeffreys, 1856)	84	56	40			1	10	12	2
Nodulus spiralis (van der Linden, 1986)						322	40	34	5
Ocinebra edwardsi (Payraudeau, 1826)				8	8			3	
Opalia crenata (Linnaeus, 1758)							1		
Pisania striata (Gmelin, 1791)						1		15	1
Pisinna glabrata (von Mühlfeldt, 1824)	8		4			424	43	207	8
Plagyostila asturiana Fischer, 1872			4						
Pusillina philippi (Aradas & Maggiore, 1844)	20	28	16	48	20				
Rissoa guerinii Récluz, 1843	360	300	160	168	240				
Rissoa lia (Monterosato, 1884)					4				
Rissoa similis Scacchi, 1836	332	100	8	8		36	48	42	14
Setia amabilis (Locard, 1886)	36	4						1	
Setia lacourti (Verduin, 1984)						1		4	
Setia turriculata (Monterosato, 1884)						10		2	

(*continued on next page*)

the latter is higher. This could be due to the mesolittoral stress it-self, whereas the infralittoral provides a more stable environment and the algal fronds are more developed. Conversely, the density of molluscs in the mesolittoral (2520 individuals in 0.25 m² = 10 080 ind./m²) triplicates that of the infralittoral (4048 individuals in 1.25 m² = 3267 ind./m²). This may be explained because the species which most contribute to the abundance numbers in the mesolittoral (*Pisinna glabrata, Nodulus spiralis, Skeneopsis planorbis)* are microgastropods which can fit into the densely packed algal turf, whereas in the infralittoral the most dominant species (*Rissoa guerinii, Bittium reticulatum, Musculus costulatus*) are larger.

Some of the species are exclusively found in the mesolittoral level and others in the infralittoral, therefore they define a verti-cal zonation. In the first place, the species *Pisinna glabrata* and *Skeneopsis planorbis* are the dominant ones in the mesolittoral and, nevertheless, they did not appear at all in the infralittoral or did so with very reduced numbers. Similarly, *Rissoa guerinii*,

which is a highly dominant species in the infralittoral, has not been collected in the mesolittoral whereas another species of the same genus, *Rissoa similis*, does have a good representation at both levels. Second, there is a striking pattern of mutual re-placement among species of the genera *Tricolia* and *Nodulus*. In the mesolittoral we find *Tricolia miniata* and *Nodulus spiralis*, while in the infralittoral they are replaced by *Tricolia pullus* and *Nodulus contortus* (Fig. 2), all of them dominant in their respective levels. Most of these species have a broad Atlanto-Mediterranean distribution.

Even if the two sampling events took place at different times, we did not notice any major perturbation in the study area and, as noted above, interannual variations are not likely to change drastically species composition and richness.

The replacement of invertebrate species along a shore zona-tion has been observed repeatedly in molluscs (e.g. Della Santina et al., 1993; Stenseng et al., 2005) and other groups (e.g. Jansen, 1971; Grosberg, 1982; Jensen and Armstrong, 1991). Competition

Table 1 (continued).

SPECIES	IF1	IF2	IF3	IF4	IF5	IM1	IM2	IM3	IM4
Similiphora similior (Bouchet & Guillemot, 1978)		4	8						
Skeneopsis planorbis (Fabricius, 1780)						285	93	43	10
Tritia cuvierii (Payraudeau, 1826)			4						1
Tritia incrassata (Ström, 1768)	12	20	8	16	4				
Tritia reticulata (Linnaeus, 1758)	4								
Vermetus rugulosus Bivona, 1832						1			1
Vitreolina incurva (Buquoy, Dautzenberg & Dollfus, 1883)			12						
Vitreolina philippi (de Rayneval & Ponzi, 1854)	8								
Class Gastropoda, subclass Heterobranchia									
Ammonicera fischeriana (Monterosato, 1869)						1			
Aplysia sp.	16	40	20				4	2	
Haminoea sp.						1	13	3	10
Odostomella doliolum (Philippi, 1844)						2		2	
Odostomia turrita Hanley, 1844					4	2		3	
Parthenina emaciata (Brusina, 1866)			4						
Parthenina monozona (Brusina, 1866)								4	
Rissoella diaphana (Alder, 1848)						5	13	7	
Runcina sp.			4						
Philine iris Tringali, 2001	4	8					1	4	1
Retusa truncatula (Bruguière, 1792)	4	4	4	4			6		1
Williamia gussonii (Costa O.G., 1829)							2		
Class Bivalvia									
Anomia ephippium Linnaeus, 1758		4							
Arca noae Linnaeus, 1758		4			4				
Cardita calyculata (Linnaeus, 1758)		4				39	28	59	
Crenella prideauxi (Leach, 1815)	8	8			8				
Flexopecten flexuosus (Poli, 1795)					4				
Gregariella semigranata (Reeve, 1858)			8			1		6	
Hiatella arctica (Linnaeus, 1767)	4		8		4	3		2	
Irus irus (Linnaeus, 1758)						15		9	
Kellia suborbicularis (Montagu, 1803)			4						
Lasaea adansoni (Gmelin, 1791)						18		3	1
Limaria tuberculata (Olivi, 1792)		4							
Lyonsia norwegica (Gmelin, 1791)			4						
Modiolus barbatus (Linnaeus, 1758)						1		1	
Modiolus lulat (Dautzenberg, 1891)		4	4		4			1	
Musculus costulatus (Risso, 1826)	84	64	100	72	72	6	8	10	1
Musculus subpictus (Cantraine, 1835)	12				4				
Mytilaster minimus (Poli, 1795)		4		4		11	2	6	2
Mytilus galloprovincialis Lamarck, 1819		4				10		1	3
Parvicardium scabrum (Philippi, 1844)	4								
Parvicardium scriptum (Bucquoy, Dautzenberg & Dollfus, 1892)		4	8	8		5	6		
Striarca lactea (Linnaeus, 1758)		4							
Tapes rhomboides (Pennant, 1777)	4								
Venerupis geographica (Gmelin, 1791)					8				

Table 2

Ecological indices and total abundance for molluscs in winter mesolittoral samples (IM1 to IM4) and winter infralittoral samples (IF1 to IF5; data from Urra et al. (2013)) from the SAC Calahonda.

| Index	IM1	IM2	IM3	IM4	Pooled	IF1	IF2	IF3	IF4	IF5	Pooled
Species richness (S)	30	23	35	20	45	33	35	29	20	23	66
Abundance (N)	1271	505	581	163	2520	1380	1056	668	468	512	4084
Shannon-Wiener index (H′ log 2)	2.66	3.24	3.54	2.71	3.33	3.48	3.67	3.57	3.25	2.92	3.38
Evenness (J)	0.54	0.72	0.68	0.63	0.60	0.69	0.72	0.73	0.75	0.65	0.70

for space and resources or different cues for larval settlement are generally invoked as possible causes for non-overlapping vertical distributions. Different physiological capabilities have also been reported among mutually exclusive species (Jansen, 1971; Jensen and Armstrong, 1991; Stenseng et al., 2005) but it is not always clear if those are adaptations which were selected after the stratification became established, or if they are the original cause for the non-overlapping ranges. Escape from selective predators (e.g. crabs) could make sense for *Tricolia miniata* which has a small and relatively fragile shell, whereas *T. pullus* is larger and more sturdy, but not in the case of *Nodulus* spp. which have an essentially similar build of their shell. In any case, this occurrence at non-overlapping levels can be seen as a case of character

displacement triggered by the sympatric occurrence of species with similar ecological function and trophic requirements.

Regarding the other fauna associate to the algal turf of the mesolittoral, it is interesting to point out the high number of cumaceans present in the samples (more than 1500 ind./m²). Other studies of peracarids associated with *E. elongata* were carried out in the Strait of Gibraltar, where no cumaceans were recorded (Guerra-García et al., 2009), and along the entire Iberian Peninsula, where only 1 species with very low abundance (<10 ind.) was obtained (Izquierdo and Guerra-García, 2011).

From a conservation and management point of view, our study demonstrates the existence of small-scale spatial heterogeneity and the need for a detailed assessment of different microhabitats
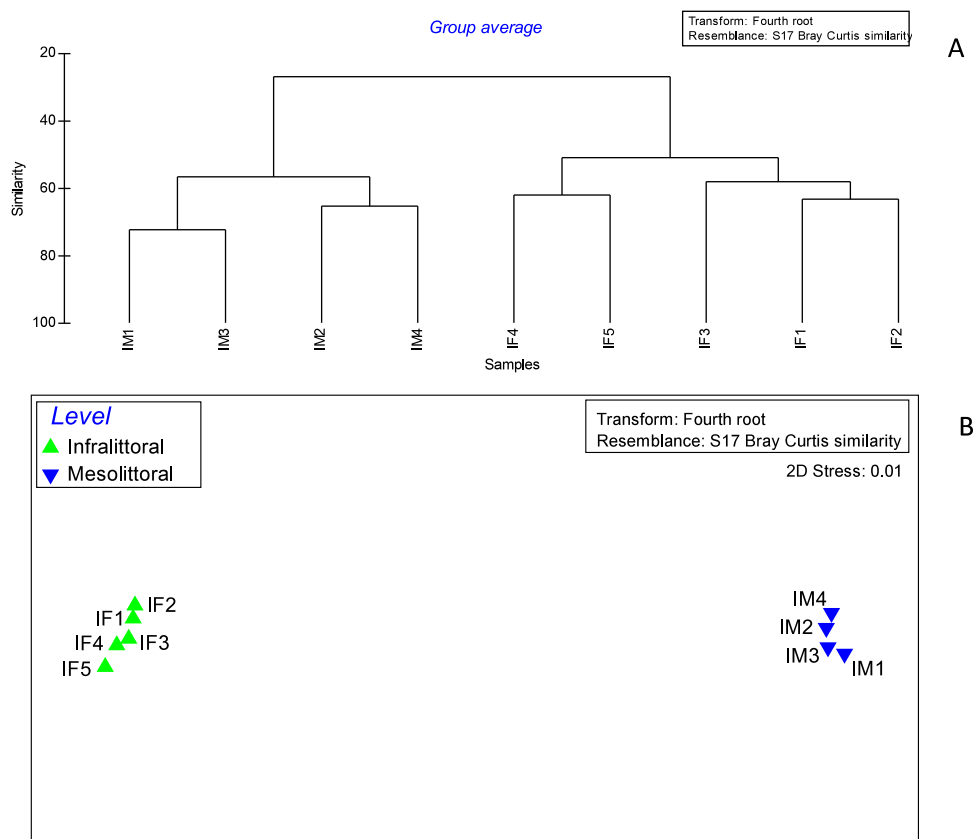
Fig. 3. Dendrogram (or Cluster) (A) and MDS ordering (B) showing the affinity degree between the samples of the mesolittoral (blue triangles) and the infralittoral (green triangles). The stress index of 0.01 represented on the MDS graph indicates a high level of significance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in order to assess properly the biodiversity of a marine (protected or not) area. Recent studies also pose the question of how climate change could affect the habitat-forming coralline algae and their associated fauna (Marchini et al., 2019; Rindi et al., 2019; Ragazzola et al., 2021; Peña et al., 2021; Kelaher et al., 2022). Marchini et al. (2019) conclude that "species-rich Mediterranean assemblages associated to *Ellisolandia elongata* should be considered at risk" due to acidification of the oceans and high-temperatures, which would reduce coralline algal growth and, therefore, complexity and diversity of faunal assemblages. In the case of molluscs, they would be double affected, directly in shell formation and by loss of their habitat (Kelaher et al., 2022).

In the western Mediterranean there is a further risk where a rapid invasion of the asiatic alga *Rugulopteryx okamurae* is taking place, colonizing a huge variety of marine habitats (García-Gómez et al., 2020; Estévez et al., 2022) but apparently failing to invade the mesolittoral zone. Therefore, such readily accessible communities are also highly recommendable as sentinel habitats for the monitoring of forthcoming changes.

5. Conclusion

Our study demonstrates a sharp faunal turnover between the apparently similar algal turfs of the meso- and infralittoral levels, and the uniqueness of the mesolittoral algal turf among the many habitats present in Calahonda, which have already promoted their protection and recognition as Special Area of Conservation.

In the context of climate change and *R. okamurae* invasion, an accurate knowledge of pristine molluscan communities could provide valuable information in futures impacts evaluations.

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.

Data availability

Data will be made available on request.

References

Augustin, D., Galzin, R., Legendre, P., Salvat, B., 1997. Interannual variability of the Tiahura barrier reef communities (Moorea Island, French Polynesia). Oceanol. Acta 20, 745–758.

Ávila, S.P., Santos, A.C., Penteado, A.M., Rodrigues, A.M., Quintino, I., Machado, M.I., 2005. The molluscs of the intertidal algal turf in the Azores. Iberus 23, 67–76. http://dx.doi.org/10.5281/zenodo.4521428.

Azevedo, J., Manuel, N., 1992. Algae-associated marine molluscs in the Azores. Biol. J. Linn. Soc. 46, 177–187. http://dx.doi.org/10.1111/j.1095-8312.1992.tb00859.x.

Ballesteros, E., 1982. Primer intento de tipificación de la vegetación marina y litoral sobre sustrato rocoso de la Costa Brava. Oecol. Aquat. 6, 163–173.

Bellan-Santini, D., 1965. Méthode de récolte et d'étude quantitative des peuplements sur substrat dur dans la zone d'agitation hydrodynamique. In: Comité du Benthos (Ed.), Colloque Méthodes Quantitatives d'Études du Benthos et Échelle Dimensionnelle des Benthontes (Marseille novembre 1963). Commission Internationale pour l'exploration Scientifique de la Mer Méditerranée, Monaco, pp. 23–24.

Bray, R.J., Curtis, J.T., 1957. An ordination of the uplands forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–347.

Brown, P.J., Taylor, R.B., 1999. Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal. J. Exp. Mar. Biol. Ecol. 235, 45–53. http://dx.doi.org/10.1016/S0022-0981(98)00186-5.

Cain, S.A., Castro, G.D., 1959. Manual of Vegetation Analysis. Harper, New York, p. 325.

Catra, M., Alongi, G., Leonardi, R., Negri, M.P., Sanfilippo, R., Sciuto, F., Serio, D., Viola, A., Rosso, A., 2019. Degradation of a photophilic algal community and its associated fauna from eastern Sicily (Mediterranean Sea). Med. Mar. Sci. 20, 74–89. http://dx.doi.org/10.12681/mms.17765.

Chapman, G., 1955. Aspects of the fauna and flora of the Azores. VI. The density of animal life in the coralline alga zone. Ann. Mag. Nat. Hist. 12, 801–805. http://dx.doi.org/10.1080/00222935508655700.

Chemello, R., Milazzo, M., 2002. Effect of algal architecture on associated fauna: some evidence from phytal molluscs. Mar. Biol. 140, 981–990. http://dx.doi.org/10.1007/s00227-002-0777-x.

Ciércoles, C., García-Ruiz, C., González, M., López-González, N., Tuite, P., Ortiz De Urbina, J., Rueda, J., 2016. Spatial distribution, inter-annual variability and influence of abiotic factors on molluscan assemblages collected with otter trawl in the northen Alborán Sea. In: Front. Mar. Sci. Conference Abstract: XIX Iberian Symposium on Marine Biology Studies. http://dx.doi.org/10.3389/conf.FMARS.2016.05.00016.

Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach To Statistical Analysis and Interpretation. Plymouth Marine Laboratory. Bourne Press Ltd., Bournemouth, p. 144.

Della Santina, P., Sonni, C., Sartoni, G., Chelazzi, G., 1993. Food availability and diet composition of three coexisting Mediterranean limpets (*Patella* spp.). Mar. Biol. 116, 87–95. http://dx.doi.org/10.1007/BF00350735.

Estévez, R.M., Palacios, M., Cervera, J.L., González-Duarte, M.M., 2022. Expansion of the invasive alga *Rugulopteryx okamurae* (Dictyotaceae, Ochrophyta) in the Mediterranean Sea: first evidence as epiphyte of the cold-water coral *Dendrophyllia ramea* (Cnidaria: Scleractinia). BioInvasions Rec. 11, 925–936. http://dx.doi.org/10.3391/bir.2022.11.4.11.

Fernández, E., Anadón, R., Fernández, C., 1988. Life histories and growth of the gastropods *Bittium reticulatum* and *Barleeia unifasciata* inhabiting the seaweed *Gelidium latifolium*. J. Moll. Stud. 54, 119–129. http://dx.doi.org/10.1093/mollus/54.1.119.

García-Gómez, J.C., Sempere-Valverde, J., González, A.R., Martínez-Chacón, M., Olaya-Ponzone, L., Sánchez-Moyano, E., Ostalé-Valriberas, E., Megina, C., 2020. From exotic to invasive in record time: The extreme impact of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in the strait of Gibraltar. Sci. Total Environ. 704, 135408. http://dx.doi.org/10.1016/j.scitotenv.2019.135408.

García-Raso, J.E., Gofas, S., Salas Casanova, C., Manjón-Cabeza, M.E., Urra, J., García Muñoz, J.E., 2010. El mar más rico de Europa: Biodiversidad del litoral occidental de Málaga entre Calaburras y Calahonda. In: Junta de Andalucía, Consejería de Medio Ambiente. Sevilla, p. 138.

Gladstone, W., 2002. The potential value of indicator groups in the selection of marine reserves. Biol. Cons. 104, 211–220. http://dx.doi.org/10.1016/S0006-3207(01)00167-7.

Gofas, S., Moreno, D., Salas, C., 2011. Moluscos Marinos de Andalucía. Servicio de Publicaciones e Intercambio Científico, Universidad de Málaga, Málaga, p. 798.

Grosberg, R.K., 1982. Intertidal zonation of barnacles: The influence of planktonic zonation of larvae on vertical distribution of adults. Ecology 63, 894–899. http://dx.doi.org/10.2307/1937228.

Guerra-García, J.M., Cabezas, M.P., Baeza-Rojano, E., Espinosa, F., García-Gómez, J.C., 2009. Is the north side of the Strait of Gibraltar more diverse than the south side? A case study using the intertidal peracarids (Crustacea: Malacostraca) associated to the seaweed *Corallina elongata*. J. Mar. Biol. Assess. U.K. 89, 387–397. http://dx.doi.org/10.1017/S0025315409002938.

Hawkins, S.J., Jones, H.D., 1992. Marine Field Course Guide. 1. Rocky Shores. Marine Conservation Society. Immel Publishers, London, p. 144.

Izquierdo, D., Guerra-García, J.M., 2011. Distribution patterns of the peracarid crustaceans associated with the alga *Corallina elongata* along the intertidal rocky shores of the Iberian Peninsula. Helgol. Mar. Res. 65, 233–243. http://dx.doi.org/10.1007/s10152-010-0219-y.

Jansen, K.P., 1971. Ecological studies on intertidal New Zealand Sphaeromatidae (Isopoda: Flabellifera). Mar. Biol. 11, 262–285. http://dx.doi.org/10.1007/BF00401274.

Jensen, G.C., Armstrong, D.A., 1991. Intertidal zonation among congeners: factors regulating distribution of porcelain crabs *Petrolisthes* spp.(Anomura: Porcellanidae). Mar. Ecol. Prog. Ser. 73, 47–60.

Kelaher, B.P., Mamo, L.T., Provost, E., Litchfield, S.G., Giles, A., Butcherine, P., 2022. Influence of ocean warming and acidification on habitat-forming coralline algae and their associated molluscan assemblages. Glob. Ecol. Conserv. 35, e02081. http://dx.doi.org/10.1016/j.gecco.2022.e02081.

Krebs, C.J., 1989. Ecological Methodology. Harper and Row, New York, p. 654.

Kruskal, J.B., Wish, M., 1978. Multidimensional Scaling. Sage Publications, Beverley Hills, California, p. 93.

Marchini, A., Ragazzola, F., Vasapollo, C., Castelli, A., Cerrati, G., Gazzola, F., Jiang, C., Langeneck, J., Manauzzi, M.C., Musco, L., Nannini, M., Zekonyte, J., Lombardi, C., 2019. Intertidal Mediterranean coralline algae habitat is expecting a shift toward a reduced growth and a simplified associated fauna under climate change. Front. Mar. Sci. 6 (106), http://dx.doi.org/10.3389/fmars.2019.00106.

Nicolaidou, A., Petrou, K., Kormas, K.A., Reizopoulou, S., 2006. Inter-annual variability of soft bottom macrofaunal communities in two Ionian Sea lagoons. Hydrobiologia 555, 89–98. http://dx.doi.org/10.1007/s10750-005-1108-2.

Peña, V., Harvey, B.P., Agostini, S., Porzio, L., Milazzo, M., Horta, P., Le Gall, L., Hall-Spencer, J.M., 2021. Major loss of coralline algal diversity in response to ocean acidification. Glob. Chan. Biol. 27, 4785–4798. http://dx.doi.org/10.1111/gcb.15757.

Pérès, J.M., 1982. Zonations. In: Kinne, O. (Ed.), Marine Ecology, Vol. 1. John Wiley, Chichester, London, pp. 9–46.

Pérès, J.M., Picard, J., 1964. Nouveau manuel de bionomie benthique de la Méditerranée. Rec. Trav. St. Mar. Endoume 31, 1–137.

Pielou, E.C., 1969. An Introduction To Mathematical Ecology. Wiley-Interscience, New York, p. 285.

Raffaelli, D., Hawkins, S., 1996. Intertidal Ecology. Chapman and Hall, London, p. xi+356.

Ragazzola, F., Marchini, A., Adani, M., Bordone, A., Castelli, A., Cerrati, G., Konzelburg, R., Langeneck, J., Di Marzo, C., Nannini, M., Raiteri, G., Romanelli, E., Santos, M., Vasapollo, C., Pipitone, C., Lombardi, C., 2021. An intertidal life: Combined effects of acidification and winter heatwaves on a coralline alga (*Ellisolandia elongata*) and its associated invertebrate community. Mar. Env. Res. 169, 105342. http://dx.doi.org/10.1016/j.marenvres.2021.105342.

Rindi, F., Braga, J.C., Martin, S., Peña, V., Le Gall, L., Caragnano, A., Aguirre, J., 2019. Coralline algae in a changing Mediterranean Sea: how can we predict their future, if we do not know their present? Front. Mar. Sci. 6, 723. http://dx.doi.org/10.3389/fmars.2019.00723.

Ros, J., Romero, J., Ballesteros, E., Gili, J.M., 1989. Buceando en aguas azules. El Bentos. In: Margalef, R. (Ed.), El Mediterráneo Occidental. Omega, Barcelona, pp. 235–297.

Sarhan, T., García Lafuente, J., Vargas, M., Vargas, J.M., Plaza, F., 2000. Upwelling mechanisms in the northwestern Alboran Sea. J. Mar. Syst. 23, 317–331. http://dx.doi.org/10.1016/S0924-7963(99)00068-8.

Sierra, F., Fernández, C., 1984. El horizonte de *Corallina elongata* en la costa central de Asturias (N de España). I. Área mínima y distribución espacial. Inv. Pesq. 48, 255–268.

Smith, S.D., 2005. Rapid assessment of invertebrate biodiversity on rocky shores: where there's a whelk there's a way. Biodivers. Conserv. 14, 3565–3576. http://dx.doi.org/10.1007/s10531-004-0828-3.

Stenseng, E., Braby, C.E., Somero, G.N., 2005. Evolutionary and acclimation-induced variation in the thermal limits of heart function in congeneric marine snails (genus *Tegula*): implications for vertical zonation. Biol. Bull. 208, 138–144. http://dx.doi.org/10.2307/3593122.

Templado, J., Ballesteros, E., Galparsoro, I., Borja, A., Serrano, A., Martín, A., 2012. Guía Interpretativa. Inventario Español de Hábitats Marinos. Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, p. 229.

Urra, J., Rueda, J.L., Mateo Ramírez, Á., Marina, P., Tirado, C., Salas, C., Gofas, S., 2013. Seasonal variation of molluscan assemblages in different strata of photophilous algae in the Alboran Sea (western Mediterranean). J. Sea. Res. 83, 83–93. http://dx.doi.org/10.1016/j.seares.2013.05.016.

Waters, L.J., Hadfield, M.G., Smith, C.M., 1996. Waterborne chemical compounds in tropical macroalgae: positive and negative cues for larval settlement. Mar. Biol. 126, 383–393. http://dx.doi.org/10.1007/BF00354620.

WoRMS, 2022. WoRMS Editorial Board. World Register of Marine Species, http://www.marinespecies.org/ Accessed 2022.