

# Drastic changes in macrofaunal communities of intertidal boulder fields' habitat during the last decade in the south of the Bay of Biscay

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## Abstract

The cumulative effects of environmental and anthropogenic pressures on marine environments are endangering the biocoenosis that inhabit them. Identifying and understanding the impacts of global changes are key challenges for maintaining the habitats in good working state and require the use of standardized monitoring and reliable indicators.

Between 2014 and 2023, as part of various research programs, macrofaunal communities were inventoried in the boulder fields in the Southeastern Bay of Biscay, in an area devoid of fishing pressure. Following a stratified random sampling design, the mobile and sessile macrofaunal of the upper and lower medio littoral zones were identified annually between March and July. The results reveal significant changes over the study period, with a transitional year in 2020. Changes in biodiversity, functionality and indicator species of the habitat are observed, with the decline or even disappearance of species. In functional aspects, the abundance of grazers declines in favour of scavengers. The transition to a new state coincides with changes in environmental parameters (water temperature, salinity, etc.) and confirms the ability of this monitoring method to characterize changes and emerging pressures. The effect of the change and the transition to a new state on ecosystem functioning are discussed.

These results underscored the importance of ongoing monitoring for the management and conservation of coastal ecosystems in the Southeastern Bay of Biscay.

*Keywords:* macrobenthos, biodiversity, biological traits, boulder fields, intertidal environment, Bay of Biscay

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## 1. Introduction

Intertidal rocky reefs are one of the most common coastal habitats across the globe. At the interface between the continental and marine realms, they have been described as "superb natural laboratories" (Branch, 2001). Among this habitat, the "medio littoral boulder fields" are home to a wealth and diversity

of macrofauna (Murray et al., 2006). Through its position at the land-sea interface and its structural heterogeneity (size and shape of boulders), this ecosystem plays an important ecological role: shelter/refuge, reproduction/nursery, feeding. Yet, these coastal zones suffer from chronic or one-off stress events caused by a combination of environmental and anthropogenic pressures (Chapman, 2017). Species need to be able to adapt to extreme conditions, such as dewatering, temperature variations and irradiance. In addition, global changes have an impact on these areas: rising sea levels (Cazenave et al., 2014), increasing surface temperatures (Costoya et al., 2015), wastewater discharges (Cabral-Oliveira et al., 2014; Huguenin et al., 2019) - all threats that are destabilising the biological structure. The complexity of this habitat also makes it difficult to study; hence, few studies describe its biological functions.

Over the last few decades, European Directives such as Water Framework Directive (WFD, 2000/60/EC) and Marine Strategy Framework Directive (MSFD, 2008/56/EC) aimed to determine the ecological status of coastal waters and their communities. To assess the conservation status of rocky foreshore, samplings are primarily based on macroalgae, phytoplankton or benthic invertebrates (Ar Gall et al., 2016; Bianchi et al., 2003; Blanchet et al., 2008; Casamajor (de) et al., 2019; Díez et al., 2012a; Frascetti et al., 2005; Huguenin et al., 2019; Rees et al., 2006; Sagert et al., 2005). The key objective of these directives is to protect, restore and prevent deterioration of water bodies by identifying the pressures being exerted on it. Because of its accessibility, the rocky foreshore is particularly suitable for shore fishing and stamping (Bernard, 2012; Bernard and Poisson, 2024; Rossi et al., 2007). In the southern part of the Bay of Biscay, these activities are rarely practised, and benthic communities are mainly affected by abiotic factors such as hydrodynamics (Abadie et al., 2005; Sousa, 1979) and physico-chemical quality (Huguenin et al., 2019; Piló et al., 2018). Inputs of continental water and discharges of urban water affect them (Zubikarai et al., 2014). Biotic factors, such as predation and competition, also play an important role in the structuring and evolution of these biocenoses (Le Hir and Hily, 2005).

Boulder fields are a component of the “reef” habitat and as such, are considered as a remarkable habitat. The instability and the mobility of the boulders lead to a low representation of complex structure macroalgae in favour of simple and opportunistic algae (Díez et al., 2012a). As a result, unlike the platform habitat, faunal diversity is greater than floral diversity (Chapman, 2017). The specific algal belts to the biogeographic zone, as defined in the WFD, are used to define two littoral habitats. The lower and upper mediolittoral are defined by algal belts, covered respectively by *Gelidium* spp. and *Halopteris scoparia*, and *Corallina* spp. and *Caulacanthus* spp. (Ar Gall et al., 2016). These structuring algae contribute to the biogenic power of the foreshore, providing refuge, food and nesting for macrofauna (Chemello and Milazzo, 2002; Vieira et al., 2018). Benthic macrofauna is widely used for soft substrates as it is a reliable bioindicator that responds significantly to environmental pressures and is commonly applied in assessments (Arshad and Farooq, 2018; Borja et al., 2000; Desrosiers et al., 2013; Salas et al., 2006; Siddig et al., 2016). However, it is not considered in the evaluation of boulder fields. Developing specific tools to boulder fields is necessary to characterise the quality of this habitat as a complement to WFD monitoring.

The seasonality in the dynamics of benthic communities can be explained by more or less regular annual changes as a result of mortality, recruitment, growth, seasonal migration and behavioural patterns (Coma et al., 2000; Hartnoll and Hawkins, 1980). This variability could make the sampling and the deductions more complex. Indicator Species Analysis (ISA) is a useful and commonly used for ecological research (Bakker, 2008; Rentch et al., 2005), based on statistical analyses that allow to determine characteristic species of a habitat (Dufrêne and Legendre, 1997). Monitoring the abundance of these species reflects environmental changes without having to survey all the biodiversity. An alternative approach of systematic criteria is to group species with similar characteristics (Murray et al., 2006). Species that use similar resources should be indicative of the processes that control those resources (Underwood and Petraitis, 1993). Hence, functional ecology based on trophic guilds allows the understanding of ecological processes from the organismic scale (Keddy, 1992). Changes in

biological group composition according to their biological traits reflect environmental changes (Borja et al., 2000; Podraza et al., 2000; Thompson et al., 2020).

In the Bay of Biscay, the presence of boulder fields contributes to intertidal zone diversity. Given the need for knowledge and the interest in this habitat, various monitoring programmes have been set up over the last two decades in this workshop site. The protocols used differed according to the study issues: definition of the good ecological status of coastal water bodies as part of the Water Framework Directive (WFD) on homogenous rocky platform habitat (Ar Gall et al., 2016), impact of oil spills (Castège et al., 2014), characterisation of biodiversity and definition of indicators (Huguenin et al., 2018).

Several criteria warrant the development of a protocol on this workshop site: site management, previous knowledge (Castège et al., 2014; Evans, 1957), European Directive reference station, biogeographic specificities (Sous et al., 2024). Over the last twenty years, studies in the southern part of the Bay of Biscay have shown profound changes in coastal algal communities (Borja et al., 2013; Casado-Amezúa et al., 2019; Díez et al., 2012b; Díez et al., 2003) and degradation of coastal water bodies (Casamajor (de) et al., 2024, 2022). Benthic macrofauna of boulder fields of the study site was described in 2017 as part of the LIFE Marine Habitat (LIFE MarHa) project, which aims to develop a protocol for assessing environmental changes, whatever the pressures exerted on the environment. To do this, abundance of individuals, taxonomic richness and indicator assemblages were defined using a major sampling effort (Huguenin et al., 2018). The heterogeneous distribution of organisms bears witness to the variability of conditions.

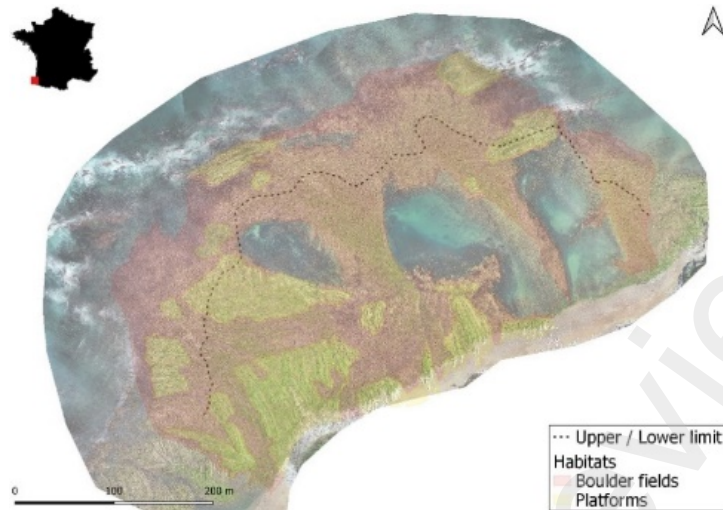
Linked with the objectives of the exploratory project, this study investigated over a 10-year period the biodiversity and the functionality of boulder field habitat. The aims are to (i) assess changes in macrofaunal assemblage, functional traits and indicator species of habitat, and (ii) evaluate the reliability of the protocol to detect changes of environment conditions. The response of benthic communities to environment and anthropic pressures are discussed.

## **2. Material and methods**

### **2.1 Study area**

The sampling site is located in the South of the Bay of Biscay (Alcyons beach, Guéthary city, Figure 1). It is included in a Marine Protected Area (MPA), the Natura 2000 "Cliff from Saint-Jean-de-Luz to Biarritz" (FR7200776) and the Natural Zone of Ecological, Faunistic and Floristic Interest (ZNIEFF) "Coastal environments from Biarritz to the Pointe de Sainte-Barbe". In addition, a council decree prohibiting fishing completes this protection regulatory scheme.

Hard substrates dominate the Basque coast represented mainly by boulders and flysch foreshores (Alexandre et al., 2003). The South-West of the Bay of Biscay is marked by characteristic meteorological and oceanic conditions. The orientation of the coast exposes the foreshore to intense swell phenomena and to desalination due to the numerous coastal tributaries. The strongest hydrodynamic features of the French coastline with an average height of 1.8 m for a period of 9.6 s batters the coasts (Alexandre et al., 2003; Delpy et al., 2021). Tides over the area are semidiurnal. Tidal amplitudes between 1.85–3.85 m form a mesotidal system (Augris et al., 2009; Borja and Collins, 2004). Many rivers flow into the coast and increase the supply of nutrients (Defontaine et al., 2019). Sea surface temperature shows seasonality, varying between 8 and 15°C during winter, and reaching 22°C and more during summer (Valencia et al., 2004). These conditions influence the primary production and community structure of coastal ecosystems.



**Figure 1** Sampling site location ( $43^{\circ} 25' 36.475''\text{N}$ – $1^{\circ} 36' 58.445''\text{W}$ ) and area (red zone). The dotted line represents the midlittoral zone boundary. Orthomosaic made with a drone (DJI phantom 4 RTK) for the European MarHa project. The map identifies two habitats, described by ‘Cahiers d’habitats Natura 2000 – Habitats côtiers’ as ‘Boulder fields – Atlantic coast (11-70-9)’ and ‘Exposed mediolittoral rocky shore – Atlantic coast (1170-3)’ (Bensettiti, 2005). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

## 2.2 Sampling

Sampling took place in the intertidal zone of the "mediolittoral boulder fields" habitat (European reference system MA123 EUNIS, national repository HabRef A1-8, Tauran and Grall, (2022)) on both upper and lower mediolittoral levels defined by the WFD algal belt (Ar Gall et al., 2016). Inventories were done between 2014 and 2023 in spring and early summer (March to July).

A two-stage stratified random sampling design was used to determine the structure of the benthic communities. Mobile and sessile taxa were inventoried in 33 x 33 cm quadrats, *i.e.* the same sampled size area as for the WFD sampling (Ar Gall et al., 2016), and characterised by count and percentage cover respectively. In order to compare the blocks size by minimizing bias, the surface area of boulders surveyed was equivalent to that of the quadrat, *i.e.* 0.1 m<sup>2</sup>. Only organisms that can be identified with the naked eye and larger than 1 cm have been inventoried. The term 'macrofauna' is used in comparison with the Huguenin et al. (2018) results and meets the definition given by Cochran et al. (2019), “macrofauna are a group of animals defined by their size, [...] between 500 μm (0.5 mm) and 5 cm”. The majority of species were identified *in situ*; for those that could not be directly identified, an individual was sampled and determined *a posteriori* in the laboratory. Considering habitat conservation, not all individuals were sampled in every quadrat, leading to varying levels of identification (family, genus, or species).

The database from inventories were banked into two datasets named “Global assemblage matrices”: the mobile macrofauna corresponds to the individuals that could be counted (abundance) and the sessile macrofaunal groups together the uncountable individuals characterised by their surface coverage per quadrat in class of percentage as proposed by Kuchler et al. (1976).

As this habitat is not monitored on a permanent basis, numerous projects have been necessary to acquire the database (Table 1). At the beginning of the sampling period, a baseline study was conducted between 2015 and 2016. The results of this study, presented in Huguenin et al. (2018), describe in detail the sampling design chosen. (Caill-Milly et al., 2016)

**Table 1** Inventory of the number of quadrats per campaign year and associated projects

Year	Number of quadrats			Project	Funding
	Lower	Upper	Total		
2014	15	0	15	BIGORNO	Département Pyrénées- Atlantiques And OFB
2015	123	110	233		
2016	106	73	179		
2017	24	27	51	DESCARTES	DS ifremer
2018	0	0	0	No project	
2019	10	10	20	MarHa	Life
2020	14	18	32		
2021	30	30	60		
2022	30	30	60		
2023	0	15	15		
Total	352	313	665		

### 2.3 Environmental conditions

Data concerning environmental conditions aggregates: sea surface temperature ( $^{\circ}\text{C}$ ), salinity (PSU), orbital velocity ( $\text{m}\cdot\text{s}^{-1}$ ) and tidal range (m) simulated by the hydrodynamic model MARS developed by the French Research Institute for Exploitation of the Sea (Ifremer) , and (ii) rainfall (m) in Ciboure station (infoclimat.fr). Only months from May to September were considered in the dataset on environmental conditions. Several reasons can explain this choice. It is the breeding period for a large number of species (Flores and Paula, 2002; Tudge et al., 2007; Weber et al., 2014). It is the summer season, when tourist pressure is the greatest and more important on benthic communities (Mejjad et al., 2022). Lastly, when storms are not occurring, there is less overturning of the blocks by the swell, so the populations are more stable.

Modelled data are averaged per day. All environmental conditions play a role in community structure; these ones are available for the workshop site. Rainfall reflects rivers flow and potentially nutrient inputs. Measures come from Ciboure station.

A Principal Component Analysis (PCA) was performed to visualize the most descriptive conditions and to highlight interannual variation of environmental data, using the *dudi.pca* function of the “ade4” package. Anomaly detection graphs, done on environmental parameters averages, allow visualizing of the annual trend. Mann-Kendall test of the “Kendall” package allowed us to verify the observed trends for environmental parameters.

Analyses were processed on R Studio® version 4.1.2.

### 2.4 Structure of benthic communities

#### 2.4.1 Nomenclature

Taxonomic nomenclature follows WoRMS (WoRMS Editorial Board, 2024). To avoid problems of unidentified species, analyses were conducted on aggregated data containing taxonomic level mixing (species, genus, family, class). When identification was provided at the highest taxonomic category possible (genus, family or class), individuals were named by the lowest taxonomic category using the same taxonomic name.

#### 2.4.2 Data analysis

Analyses were computed separately for each database (mobile and sessile macrofauna), because mobile and sessile organisms react differently to disturbance and the units used to characterise them are different.

To evaluate the functionality of the habitat based on the macrofauna, the “Trophic guilds matrix” was designed, from on the “Global assemblage matrix”, by summing the abundances of taxa by their diet. Seven diets were defined: deposit feeder, filter feeder, grazer, omnivorous, predator, scavenger and NA for taxa with undefined trophic guild, based on WoRMS Editorial Board, 2024, Zubikarai et al. (2014) and Compaire et al. (2016). Since coverage classes cannot be added together and all sessile organisms are filter feeders, sessile taxa were not studied according to their diet.

To evaluate the reliability of indicator species to monitor the environmental quality, the “Indicator Species matrix” was designed for each database (mobile and sessile macrofauna), from on the “Global assemblage matrix”, by selecting only the most highly significant ( $p < 0.01$ ) indicator species of the habitat identified by Huguenin et al. (2018).

Non-metric MultiDimensional Scaling (nMDS) representations using *metaMDS* function of the “vegan” package, based on Hellinger distance matrix (Legendre and Legendre, 2012) were performed to highlight trends by years in benthic community structure. or reasons of data representativeness, only “Trophic guild matrix” and “Indicator Species matrix” of mobile macrofauna, were processed in order to identify the similarities and dissimilarities between each of the approaches and to characterise the complementary nature of the methods.

To determine whether there are statistically significant differences between periods, Analyses of Similarities (ANOSIM) were performed using *anosim* function of the “vegan” package (999 permutations) (Clarke and Green, 1988). To identify which taxa or trophic guilds that contribute the most in the dissimilarities, Similarity Percentages tests (SIMPER) using *simper* function from the “vegan” package (999 permutations) were used. Taxa with a cumulative contribution (cumsum) of more than 20% were defined as having the greatest influence on the overall dissimilarities (Clarke, 1993; Clarke and Warwick, 2001; Encarnaç o et al., 2015).

Single species/taxa were identified as indicators of upper and lower mediolittoral zones by Huguenin et al. (2018) using statistical analyses. Two independent Indicator Species Analyses (ISA) were conducted on mobile and sessile macrofauna associated with their mediolittoral level, using the ‘indicspecies’ package (C aceres, 2020). This preliminary study done on 2015-2016 inventories, allowed to define 10 Indicator Species.

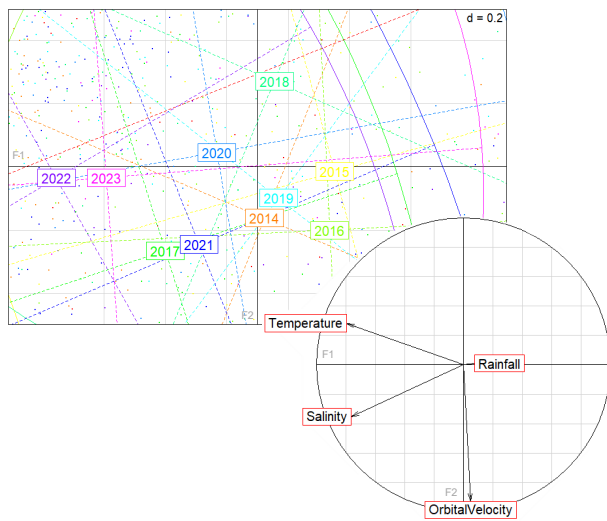
To assess the capacity of the ISA to provide conclusive information in relation to the overall inventory and the functionality based on trophic guilds, the “Indicator Species matrices” (Hellinger transformed) were compared with the “Global assemblage matrix” and “Trophic guilds matrix” (Hellinger transformed) by a Mantel-type test using the RELATE function (Spearman correlation) of the PRIMER-e software. The Spearman coefficient ( $\rho$ ) measures the strength of the relationship between the two matrices. A high  $\rho$  value indicates a high degree of similarity between the two matrices. The p-value indicates whether the correlation observed between the two matrices is significant, based on 9999 permutations.

The analyses were processed on Excel  2016, R Studio  version 4.1.2 and PRIMER7 .

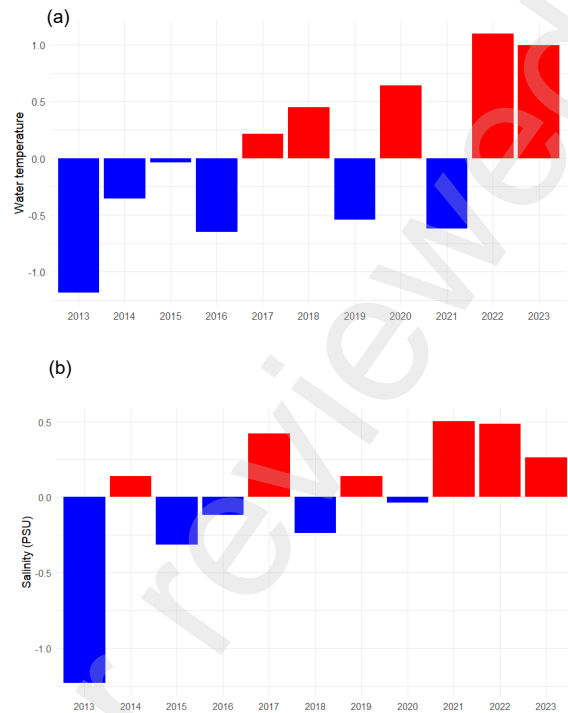
### 3. Results

#### 3.1 Environmental conditions

Environmental parameters differ significantly over the study period. PCA, represented in Figure 6, explains 57.1% of cumulative variance in two components, of which dimension 1 and 2 exhibit 30.5% and 26.7% variance, respectively.



**Figure 2** Principal Component Analysis (PCA) of the environmental variables between 2014 and 2023.  $F1 \times F2 = 52.8\%$  of variability.



**Figure 3** Anomaly in mean temperature (a) and mean salinity (b), May to September, 2013 to 2023.

Distinct cluster group formation is observed across different years. The years are structured mainly along dimension 1 (Fig. 2). Temperature of sea surface (Temperature) and salinity of sea (Salinity) show a strong positive association in dimension 1 (51.71% and 47.62% of respective contribution), with 2017, 2020, 2021, 2022, 2023. This suggests the raise of sea surface temperatures over the study period (*Mann-Kendall test*:  $\tau = 0.564$ ,  $p = 0.019$ ). Over the recent period (2020-2023), it averaged  $20.4 \pm 2.4$  °C between May and September versus  $19.5 \pm 2.4$  °C previously (2013-2019) (Fig. 3.a).

Similarly, orbital velocity has significant positive loadings in dimension 2 (80.75%) and contributes negatively to 2018.

Environmental parameters show a trend over the sampling period, with overall changes taking place between 2019 and 2020. The year 2017 shows environmental conditions close to the recent period, mainly marked by high sea surface temperatures and high salinity.

### 3.2 General structure of communities

During the study period, a total of 114 taxa were recorded, 15 780 mobile individuals among 89 taxa and 42.6 m<sup>2</sup> of 25 sessile taxa were inventoried in the 665 quadrats surveyed during the campaigns from 2014 to 2023, in the boulder field of the workshop site (Supplementary material 1). 36 taxa were observed less than twice.

According to their total abundance proportions, Arthropodia (49.9%) and Mollusca (43.7%) mostly characterise mobile macrofauna. Echinodermata, Cnidaria, Chordata and Annelida are the other phyla, less present. *Paguridae*, *Steromphala* spp. and *Porcellana platycheles* are the most abundant taxa.

For sessile macrofauna, Annelida (47.8%), Arthropodia (21.9%) and Cnidaria (10.9%) are the most abundant phyla particularly represented by the following taxa, *Janua heterostropha*, *Spirobranchus* spp., *Chthamalus* spp and *Sertularella* spp.

### 3.3 Temporal variability in mobile macrofaunal structure

To find the best compromise between feasibility of the protocol, long-term implementation and relevance of the data collected, the inventories carried out from 2014 to 2023 are represented according to their temporal variability. Three levels of expertise are analysed, according to the three matrices, biodiversity, functionality and Indicator Species/Taxa. These different methods will make it possible to identify the contribution of each to understanding the macrofaunal structures and their responses to pressures.

- On the “Global assemblage matrix”

For the mobile macrofauna, the data representation by nMDS is bad (stress > 0.2). However, two periods are significantly different in terms of structure in both the upper and lower mediolittoral zones: from 2015 to 2019 and from 2020 to 2022 (*ANOSIM test*:  $R_{upper} = 0.301$ ,  $p_{upper} = 0.001$ ;  $R_{lower} = 0.316$ ,  $p_{lower} = 0.001$ ). The taxa most affected by these differences are gibbula (*SIMPER test*:  $cumsum = 0.232$ ) and Paguroidea (*SIMPER test*:  $cumsum = 0.228$ ) in both zones.

For the sessile macrofauna, the data representation by nMDS is also poor (stress > 0.2). The previously defined periods do not show significant differences (*ANOSIM test*:  $R_{upper} = -0.039$ ,  $p_{upper} = 0.921$ ;  $R_{lower} = 0.011$ ,  $p_{lower} = 0.001$ ).

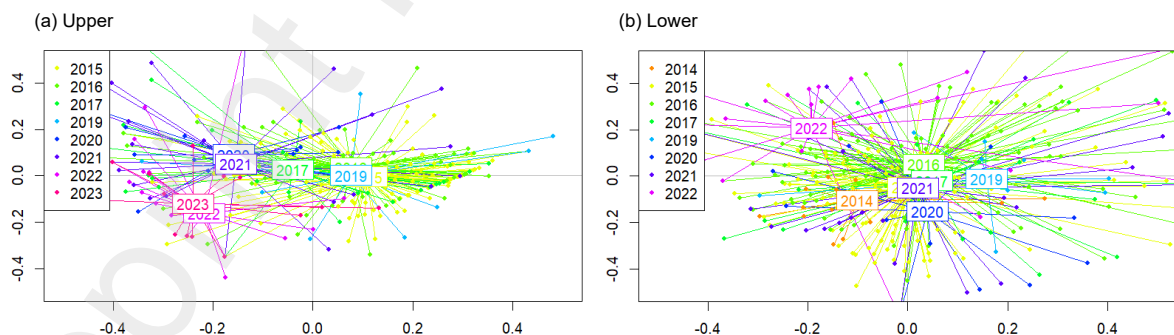
The presence and abundance of species is sometimes sporadic, as evidenced by the number of species sporadically found. Functionality according to trophic guilds allows us to overcome taxonomic limitations.

- On the “Trophic guilds matrix”

To focus on functionality of the ecosystem, taxa were classified according to their trophic guild. Figure 4 represents the nMDS computed on trophic guilds matrix. The level of representativeness is good (stress < 0.2). The same temporal patterns as previously observed emerged: from 2015 to 2019 and from 2020 to 2023.

This temporal structuring is significant in both the upper (*ANOSIM test*:  $R = 0.299$ ,  $p = 0.001$ ) and lower (*ANOSIM test*:  $R = 0.287$ ,  $p = 0.001$ ) levels.

In the upper zone, the most represented trophic guilds in 2015-2019 are grazers (54.1%), scavengers (31.7%) and filter feeders (9.2%). In 2020-2022, scavengers (48.1%), predators (21.8%), filter feeders (14.4%) are the most abundant. Trophic guilds that contribute the most to differences between the two periods are grazers (*SIMPER*:  $cumsum$  0.329) and scavengers (*SIMPER*:  $cumsum$  0.291). These same guilds are the most affected in the lower zone.



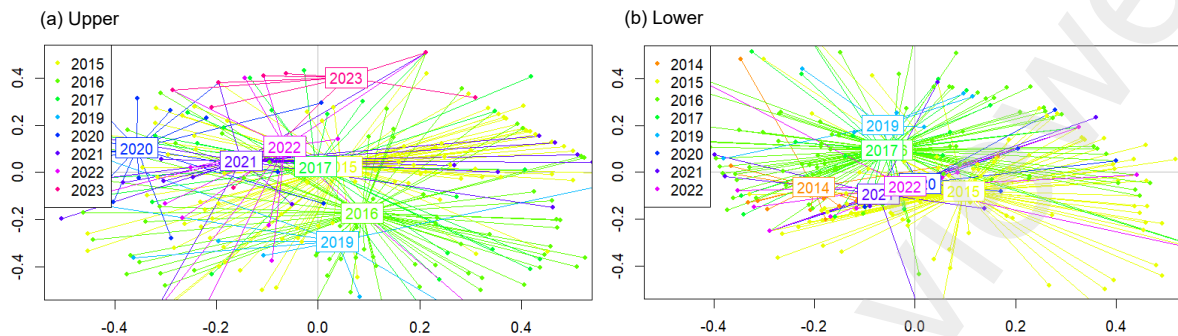
**Figure 4** nMDS (Hellinger dissimilarity matrix, euclidean distance) computed on trophic guilds of mobile fauna for upper (stress = 0.127) (a) and lower (stress = 0.175) (b) mediolittoral zones between 2014 and 2023. Dimensions 1 and 2 are used to describe the dataset, higher dimension do not substantially decrease stress values.

This approach confirms the two periods identified previously and makes it possible to specify which trophic groups are impacted by this change.



- On the “Indicator Species matrix”

The nMDS computed on indicator species of mobile macrofauna (Figure 5) shows a good level of representativeness (stress < 0.2). The same temporal patterns as previously emerged in the upper zone: from 2015 to 2019 and from 2020 to 2023.



**Figure 5** nMDS (Hellinger dissimilarity matrix, euclidean distance) computed on indicator species of mobile macrofauna (Huguenin et al., 2018) for upper (stress = 0.184) (a) and lower (stress = 0.147) (b) mediolittoral zones between 2014 and 2023. Dimensions 1 and 2 are used to describe the dataset, higher dimension do not substantially decrease stress values.

This temporal structuring is significant in the both levels and more pronounced in the upper (*ANOSIM test*:  $R = 0.215$ ,  $p = 0.001$ ) than in the lower (*ANOSIM test*:  $R = 0.152$ ,  $p = 0.001$ ) level.

The results of ordination based on each of the three matrices (all taxa, trophic guild of all taxa and indicator species) show similar trend. The change in the structure of the mobile macrofauna is more marked in the upper than in the lower zone. In upper mediolittoral, a clear difference is observed between 2019 and 2020. The year 2017 is particular, the structure of macrofauna is intermediate between that of the 2015-2019 and 2020-2023 periods. Conversely, no marked structural change is visible in the lower zone, whatever the representation.

According to these results, the three methods complement each other and using indicator species to monitor structural change is relevant.

### 3.4 Indicator species

The trends depend on the mobility of taxa. Abundance of mobile macrofauna decreases between the two periods (Tab 2.a). It is divided by 3 to 18 times, even leading to the complete disappearance of characteristic species such as *Ophioderma longicaudum* in the recent inventories. The percentage cover of sessile macrofauna is stable, even increasing. In 2021-2022, there are 3 times more *Sertularella* spp. than in the 2015-2016 inventories (Tab 2.b). Not all organisms from all quadrats were sampled for laboratory identification, for *Sertularella* spp. all of which have the same appearance as those collected, the majority are *Sertularella mediterranea*.

**Table 2** Abundance (mobile fauna) and percentage cover (sessile fauna) (average and standard deviation) per quadrat of single taxa indicator species for mobile (a) and sessile macrofauna (b), defined in 2015-2016 by Huguenin et al., 2018. Level factor refers to mediolittoral level. Indicator taxa have high significance ( $p$ -value < 0.001), are specific ( $A \geq 0.6$ ) and common ( $B \geq 0.2$ ) in their habitat. Trophic guilds are taken from (1) Zubikarai et al., 2014, (2) WoRMS Editorial Board, 2024 and (3) Compaire et al., 2016.

Indicator species of defined in 2015-2016	Level	Ab. / Cover. in 2015-2016		Ab. / Cover. in 2021-2022		Trophic guild	Pollution sensitivity
		Av.	SD	Av.	SD		
<b>(a) Mobile macrofauna (abundance)</b>							
<i>Patella</i> spp.	Upper	3.72	4.82	0.73	2.11	Grazer (2)	Very sensitive
<i>Pachygrapsus marmoratus</i>	Upper	2.53	2.47	0.80	0.86	Scavenger (1)	Indifferent
<i>Paguridae</i>	Lower	9.44	14.97	1.68	2.79	Scavenger (1)	Indifferent
<i>Porcellana platycheles</i>	Lower	5.13	6.76	0.62	1.09	Filter feeder (1)	Very sensitive
<i>Tritia</i> spp.	Lower	2.20	4.64	0.12	0.37	Scavenger (2)	Indifferent
<i>Lepadogaster lepadogaster</i>	Lower	0.24	0.64	0.03	0.18	Predator (3)	-
<i>Ophioderma longicaudum</i>	Lower	0.77	1.70	0.00	0.00	Predator (1)	Indifferent
<b>(b) Sessile macrofauna (percentage cover)</b>							
<i>Chthamalus</i> spp.	Upper	6.87	12.39	5.43	9.07	Filter feeder (2)	Very sensitive
<i>Mytilus</i> spp.	Upper	1.31	4.15	0.72	2.22	Filter feeder (2)	Tolerant
<i>Sertularella</i> spp.	Lower	1.68	6.03	5.27	12.11	Filter feeder (2)	Indifferent

The correlation between matrices, as shown in Table 3, reveals that indicator species matrix have a strong positive correlation with global assemblage matrix ( $\rho \approx 0.8$ ) whatever the factor (year, zone or both). Inventories of indicator species are just as informative as inventories of all species, when it comes to identifying global changes. Conversely, trophic guilds of indicator species matrix do not have correlation with trophic guilds of global assemblage ( $\rho \approx 0.1$ ) whatever the factor (year, zone or both). Indicator Species functionality is not sufficient to explain overall functionality.

**Table 3** Results of matrix correlation tests applied on the matrices “Global assemblage” and “Indicator Species”. Levels are based on 9999 permutations.

Hellinger transformed matrices	Factor	$\rho$	Significance level
“Global assemblage matrix” x “Indicator Species matrix”	Year	0.78	0.01
	Zone	0.82	0.01
	Year x zone	0.82	0.01
“Trophic guilds matrix” x “Indicator Species’ trophic guilds matrix”	Year	0.19	0.01
	Zone	0.12	0.01
	Year x zone	0.11	0.01

## 4. Discussion

Implementation of this benthic macrofauna sampling protocol in boulder fields aims to characterize community structures, identify possible changes, and understand how communities respond to environmental and demographic pressures. This step is essential for assessing conservation status and considering restoration measures. The geographic location of the sample site allows disregarding of the impact of shore fishing, which is prohibited and thus negligible for these communities.

### 4.1 Biodiversity and functionality changes in boulder fields

The protocol implemented over the last decade has provided the necessary data for studying the boulder fields habitat and results has revealed significant changes in faunal community structures. Both

in terms of biodiversity and functionality, the results differ between the preliminary study conducted in 2015-2016 (Huguenin et al., 2018) and the recent ones, with 2020 standing out as a transition year.

In terms of biodiversity, some biological groups have completely disappeared from the inventories, such as brittle stars. Among them, *Ophioderma longicaudum* has not been observed since 2021, even though Huguenin et al. (2018) previously classified it as an Indicator Species for the lower mediolittoral zone. The ability of organisms to persist in their environment depends on the environment's ability to meet their physiological needs (Roth and Wilson, 1998). The thermotolerance of brittle stars is greatly influenced by local population adaptations (Weber et al., 2013). Since 2020, the average surface temperature at the study site between May and September has been 20.4°C, which is one degree higher than during the 2013-2019 period. It has been shown that temperature increases lead to higher larval mortality in echinoderms (Byrne et al., 2009; Jangoux and Lawrence, 1996). While some taxa have declined in abundance, others have increased. This is particularly noticeable for species with a Southern affinity, such as *Sertularella mediterranea*, whose prevalence has been demonstrated in the Southern Bay of Biscay (Aguirrezabalaga et al., 1984).

Observations at the biodiversity level suggest a structural shift towards communities better adapted to warmer temperatures than before. This hypothesis of a "Meridionalization" of communities needs to be supported by species-specific identification and a deeper analysis of the thermal thresholds of these organisms. An approach based on the distribution range of observed species could be valuable for further research.

The functional approach by trophic group reveals significant structural changes over the study period. This habitat was initially dominated by grazers (Huguenin et al., 2018). However, recent inventories after 2020 are primarily composed of scavengers, while grazer abundance has plummeted. Grazers are regulators, and their scarcity can lead to the proliferation of opportunistic algae and associated socio-economic consequences (Puppin et al., 2024). The decline in grazer populations coincides with the first reports of the toxic dinoflagellate *Ostreopsis ovata* in 2020 (Chomérat et al., 2022). Environmental factors predisposing blooms include surface temperature (25°C), calm hydrodynamics (swell and wind), and salinity (37-38 PSU in the NW Mediterranean Sea, Tawong et al. (2015), 31-39 PSU in the Northern Adriatic Sea, Accoroni et al. (2015)).

When ingested during feeding, this microalgae and/or its produced compounds cause poisoning in organisms, as demonstrated in limpets (Blanfune et al., 2012). The toxins produced by *O. ovata* affect the larval development stages of filter feeders, reducing juvenile recruitment from one year to the next (Pavaux et al., 2020). *O. ovata*-related poisonings are not limited to the lower levels of trophic chains. Cascade effects are observed in higher-level organisms such as carnivores through biomagnification and bioaccumulation in food webs (Boisnoir et al., 2020). It is, therefore, possible that all organisms are affected, and specific studies are necessary to detect the presence of the microalgae in organisms and its effects throughout the trophic chain.

The development of marine mucilage and *O. ovata* blooms are two linked environmental pressures that should also be jointly integrated into the assessment of macrofauna dynamics. Their combination can cause mortality in benthic communities (Karadumuş and Sari, 2022; Vilà and Hulme, 2017). During its development phases, the microalga produces mucus. This mucilage then acts as a vector for transmitting toxicity, increasing the contact surface between *O. ovata* cells, substrates, and benthic organisms (Giussani et al., 2015). The mucilage itself, when deposited on these organisms, can lead to their death by suffocation (Devescovi and Iveša, 2007).

At the water body scale, simultaneous changes are occurring in the structure of characteristic algae. The results of the Water Framework Directive (WFD) for the "intertidal macroalgae" parameter, calculated at the same station but on the rocky shore habitat, downgrade the ecological status to "moderate" for the second consecutive period since 2018 (Casamajor (de) et al., 2022). Algae, as primary

producers, represent a key in biological component for environmental quality monitoring. Their development conditions grant them an effective bioindicator status for assessing the quality of aquatic environments (Ar Gall et al., 2016; Gökçe, 2016). However, these surveys are conducted every three years and provide results that are too sporadic for the study period. Moreover, they do not concern the same habitat, as boulders do not provide a stable enough environment to allow the development of entire macroalgal communities.

Regardless of the approach, the results show more pronounced changes in the upper mediolittoral zone than in the lower zone. This zonation has been widely described (Boudouresque, 1971; Parry-Wilson et al., 2024). Biotic and abiotic factors govern the vertical distribution of organisms. The lower level is subject to tides and wave action, which can lead to the temporary migration of organisms. In contrast, the upper level hosts species particularly adapted to extreme conditions, including variations in water and air temperature (Chappuis et al., 2014). Upper mediolittoral communities therefore endure long periods of emersion, leading to air temperature peaks that can be low in the winter (below  $-10^{\circ}\text{C}$ ) and very high in the summer (above  $35^{\circ}\text{C}$ ) (Durand and Mallet, 2004). Lower mediolittoral communities are less exposed to these extreme conditions. To better understand the conditions governing the spatial distribution of organisms, it would be interesting to couple these analyses with precise temperature measurements at each of the two levels. It is not possible to identify a single factor as solely responsible for this zonation. Integrating wave exposure, coastline orientation, wind, or food availability is important, as these parameters also play a role in the dynamics of benthic structures (Baker, 1909; Carcedo et al., 2017; Reichert et al., 2008).

#### 4.2 Environmental context: simultaneous changes

The multivariate analysis of environmental parameters reveals a significant shift beginning in 2020, characterized by an increase in surface water temperatures and conditions favourable to mucilage development. Simultaneously, changes are observed in the composition of macrofaunal assemblages within the study area, including a collapse of herbivore populations in favour of scavengers, and a general decline in organism abundance. Indicator taxa show similar trends, with a decline in species such as *Patella* spp. and *Porcellana platycheles*. Therefore, monitoring these species seems sufficient to track changes in macrofaunal structures relative to environmental parameters. However, from a functional perspective, focusing only on these organisms is too reductive and represents a limitation of a purely statistical approach in selecting indicator species (Lindenmayer and Likens, 2011). It would be more appropriate to include representatives of trophic guilds at each medio littoral level among the indicator taxa, creating a pool of taxa that reflects both biodiversity and functionality.

For sustainable monitoring practices, focusing solely on indicator taxa provides a general understanding of changes within the "boulder fields" habitat. However, a comprehensive inventory of the entire macrofaunal yields more detailed insights, particularly regarding ecosystem functionality. These two approaches are therefore complementary, enabling a holistic assessment of ecosystem conservation status and its response to pressures.

Current inventories do not distinguish species based on their mobility-related physiological traits, instead categorizing them by organism count. Countable organisms are considered mobile, while encrusting species are classified as sessile. To optimize the protocol, future analyses should incorporate more precise biological and environmental data. Mobility influences community structure, with dispersal capabilities after settlement-increasing organisms' resilience to an unstable environment (Van Der Wal et al., 2017). In other words, mobile taxa can move between shore levels and microhabitats when disturbed (Davidson et al., 2003). Sessile species, however, lack this ability and must adapt through colonization techniques, such as larval dispersal (Archambault et al., 2018). Monitoring sessile species is therefore crucial for characterizing changes on large spatiotemporal scales (Barnes and Hughes, 1999). Future inventories should consider taxa based on their actual mobility, with a particular focus on sessile communities while highlighting their functional groups.

Additionally, to improve community descriptions, a more precise taxonomic identification would enhance our understanding of ecosystem functioning. Not all species within the same genus share the same ecological requirements, and the meridional distribution of each species is an important factor in the context of global change. For example, the three species of *Steromphala* commonly found on this rocky shore—*S. cineraria*, *S. pennanti*, and *S. umbilicalis*—demonstrate different thermal tolerance limits. Parry-Wilson et al. (2024) show that on the English rocky shore, the lethal thermal tolerance limit for *S. umbilicalis* ranges from 41.8 to 42.1°C, compared to 35.5 to 36.2°C for *S. cineraria*. However, *S. umbilicalis* is a generalist species in the Bay of Biscay, while *S. pennanti* is favoured by certain habitats, such as fucoid algae (Wort et al., 2019). Due to their physiological constraints, these species allow for a more precise assessment of ecosystem conservation status.

Lastly, regarding the functional traits of organisms, the trophic guilds defined in the literature are not sufficiently precise. For instance, they do not differentiate sessile taxa according to their capture strategies. Under the designation of "filter feeders," species like Cirripedia, Annelida, or Actinia deploy external appendages into the water column to capture prey, classifying them as "active filter feeders" or "suspension feeders" (Chintiroglou and Koukouras, 1992; Jarrett, 2018; Rouse et al., 2022). Conversely, ascidians, bivalves, and porifera contain siphons within their bodies, without developing external capture organs, making them "passive filter feeders" or "deposit feeders" (Petersen, 2007; Riisgård et al., 2003; Vacelet and Dupont, 2004). Distinguishing these trophic classes among sessile organisms would improve the understanding of their functioning and better integrate them into analyses.

## 5. Conclusion

This study demonstrates that significant structural changes in benthic communities are already observable within just a decade; brought to light by the results presented. The protocol applied to the "mediolittoral boulder fields" habitat effectively detects alterations in community structure and assesses the conservation status of this habitat. Notably, increasing scarcity even disappearance of indicator species and profound functional changes, such as the decline of grazers in favour of scavengers, have been observed. These shifts in biological compartments coincide with environmental changes, particularly during the transition period between 2019 and 2020. In a context of high level of sea surface temperature, this phase corresponds to imbalances leading to blooms of the toxic algae *Ostreopsis ovata* and a general increase in mucilage formation in the Southern Bay of Biscay. Consequently, the results of this work highlight the importance of targeting future studies to assess the actual impact of pressures, such as toxic microalgal blooms, on the benthic communities of rocky shores.

Considering those results and the drastic changes observed, it seems likely that this marine habitat is in a transitional phase, evolving towards a new state that needs to be described. In the context of global change, this study underscores the importance of continuing long-term monitoring through the application of this protocol for the surveillance of this habitat, in conjunction with *in situ* measurements of environmental parameters. To harmonize this work and assess pressures on a larger scale, the protocol should be implemented at other sites along the Atlantic coast. The recommendations provided will help to optimize the protocol and refine the information collected for better coastal heritage management.

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## Supplementary materials

**Supplementary material 1.** List of taxa identified in inventories, their trophic guilds from WoRMS Editorial Board (2024) (1), Zubikarai et al. (2014) (2), and Froese, R. and D. Pauly (2024) (3).

Taxa	Phylum	Trophic guild
<b>(a) Mobile macrofauna</b>		
Annelida undefined	Annelida	
<i>Eulalia viridis</i>	Annelida	Predator (1)
<i>Hesionella splendida</i>	Annelida	Deposit feeder (1)
<i>Alpheus</i> spp.	Arthropoda	Grazer (1)
<i>Alpheus macrocheles</i>	Arthropoda	Grazer (1)
<i>Athanas</i> spp.	Arthropoda	Omnivorous (1)
<i>Athanas nitescens</i>	Arthropoda	Omnivorous (1)
<i>Eriphia verrucosa</i>	Arthropoda	Predator (2)
<i>Galathea squamifera</i>	Arthropoda	Deposit feeder (1)
<i>Herbstia condyliata</i>	Arthropoda	Grazer (1)
<i>Macropodia</i> spp.	Arthropoda	Scavenger (1)
<i>Necora puber</i>	Arthropoda	Omnivorous (1)
<i>Pachygrapsus marmoratus</i>	Arthropoda	Scavenger (1)
Paguridae	Arthropoda	Scavenger (1)
<i>Palaemon elegans</i>	Arthropoda	Predator (1)
<i>Pisa</i> spp.	Arthropoda	Grazer (1)
<i>Pisidia longicornis</i>	Arthropoda	Filter feeder (1)
<i>Porcellana platycheles</i>	Arthropoda	Filter feeder (1)
<i>Xantho</i> spp.	Arthropoda	Scavenger (1)
<i>Lysmata seticaudata</i>	Arthropoda	Predator (1)
Blenniidae undefined	Chordata	Predator (3)
<i>Coryphoblennius galerita</i>	Chordata	Grazer (1)
Gobiidae undefined	Chordata	Predator (3)
<i>Gobius paganellus</i>	Chordata	Predator (3)
<i>Lepadogaster candolii</i>	Chordata	Predator (3)
<i>Lepadogaster lepadogaster</i>	Chordata	Predator (3)
<i>Lipophrys pholis</i>	Chordata	Predator (3)
<i>Lipophrys trigloides</i>	Chordata	Predator (3)
<i>Parablennius sanguinolentus</i>	Chordata	Grazer (1)
<i>Salaria pavo</i>	Chordata	Predator (2)
<i>Actinia equina</i>	Cnidaria	Predator (1)
<i>Actinia fragacea</i>	Cnidaria	Predator (1)
<i>Actinia prasina</i>	Cnidaria	Predator (1)
<i>Actinotoxoa sphyrodeta</i>	Cnidaria	Predator (1)
<i>Aiptasia mutabilis</i>	Cnidaria	Predator (1)
<i>Anemonia sulcata</i>	Cnidaria	Predator (1)
<i>Anthopleura ballii</i>	Cnidaria	Predator (1)
<i>Anthopleura thallia</i>	Cnidaria	Predator (1)
Anthozoa undefined	Cnidaria	
<i>Balanophyllia regia</i>	Cnidaria	Filter feeder (1)
<i>Corynactis viridis</i>	Cnidaria	Filter feeder (1)
<i>Cylista elegans</i>	Cnidaria	Predator (1)
<i>Amphipholis squamata</i>	Echinodermata	Deposit feeder (1)
<i>Asterina gibbosa</i>	Echinodermata	Omnivorous (1)
<i>Asterina phylactica</i>	Echinodermata	Omnivorous (1)
<i>Coscinastris tenuispina</i>	Echinodermata	Predator (1)
<i>Holothuria tubulosa</i>	Echinodermata	Deposit feeder (1)
<i>Holothuria</i> spp.	Echinodermata	Deposit feeder (1)
<i>Marthasterias glacialis</i>	Echinodermata	Predator (1)
<i>Ophiothrix fragilis</i>	Echinodermata	Deposit feeder (1)
<i>Ophioderma longicaudum</i>	Echinodermata	Predator (1)
<i>Paracentrotus lividus</i>	Echinodermata	Grazer (1)
<i>Psammechinus miliaris</i>	Echinodermata	Predator (1)
<i>Acanthochitona crinita</i>	Mollusca	Grazer (2)
<i>Acanthochitona fascicularis</i>	Mollusca	Grazer (2)
<i>Acanthochitona</i> spp.	Mollusca	Grazer (2)
<i>Aeolidia papillosa</i>	Mollusca	Predator (2)
<i>Aplysia punctata</i>	Mollusca	Grazer (2)

<i>Berthellina edwardsii</i>	Mollusca	Predator (1)
<i>Bittium reticulatum</i>	Mollusca	Grazer (1)
<i>Calliostoma zizyphinum</i>	Mollusca	Grazer (1)
<i>Cerithium</i> spp.	Mollusca	Predator (2)
<i>Chiton</i> spp.	Mollusca	Grazer (2)
<i>Diodora gibberula</i>	Mollusca	Predator (2)
<i>Discodoris rosi</i>	Mollusca	Predator (2)
<i>Doris verrucosa</i>	Mollusca	Predator (2)
<i>Facelina auriculata</i>	Mollusca	Predator (2)
<i>Felimare cantabrica</i>	Mollusca	Predator (2)
<i>Gibbula</i> spp.	Mollusca	Grazer (2)
<i>Haliotis tuberculata</i>	Mollusca	Grazer (2)
<i>Lepidochitona cinerea</i>	Mollusca	Grazer (2)
<i>Limaria hians</i>	Mollusca	Filter feeder (1)
<i>Melarhapha neritoides</i>	Mollusca	Grazer (1)
<i>Nassarius</i> spp.	Mollusca	Scavenger (2)
<i>Nudibranchia</i> undefined	Mollusca	Predator (2)
<i>Ocenebra erinaceus</i>	Mollusca	Predator (2)
<i>Ocenebra</i> spp.	Mollusca	Predator (2)
<i>Ocenebra edwardsii</i>	Mollusca	Predator (2)
<i>Opalia crenata</i>	Mollusca	Grazer
<i>Patella</i> spp.	Mollusca	Grazer (2)
<i>Phorcus lineatus</i>	Mollusca	Grazer (2)
<i>Spurilla neapolitana</i>	Mollusca	Predator (2)
<i>Steromphala cineraria</i>	Mollusca	Grazer (2)
<i>Steromphala pennanti</i>	Mollusca	Grazer (2)
<i>Steromphala umbilicalis</i>	Mollusca	Grazer (2)
<i>Stramonita haemastoma</i>	Mollusca	Predator (2)
<i>Tenellia adspersa</i>	Mollusca	Predator (2)
<i>Tricolia</i> spp.	Mollusca	Grazer (2)
<i>Tritia incrassata</i>	Mollusca	Scavenger (2)
<i>Tritia reticulata</i>	Mollusca	Scavenger (2)
<i>Trivia monacha</i>	Mollusca	Predator (2)
<i>Leptoplana</i> spp.	Platyhelminthes	Predator (1)

**(b) Sessile macrofauna**

Annelida undefined	Annelida	
<i>Janua heterostropha</i>	Annelida	Filter feeder (2)
Serpulidae undefined	Annelida	Filter feeder (2)
<i>Spirobranchus</i> spp.	Annelida	Filter feeder (2)
<i>Sabellaria alveolata</i>	Annelida	Filter feeder (1)
<i>Chthamalus</i> spp.	Arthropoda	Filter feeder (2)
<i>Perforatus perforatus</i>	Arthropoda	Filter feeder (2)
Bryozoa undefined	Bryozoa	Filter feeder (2)
<i>Chartella</i> spp.	Bryozoa	Filter feeder (2)
<i>Ascidia</i> spp.	Chordata	Filter feeder (2)
<i>Botrylloides leachii</i>	Chordata	Filter feeder (2)
<i>Botryllus schlosseri</i>	Chordata	Filter feeder (2)
<i>Ectopleura larynx</i>	Cnidaria	Filter feeder (1)
Hydrozoa undefined	Cnidaria	Filter feeder (1)
<i>Botryllus schlosseri</i>	Cnidaria	Filter feeder (2)
<i>Anomia ephippium</i>	Mollusca	Filter feeder (1)
<i>Magallana gigas</i>	Mollusca	Filter feeder (2)
<i>Mytilus</i> spp.	Mollusca	Filter feeder (2)
<i>Ostrea edulis</i>	Mollusca	Filter feeder (2)
<i>Rocellaria dubia</i>	Mollusca	Filter feeder (1)
<i>Striarca lactea</i>	Mollusca	Filter feeder (1)
Porifera undefined	Porifera	Filter feeder (2)
<i>Aplysina</i> spp.	Porifera	Filter feeder (2)
<i>Cliona celata</i>	Porifera	Filter feeder (1)
<i>Sycon</i> spp.	Porifera	Filter feeder (2)