Coralline barrens and benthic mega-invertebrates: An intimate connection

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ABSTRACT

Despite considerable progress in understanding the transition from algal forests to coralline barrens, knowledge of coralline barren ecosystems in terms of community composition and functioning is still sparse and important gaps remain to be filled. Using a barren/forest patch system, we tested the hypothesis that the presence of coralline barren enhances the abundance and diversity of benthic mega-invertebrates. We also analysed trophic functional diversity through isotopic analyses of $\delta^{13}C$ and $\delta^{15}N$. The distribution of benthic mega-invertebrates biomass differed markedly between coralline barren and algal forest, being more abundant and diverse in the barren state. Isotopic diversity metrics of the benthic mega-invertebrates assemblage indicated comparable trophic structure between the two states, although higher isotopic uniqueness in coralline barren was determined by sea urchins, especially *A. lixula,* and carnivorous starfish. We showed that in a patchy coralline barren/algal forest system, a more diversified benthic mega-invertebrates assemblage in the barren caused limited trophodynamic changes. This was possibly determined by the behaviour of some trophic groups such as filter feeders, deposit feeders and omnivores. Finally, our results evidence the close association between coralline barrens and benthic mega-invertebrates, contradicting the common view of coralline barrens as depauperate habitats with low diversity and productivity.

1. Introduction

In the marine realm, overfishing in synergy with other anthropogenic stressors (i.e., habitat fragmentation, pollution, nutrient availability, global warming) is causing catastrophic regime shifts that are difficult to predict and costly to reverse (Costanza et al., 2007; Ling et al., 2015; Glasby and Gibson 2020). Notorious examples include the transition from coral reefs to macroalgal dominated habitat (McManus and Polsenberg 2004; Crisp et al., 2022), the collapse of coastal and oceanic fish stocks followed by jellyfish blooms (Purcell et al., 2007; Boero, 2013) and the shift from canopy kelp to algal turf or encrusting coralline algae (Filbee-Dexter and Scheibling 2014, Filbee-Dexter and Wernberg, 2018 and references therein). These regime shifts drive a significant erosion of ecosystem resistance and resilience to disturbance with potential dramatic consequences for ecosystem services provided (Levin and Lubchenco, 2008; Mancuso et al., 2018).

Canopy-forming brown algae (i.e. many species belonging to the order Fucales) are habitat formers that provide high-value ecosystem services with among the highest levels of primary production for submerged aquatic communities, they attract and support rich faunistic assemblages providing food and refuge for many species and enhancing

nutrient cycling, water quality and sediment stabilization (Bulleri et al., 2002; Steneck et al., 2002; Eger et al., 2023).

In the Mediterranean Sea, grazing of two common sea urchins *Paracentrotus lividus* (Lamarck, 1816) and *Arbacia lixula* (Linnaeus, 1758) can drive a transition from one complex and productive state, dominated by *Cystoseira* (*sensu lato*) spp. forests, to a simpler and less productive one, dominated by encrusting coralline algae, the so-called 'coralline barren state' (Estes et al., 2011; Bonaviri et al., 2011; Agnetta et al., 2013). It is widely accepted that coralline barrens are systems characterized by low primary productivity and complexity with prominent consequences in terms of ecosystem functioning, goods and services delivered to humans (Orfanidis et al., 2021). This paradigm intuitively conjures up in the collective imagination a "lifeless" perception of coralline barrens, where sea urchins generate an impoverishment of coastal fauna that uses *Cystoseira* (*sensu lato*) forests as shelter, recovery, food and settlement (Bianchelli et al., 2016; Cheminée et al., 2017; Pinna et al., 2020; Tamburello et al., 2022). The decline of macroalgal forest is documented in the Mediterranean Sea (Fabbrizzi et al., 2020; Tamburello et al., 2022) and there is growing interest in identifying processes that can enhance or prevent their restoration. In this context, knowledge of species composition which characterize the barren state

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can shed light on new potential interactions among species that in turn may generate self-perpetuating mechanisms (i.e., hysteresis) that maintain the barren state even if the initial conditions are restored (Scheffer and Carpenter, 2003; Baskett and Salomon, 2010; Gizzi et al., 2021; Bernal-Ibáñez et al., 2021). Notwithstanding considerable progress in understanding shifts between alternative stable states, biodiversity and trophic structure of the coralline barrens is still scant and important gaps remain to be filled. For instance, despite their low primary productivity, the smooth crustose surface of encrusting coralline algae sustains an unexpectedly diverse and abundant cryptic macro fauna (Chenelot et al., 2011). This may have in turn unforeseen effects on the overlooked benthic mega-invertebrates such as starfish, sea urchins, sponges, holothurians, bryozoans, polychaetes, echiurans, sea anemones and molluscs of large size.

Using a mosaic landscape, with interspersed patches of both coralline barren and *Cystoseira* (*sensu lato*) forests, we tested the hypothesis that the presence of coralline barrens increases the abundance and diversity of benthic mega-invertebrates. Furthermore, because of the different structure of the two algal assemblages (macroalgae vs encrusting coralline algae) a study based on stable isotopes of carbon and nitrogen was conducted to investigate the trophic structure and functioning of benthic mega-invertebrate assemblages in barren (BAR) and forest (FOR) state. In doing so, we built a possible new trophic vision (*sensu* Moore and de Ruiter 2012) of how a community at low biodiversity status can renovate thanks to the role played by neglected components such as the benthic mega-invertebrates. Such an information is important for evaluating possible solutions for the conservation and restoration of rocky shores worldwide, clarifying indirect multilayer effects, feedbacks, and emergent properties among taxonomic and ecological-functional groups.

2. Materials and methods

Study area. The study was performed during summer 2010, in the upper infralittoral of the volcanic "Ustica Island" Marine Protected Area (MPA), located in the north coast of Sicily (Western Mediterranean, $38°42'20''$ N-$10°43'43''$ E). The MPA of Ustica Island, created in 1986, encompasses a total area of 16,000 ha and contains three zones with different degrees of protection. The no take zone (zone A) extends for 65 ha along the western part of the island, whereas the general reserve (zone B) and the take zone (zone C) equally share the remaining area. Unlike other Mediterranean MPAs, the Ustica infralittoral zone developed in wide barren areas after protection enforcement (Gianguzza et al., 2006; Galasso et al., 2015) and until 2009 sea urchins, *P. lividus* and *A. lixula*, and encrusting corallines such as *Lithophyllum* spp., *Pseudolithophyllum expansum* (Philippi), *Lithothamnium* spp., *Mesophyllum coralloides* (J.Ellis) dominated the substrates of the no-take zone. In recent years, the recovery of mesopredators such *Martasterias glacialis* (L.) reduced sea urchin abundance (Galasso et al., 2015; Gianguzza et al., 2016) likely promoting the resurgence of *Cystoseira* (*sensu lato*) patches. This configuration provided a binary landscape dominated either encrusting coralline algae (BAR) and erected macro algae (FOR), forming a mosaic of interspersed patches of tens of meters in diameter (Gianguzza et al., 2010). We selected four random patches, two characterized by BAR and two by forest FOR, each 200 m apart, from a set of patches with similar orientation, water motion, and topography (Agnetta et al., 2013) (Fig. 1).

2.1. Data collection and processing

The abundance and biodiversity of benthic mega-invertebrates (invertebrates >20 mm total length *sensu* Moleon et al., 2020) were assessed in BAR and forest FOR patches to test the specific hypothesis that both variables are higher in BAR than FOR. Counts of benthic mega-invertebrates (number of individuals) were collected in the morning from 09:00 to 12:00 h by UVC (Underwater Visual Census)
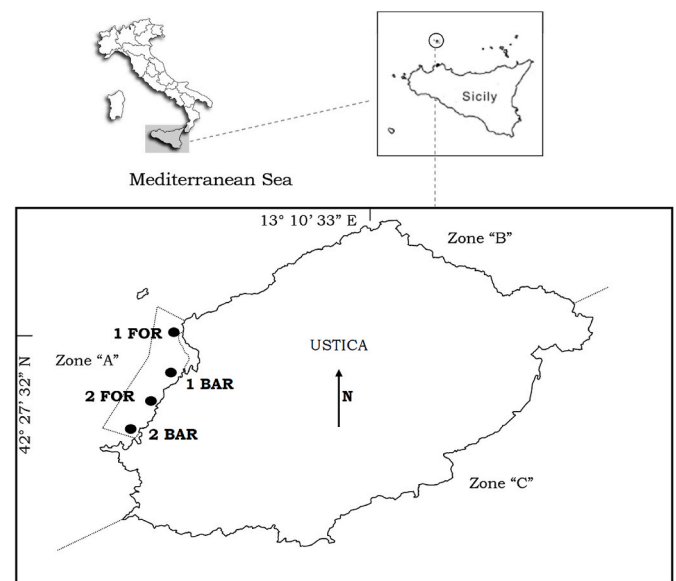

Fig. 1. Map of Ustica Island and sampling patches (1, 2) of each state (forest, FOR; barren, BAR).

along six strip transects of 50×5 m (250 m^2) parallel to the coast, at a depth of 5 m by two scuba divers. Due to cryptic behavior of some species (e.g., starfish and brittle stars), crevices and holes were carefully inspected (about 20 min per transect) while diving. Colonial taxa (e.g. Bryozoa, Porifera and Anthozoa) were sampled as number of colonies per transect (Wulff 2001).

Benthic mega-invertebrates were sampled with an experimental design that included two factors: State (St), fixed with 2 levels (FOR and BAR) and Patch (Pa), random and nested in State with 2 levels (1 and 2). There were 6 replicates for each combination of factors. Benthic mega-invertebrate abundances were compared between States by permutational MANOVA (Anderson 2001). Raw data were log transformed and analysis run on Bray Curtis similarity resemblance matrix. For each taxon ANOVAs (Underwood 1997) were also performed on Euclidean distance resemblance matrix.

Common diversity indices such as total abundance of individuals (N), number of species (S), Margalef's species richness (d), Pielou's eveness (J'), Shannon-Weaver's diversity (H' on log-e) and Simpson's index (1-λ) were calculated for each of the 24 samples, then single ANOVAs were performed for each diversity index by considering Euclidean distance resemblance matrix. All the analysis run on Primerv6 & Permanova+®.

The most important components of benthic mega-invertebrates, of each state, was also investigated by a Stable Isotope (SI) approach. Δ^{13}C and δ^{15}N data were used to test differences in isotopic functional diversity. Stable isotope (SI) analysis (primarily carbon (reported as δ^{13}C) and nitrogen (δ^{15}N) is a technique that has been used since the 1970s to characterize food webs (Deniro and Epstein 1978). Isotope fractionation events in living organisms most often result in the enrichment of the heavier isotope of nitrogen (increase in δ^{15}N) relative to food items, providing a relative estimate of trophic position. Carbon SI values show less enrichment between diet and organism and can be used to characterize carbon sources or organisms and food webs (see Peterson and Fry 1987; Hardy et al., 2010). Individuals of benthic mega-invertebrates were hand-collected by SCUBA divers from the central area of each of the 4 patches. To avoid variations in δ^{13}C and (mostly) δ^{15}N as a function of individual size, individuals of the same size were used for isotopic analysis. Given that starfishes have a remarkable capacity for arm regeneration (Lawrence and Larrain 1994; Di Trapani et al., 2020), we collected only a piece of an arm of starfishes as a replicate. In order to analyze sea urchins, the lantern muscle of *P. lividus* and *A. lixula* was extracted. The foot muscle of gastropods, muscles of holothurians and

whole body for all other species were used. The first centimeter of sediment was scraped to investigate the isotopic composition of the SOM (Agnetta et al., 2013).

All samples were sealed separately in plastic bags and preserved at −20 °C. Defrosted samples were dried at 60 °C (48 h) and ground to a fine powder (Caut et al., 2009). Samples were treated separately for $\delta^{15}N$ and $\delta^{13}C$ and prior $\delta^{13}C$ analyses, samples were acidified with drop-by-drop 2 N HCl to remove carbonates. C and N stable isotopes were analysed by a continuous-flow isotope-ratio mass spectrometer (Thermo Delta Plus XP) coupled to an elemental analyser CHN (Thermo EA 11112). Experimental precision, based on the standard deviation of replicates of the internal standard, was 0.2‰. Isotope ratios were expressed relative to PeeDee Belemnite (PDB) standard for carbon and to N_2 in air for nitrogen. Ratios were calculated by equation from literature (Peterson and Fry 1987). Bi-plots were drawn in order to visualize the isotopic structure of benthic mega-invertebrates relative to BAR and FOR. To consider the potential effect of lipid content we explored the data after applying the mathematical lipid normalization according to the equation proposed by Post et al., 2007. Normalization resulted in a $\Delta13C$ of 1.3 ± 0.5 for most organisms, therefore it was chosen to show the original isotopic values.

Moreover, the difference between the trophic structure of BAR and FOR was tested using the isotopic diversity metrics developed by Cucherousset and Villéger (2015). Accordingly, we calculated the following functional indices: i) the isotopic divergence (IDiv), that is a weighted distance between all organisms and the convex hull's centre of gravity. IDiv is minimal (i.e. tends to 0) when most of the points (weighted by species biomass) are close to the centre of gravity. On the opposite, IDiv tends to 1 when organisms with the most extreme stable isotope values dominate the food web. ii) the isotopic dispersion (IDis), a weighted deviation to the average position of points in the stable isotope space divided by the maximal distance to the centre of gravity. IDis equals 0 when all species have the same isotopic values and it increases to 1when most of the weighted points (organisms) show contrasted stable isotope values. iii) the isotopic eveness (IEve), quantifies the regularity in the distribution of organisms and of their weight along the shortest tree that links all the points. IEve tends to 1 when points are evenly distributed in the stable isotope space; iv) the isotopic uniqueness (IUni), measures how much pairs of neighbor species are isotopically different. This index equals 0 when each organism has at least one organism with the same position in the stable isotope space and tends to 1 when most of the organisms are isolated in the stable isotope space.

Finally, the total area (TA) estimated by the convex hull for BAR and FOR benthic mega-invertebrates were compared by overlap indices such as similarity and nestedness (Cucherousset and Villéger 2015), after evaluating the potential effect of the non-normal distribution of data (Fey et al., 2021, Fig.1SM). All isotopic indices and overlap were calculated in the R environment (R Core Team 2023 v. 4.3.1) following the script provided by Cucherousset and Villéger (2015).

3. Results

Abundance of benthic mega-invertebrates was significantly higher in BAR patches than in FOR ones (pseudo $F_{1,2} = 9.28$; P-MC = 0.002). A total of 14845 specimens belonging to 20 species and six taxonomic groups (Annelida, Bryozoa, Cnidaria, Echinodermata, Mollusca, Porifera) were surveyed in BAR and a total of 3961 specimens belonging to 17 species of the above-mentioned taxonomic groups were recorded in FOR. Cumulative abundance of *A. lixula* and *P. lividus* echinoids resulted the main component of the benthic mega-invertebrates (61.46% and 26.77% of the total number of benthic mega-invertebrates respectively), followed by cnidarians (*Anemonia viridis* (Forsskål, 1775) and *Aiptasia mutabilis* (Gravenhorst, 1831) 2.75% and 1.9% respectively). Univariate analysis showed that the starfish *Marthasterias glacialis* (L.), sea urchins *P. lividus* and *A. lixula*, holothurians *Holoturia tubulosa* (Gmelin, 1788) and *H. polii* (Delle Chiaje, 1824), serpulids *Protula* spp. and Arcidae were

significantly more abundant in BAR than in FOR paches. Moreover, *Coscinasterias tenuispina* (Lamarck, 1816), *Stramonita haemastoma* (Linnaeus, 1767), *Conus* spp. and *Patella caerulea* (Linnaeus, 1758) were species exclusively found in BAR whereas *Myriapora truncata* (Pallas, 1766) was met only in FOR patches (Table 1).

BAR and FOR patches are remarkably different in terms of benthic mega-invertebrate species richness (S): BAR host 8.58 ± 0.1920 (average number of species ± SE) while FOR 5.58 ± 0.35 (ANOVAs, Table 2). The other diversity indices calculated were not statistically significant (ANOVAs, Table 2).

Isotopic signatures (Fig. 2 bi-plot and Table 3) showed no separation between BAR and FOR species, while the suspended organic matter (SOM) of BAR resulted more enriched than that of FOR ($\delta^{13}C = −17.04 \pm 0.38$, $\delta^{15}N = 2.04 \pm 0.60$ and $\delta^{13}C = -18.99 \pm 0.53$, $\delta^{15}N = 1.85 \pm 0.51$ respectively) ($F_{1,2} = 19.35$, P = 0.046). Filter feeders such as Schizoporellidae, *M. truncata*, and Arciidae, were close to LM (leathery algae) in both states and to the SOM signature only in FOR. Omnivores such as *P. lividus*, *A. lixula*, *Ophidiaster ophidianus* and particulate feeders such as *Anemonia viridis* fell between SOM and EC (encrusting algae) baseline. The scavengers *Ophioderma* spp. and *Hexaplex trunculus* were at the top of trophic structures with the highest values of $\delta^{15}N$ in both

Table 1
Benthic mega-invertebrates. Mean density (ind./250 $m^2 \pm$ S.E.) values on BAR and FOR state (patches pooled) and analysis of variance between states (* = P < 0.05, ** = P < 0.01).

	BAR	FOR	ANOVA (state)	
Annelida				
Protula spp.	21.50 ± 3.86	1.08 ± 0.79	P = 0.03*	$F_{1,2} = 27.86$
Bryozoa				
Myriapora truncata	0	2.33 ± 0.85		
Schizoporellidae	5.07 ± 1.15	3.75 ± 0.99	P = 0.49	$F_{1,2} = 0.66$
Cnidaria				
Aiptasia mutabilis.	23.75 ± 5.21	26.58 ± 5.74	P = 0.79	$F_{1,2} = 0.09$
Anemonia viridis	34.04 ± 17.21	28.58 ± 19.63	P = 0.61	$F_{1,2} = 0.34$
Echinodermata				
Arbacia lixula	760.42 ± 101.27	98.33 ± 38.38	P = 0.043*	$F_{1,2} = 20.33$
Coscinasterias tenuispina	0.33 ± 0.18	0		
Holothuria spp.	7.25 ± 1.75	0.42 ± 0.22	P = 0.003**	$F_{1,2} = 349.63$
Marthasterias glacialis	2.33 ± 0.78	0.17 ± 0.11	P = 0.026*	$F_{1,2} = 35.05$
Ophidiaster ophidianus	2.92 ± 0.77	1.25 ± 0.54	P = 0.335·	$F_{1,2} = 1.55$
Ophiuroidea	3 ± 1.03	0.50 ± 0.25	P = 0.154.	$F_{1,2} = 5.17$
Paracentrotus lividus	331.25 ± 56.84	154.17 ± 46.94	P = 0.038*	$F_{1,2} = 23.73$
Mollusca				
Arcidae	21 ± 4.66	1.92 ± 0.95	P = 0.029*	$F_{1,2} = 31.31$
Buccinidae	2.5 ± 0.97	0.08 ± 0.08	P = 0.14	$F_{1,2} = 5.28$
Conus spp.	1.75 ± 0.86	0		
Hexaplex trunculus	5.83 ± 1.43	2.75 ± 1.03	P = 0.217	$F_{1,2} = 3.04$
Patella caerulea	4 ± 1.61	0		
Stramonita haemastoma	0.42 ± 0.14	0		
Porifera				
Irciniidae	0.5 ± 0.28	1.17 ± 0.44	P = 0.19	$F_{1,2} = 3.75$
Others Porifera	0.42 ± 0.18	0.17 ± 0.11	P = 0.46	$F_{1,2} = 0.79$
Spirastrella cunctatrix	7.08 ± 1.78	2.83 ± 0.69	P = 0.34	$F_{1,2} = 0.66$

Table 2

Diversity indices calculated for the two states and analysis of variance for each index. S = species richness, N = number of individuals, d = Margalef index, J' = Pielou index, H' = Shannon-Weaver index, 1-Lambda = Simpson index. Average ± E.S

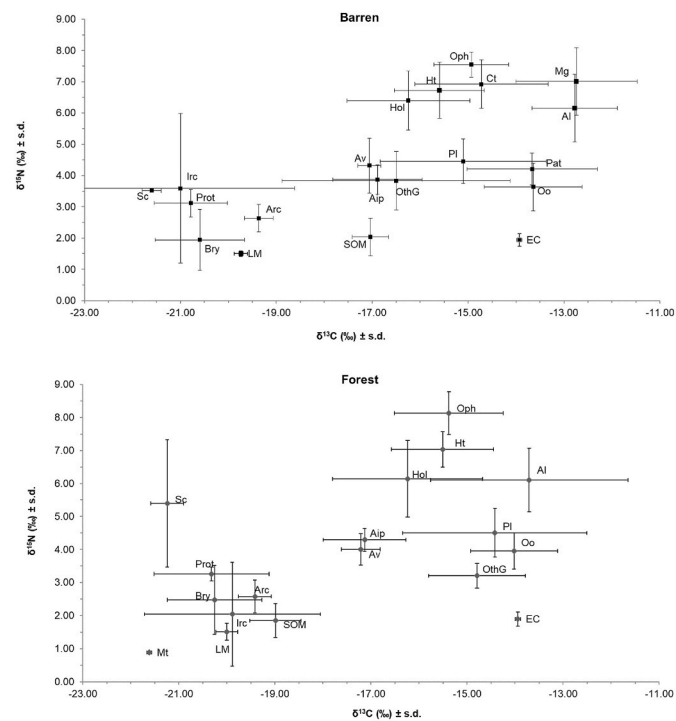|	N	S	d	J'	H'	1-λ
BAR	1237.08 ± 86.05	8.58 ± 0.19	1.07 ± 0.03	0.45 ± 0.03	0.98 ± 0.06	0.50 ± 0.04
FOR	330.08 ± 78.81	5.58 ± 0.35	0.87 ± 0.09	0.67 ± 0.04	1.14 ± 0.09	0.59 ± 0.04
ANOVA	$F_{1,2}$ = 0.009	$F_{1,2}$ = 0.019		n.s.	n.s.	n.s.

Fig. 2. Stable Isotopes diagram of benthic mega-invertebrates and SOM in barren and forest state (Aip = *Aiptasia* spp.; Al = *Arbacia lixula*; Arc = Bivalves [Arcidae]; Av = *Anemonia viridis*; Bry = Bryozoans [Schizoporellidae]; Ct = *Coscinasterias tenuispina*; Hol = *Holothuria* spp.; Ht = *Hexaplex trunculus*; Irc = Irciniidae; Mg = *Marthasterias glacialis*; Mt = *Myriapora truncata*; Oo = *Ophidiaster ophidianus*; Oph = *Ophioderma* spp.; OthG = Other gastropods; Pat = *Patella* spp.; Pl = *Paracentrotus lividus*; Prot = *Protula* spp.; Sc = *Spirastrella cuncatrix*; SOM = Sedimentary Organic Matter, *LM = *Cystoseira* spp. *sensu lato*, *EC = encrusting coralline), *data from Agnetta et al., 2013.

systems. Interestingly, the carnivores *M. glacialis* and *C. tenuispina* compound a uniqueness of barren and their position was just above the sea urchins.

IDiv and IDis isotopic diversity metrics, showed similar values comparing BAR and FOR state (Fig. 3). Sea urchins, especially *A. lixula*, and carnivorous starfish cause complementary indices such as IEv and IUni to be in the opposite direction. IEv was lower at BAR than at FOR, that is, isotopic values of points were less evenly distributed in BAR. IUni was higher (i.e. points more unique) at BAR state. Although abundant echinoderms determine several trophic differences, overall benthic mega-invertebrates in BAR and FOR yielded high overlap indices in terms of similarity and nestedness (Fig. 4).

4. Discussion

Research on encrusting coralline algae (i.e., all forms that grow

roughly radially on hard substrates and exhibit determinate thickness <1 cm) has recently expanded among marine ecologists, and geologists (McCoy and Kamenos, 2015). In most shallow temperate waters, coralline algae provide important ecosystem services: induce settlement and recruitment of numerous invertebrates and provide habitats for a variety of grazing and burrowing infauna (Chenelot et al., 2011; Adey et al., 2013). In addition, encrusting coralline algae are also of significant importance in the carbon and carbonate cycles of shallow coastal ecosystems, being major contributors to CO_2 fluxes through high community $CaCO_3$ production and dissolution (Van Der Heijden and Kamenos 2015; Noisette et al., 2013) and are used as paleo-ecological proxies (McCoy and Kamenos, 2015). Furthermore, they provide important species for contextualizing catastrophic regime shifts.

Recent studies consistently reported that loss of biodiversity is one of the major and most recurrent consequence of catastrophic regime shifts from FOR to BAR (Fabbrizzi et al., 2020; Tamburello et al., 2022). According to the 'mass ratio hypothesis' (Grime, 1998), dominant species, such as *Cystoseira* (*sensu lato*) are few in number, tall and more expansive in morphology and are considered more important in ecosystem functioning because of the large amount of biomass they produce. Subordinate species, such as encrusting coralline algae are generally more numerous, and form a low proportion of the total community biomass and thus are considered less important in ecosystem functioning.

Our results intriguingly show this was not supported by the data for benthic mega-invertebrates presented here, whose abundance and biodiversity were higher and tightly linked to the presence of encrusting corallines in BAR. BAR and FOR patches are remarkably different in terms of benthic mega-invertebrate species richness. This is due to the fact that the high number of individuals found in the BAR far exceeds the number of species and to the peculiar distribution of the number of individuals in each species (evenness), makes this state more diverse than FOR although diversity indices were not all statistically significant.

In the same way that FOR modify the *status* of macro and meio-fauna (Costa et al., 2018; Bianchelli and Danovaro, 2020) and affect the interactions with fish, BAR could play a fundamental role in attracting benthic mega-invertebrate species (Tuya et al., 2006; Rassweiler et al., 2010). Previous studies have suggested that encrusting coralline communities exhibit what is called consumer-mediated coexistence (Steneck et al., 1991; Dethier and Steneck 2001). The presence of grazers can overturn competition hierarchies by favouring grazer-resistant species over fast growing species (Steneck et al., 1991; Dethier and Steneck 2001). According to McCoy and Kamenos (2015) encrusting corallines in BAR can generally have both positive and negative interactions with grazers. They benefit from high levels of herbivory on erect species (Steneck 1983, 1986), and grazer presence may even stimulate local productivity of coralline crusts (Wai and Williams, 2005). Steneck (1983) suggested that in addition to sea urchins, limpets and chitons are able to graze coralline algae, showing several convergent adaptations for grazing hard substrates. The fact that limpets, grazers of the microalgal film, seem inhibited by the presence of erect macroalgae in FOR and they select only BAR patches as suitable habitat confirms Steneck (1983) suggestion. In contrast, the presence of an infaunal community structurally weakens the algal thallus (Steneck and Paine 1986; Adey et al., 2013) and may thus exacerbate potential effects of heavy grazing and excavating ability, above all of *A. lixula* and *P. lividus* on structural integrity of thick coralline algal crusts. Interestingly, Hind et al. (2019) showed that encrusting coralline algae, although more abundant, are significantly less diverse in urchin barrens than in macroalgal forests being dominated by few herbivore-tolerant coralline algae species.

In this consumer-mediated coexistence scenario, two types of feedback mechanisms could stabilize the BAR state and explain the benthic mega-invertebrates assemblage contribution to its diversity: processes that reduce *Cystoseira* (*sensu lato*) recruitment and processes that allow sea urchins to maintain high densities. Presence of sea urchins in BAR is enhanced by a chemical cue associated with encrusting coralline algae that induces settlement and metamorphosis of their larvae (Pearse and

Table 3

δ^{13}C and δ^{15}N mean values (‰) ± standard deviation (S.D.) of benthic mega-invertebrates at patch 1 and 2 of barren and forest state. SOM: sedimentary organic matter.

| Species/taxon | BAR | | | | | | | | | | FOR | | | | | | | | | |
| | Patch 1 | | | | | Patch 2 | | | | | Patch 1 | | | | | Patch 2 | | | | |
| | | δ^{13}C | | δ^{15}N | | | δ^{13}C | | δ^{15}N | | | δ^{13}C | | | | | δ^{15}N | | | |
	n	mean	s.d.	mean	s.d.	n	mean	s.d.	mean	s.d.	n	mean	s.d.	mean	s.d.	n	mean	s.d.	mean	s.d.
Echinodermata																				
Asteroidea																				
Marthasterias glacialis	11	−12.99	1.11	7.03	1.02	8	−12.40	1.44	6.99	1.22										
Coscinasterias tenuispina	5	−13.66	1.32	6.43	0.90	8	−15.38	1.02	7.23	0.52										
Ophidiaster ophidianus	10	−13.72	1.24	3.43	0.81	10	−13.56	0.80	3.84	0.07	5	−14.78	0.79	3.79	0.49	10	−13.64	0.72	4.04	0.58
Ophiuroidea																				
Ophioderma spp.	2	−15.30	0.09	7.79	0.46	2	−14.56	1.14	7.31	0.21	2	−14.85	1.54	7.85	0.97	2	−15.91	0.61	8.41	0.06
Echinoidea																				
Paracentrotus lividus	10	−14.84	1.62	4.62	0.55	10	−15.37	1.88	4.29	0.84	10	−15.06	1.83	4.70	0.40	10	−13.78	1.87	4.30	0.94
Arbacia lixula	10	−12.59	0.87	6.75	1.08	10	−12.96	0.92	5.56	0.73	10	−14.20	2.20	6.28	1.08	10	−13.21	1.88	5.93	0.86
Holothuroidea																				
Holothuria spp.	10	−15.50	1.36	5.86	0.88	10	−16.84	0.95	6.89	0.72	5	−16.11	0.15	7.09	0.13	8	−16.31	2.04	5.55	1.12
Mollusca																				
Hexaplex trunculus	10	−15.19	0.91	6.89	1.08	10	−16.00	0.81	6.55	0.69	6	−14.90	1.17	7.00	0.45	10	−15.87	0.86	7.05	0.60
Patella spp	9	−13.31	0.89	4.46	0.35	9	−14.02	1.69	3.96	0.55										
Arcidae	10	−19.52	0.23	2.57	0.48	6	−19.11	0.21	2.74	0.37	6	−19.55	0.43	2.68	0.38	6	−19.28	0.16	2.47	0.60
Other gastropods	5	−17.46	2.14	3.49	0.98	4	−15.30	2.34	4.26	0.81	3	−15.16	1.17	3.01	0.36	2	−14.24	0.55	3.50	0.12
Cnidaria																				
Anemonia viridis	4	−17.32	0.08	5.20	0.70	6	−16.88	0.06	3.73	0.24	6	−17.27	0.25	3.78	0.24	6	−17.15	0.53	4.23	0.56
Aiptasia spp.	10	−16.84	1.09	3.96	0.48	10	−16.93	0.80	3.78	0.45	5	−17.32	1.24	4.45	0.45	6	−16.97	0.43	4.16	0.19
Anellida																				
Protula spp.	11	−20.76	0.79	3.22	0.44	10	−20.81	0.78	3.00	0.43	4	−20.93	1.29	3.18	0.09	3	−19.50	0.28	3.37	0.30
Bryozoa																				
Schizoporellidae	6	−20.82	0.78	1.28	0.82	4	−20.26	1.16	1.24	1.07	1	−19.23		2.92		4	−20.51	0.92	2.36	1.17
Myriapora truncata											2	−21.53	0.02	0.86	0.02	2	−21.65	0.00	0.90	0.01
Porifera																				
Spirastrella cunctatrix	1	−21.74		3.50		1	−21.46		3.53		1	−21.72		3.48		4	−21.12	0.24	5.87	1.86
Irciniidae	2	−18.94	0.01	1.52	0.27	2	−23.06	0.01	5.66	0.09	2	−21.07	2.97	2.53	2.85	3	−19.10	0.06	1.72	0.70
SOM	3	−17.30	0.11	2.46	0.36	3	−16.80	0.07	1.65	0.08	3	−18.61	0.07	2.21	0.06	3	−19.31	0.11	1.86	0.65

BAR
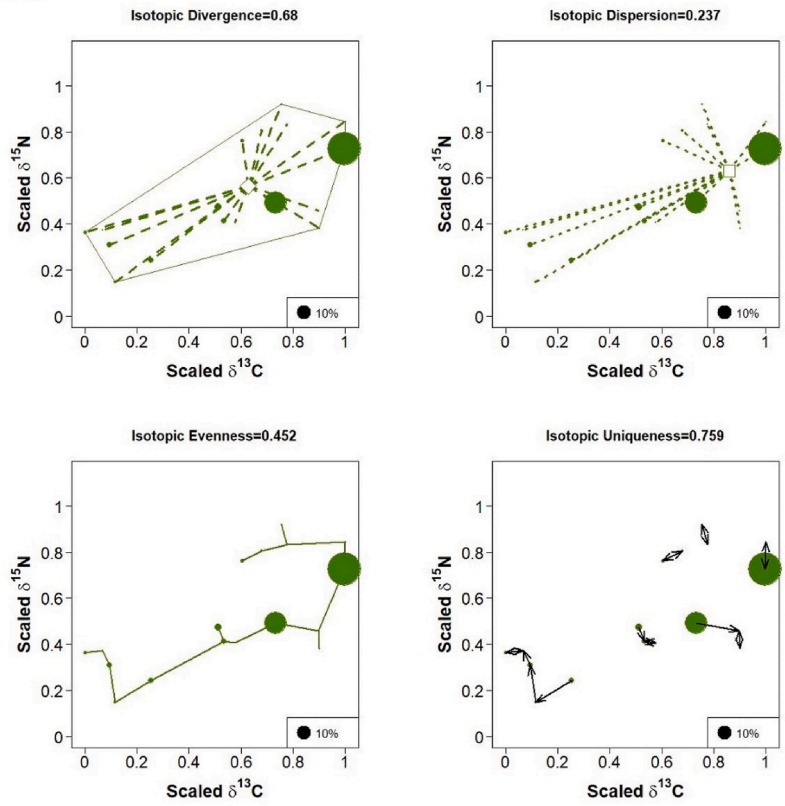
FOR
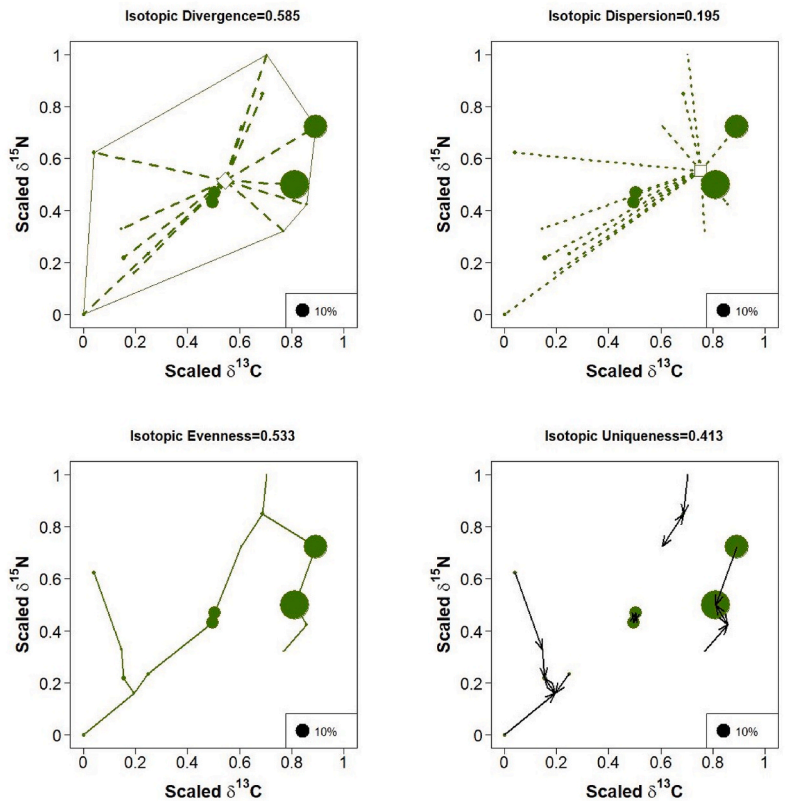
Fig. 3. Plots illustrating the four isotopic diversity metrics calculated from stable isotope values of benthic mega-invertebrates for BAR and FOR state.
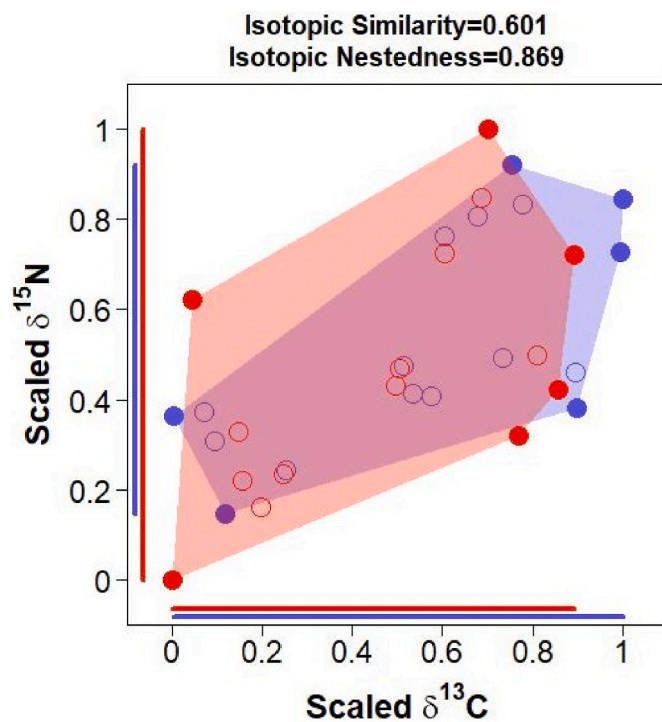
Fig. 4. Isotopic overlap metrics between organisms of benthic mega-invertebrates sampled in BAR (blu points and area) and FOR (purple points and area) in a two-dimensional isotopic space. Isotopic overlap metrics are measured using the isotopic richness of the two groups (i.e. convex hull volume represented by the red and blue areas, respectively) and the volume of isotopic space they shared (i.e. volume of their intersection, delimited by the purple line). Isotopic similarity is the ratio between the volume shared (purple area) and the volume of the union of the two convex hulls (delimited by full points). Isotopic nestedness is the ratio between the volume shared and the volume of the smallest convex hull (here in blue). Isotopic overlap on each stable isotope axis is illustrated by the overlap of the colored segments symbolizing range of values for each group.

Scheibling, 1990; Privitera et al., 2011). Therefore, by preventing *Cystoseira (sensu lato)* and other fleshy or filamentous macroalgae from overgrowing and outcompeting corallines, sea urchin grazing in barrens facilitates the supply of new individuals to the local population (Miner et al., 2006; Hernández et al., 2010). Thus, in BAR recruitment enhancement is a species-specific process that could favour a set of facilitation processes at local scale for some benthic mega-invertebrates (sea urchin and carnivorous starfish) species. Intense sea urchin grazing may drive change in rocky shore ecosystems by acting as a constraint for sessile epiphytic species associated to FOR (i.e. stressor), whilst providing opportunity for accumulation of benthic mega-invertebrates species particularly echinoderms in BAR (i.e. resource). Several studies carried out at Ustica Island suggested a facilitation model between the two co-occurring species *P. lividus* and *A. lixula* in the development of coralline barren, which in turn triggers their increase in density and biomass, facilitating and challenging food access for meso-predators (Bonaviri et al., 2009; Gianguzza et al., 2010, 2016; Agnetta et al., 2013, Agnetta et al., 2015). This is particularly true for the two large carnivore starfish *M. glacialis* and *C. tenuispina* that are found on the BAR almost exclusively. The strong trophic relationship between starfish and sea urchins, indeed, was seen in the isotopic signatures reported here and which was recently demonstrated for *M. glacialis* (Galasso et al., 2015; Gianguzza et al., 2016). The observed pattern can be explained by the opportunistic feeding behavior of this starfish that, as suggested by Branch (1978), selects its prey in relation to their abundance in the field.

In the BAR, the negligible presence of *Cystoseira (sensu lato)* and the

lack of its associated macrofauna may have allowed the development of particular detritus pathways in favour of filter feeders such as Arcidae, *A. mutabilis*, *A. viridis*, *Protula* spp, where in the BAR they easily met carrion deriving primarily from the carnivore starfish predation (Agnetta et al., 2013).

Also, the high abundance of deposit-feeders such holothurians in BAR could confirm the above-mentioned hypothesis, reinforcing the positive correlation among the great availability of profitable detritus presents in this habitat and some benthic mega-invertebrate species. A strong positive correlation between holothurians and sea urchins has been already documented (Tuya et al., 2006; Rassweiler et al., 2010). In particular, Tuya et al. (2006) argued that holothurians may profit of considerable amount of fresh particulate organic matter (POM) made available mainly from sea urchin's fecal pellets. In this study, isotopic signature of holothurians fitted only partially with SOM from BAR suggesting the SOM we collected did not totally coincide with the signature of sea urchin's fecal pellets or holothurians implemented their diet with other food items especially with regard to nitrogen provision. One possible explanation is that sea urchin fecal pellets are non-randomly distributed in the studied habitat but, rather, they show a patch distribution and should be collected as a separate source of food.

In the absence of erect macroalgae, sea urchins may alter their behaviour from passively feeding on drift-algae to actively roaming and scraping encrusting coralline and sessile invertebrates (Harrold and Reed, 1985). Recent studies highlighted that encrusting coralline in BAR can support a rich cryptic invertebrate community, partially composed by sipunculids (Chenelot et al., 2011). Results of a previous work showed that sipunculids were the main food assimilated by *A. lixula* providing 71% $\pm$ 7% (55%–88%) of the carbon and nitrogen while other guilds (suspension feeders, corticated foliose, calcareous algae, crustaceans omnivores, meso-herbivores, and particulate feeders, represented $\approx$5% each (Agnetta et al., 2013). This reinforces the hypothesis that infaunal borers could support the trophic web structure of the benthic mega-invertebrates in BAR. However, there is still a need for future investigation to evaluate the suggested hiding trophic interactions. This study suffers from the fact that it was carried out only during the summer season and that cryptic invertebrate community living under thick encrusting coralline stratum, despite its bare and barren appearance, was not sampled and included in the SI.

Despite the depauperate appearance of BAR, considered a system with lower biodiversity and production than FOR state, this study showed significantly higher species richness and abundance of benthic mega-invertebrate assemblages in BAR than in FOR patches. Our finding fit well with a recent study of Kingsford and Byrne (2023) conducted in the rocky reefs of New South Wales (NSW). These are characterized by a mosaic of habitats, including kelp forest and urchin-grazed barrens. These habitats support a diversity of dependent species. Decades of research have demonstrated that kelps form extensive forests with distinctive fish and invertebrate faunas and the 'barrens' boulder habitat provides shelter and other resources for commercial fishes, charismatic fishes and invertebrates; thus the barrens are not deserts (Kingsford and Byrne 2023). Since diversity of coralline crust assemblage (both taxonomic and functional) is affected by the shift from FOR to BAR state (Hind et al., 2019), it will be valuable in the future to understand how this diversity change drives ecological process (e.g.: structural-, chemical-, trophic-mediated process) involved in the relationship/link between coralline barren and its benthic fauna.

Stable isotopes indicated limited difference between state in isotopic diversity, this means that several sessile species could have acquired a mix of detritus coming from the two states. Mobile organisms instead, may have consumed food across different patches (Agnetta et al., 2013; Di Trapani et al., 2020) or, alternatively, it can be hypothesized that the organisms collected in FOR state were feeding mainly in the other state (e.g. BAR). The strength of trophic links is mediated by the biomass of predators and prey and since distribution of benthic mega-invertebrates was skewed in favour of BAR and several organisms appeared only in

these patches (i.e. carnivorous starfish), the last hypothesis seems to be more plausible and may explain the isotopic uniqueness resulting for coralline barren functional diversity. As subordinate species, encrusting coralline algae have no access to patches occupied by dominants erect macroalgae in FOR, but probably their better resource efficiency ("filter effects", Grime, 1998) allows them to establish in patches that dominants are not able to colonize. This mechanism leads towards spatial niche differentiation between BAR and FOR state and resource complementarity instead of resource competition.

Species diversity has two primary components: species richness (the number of species in a local community) and species composition (the identity of the species presents in a community) (Cleland, 2011). Although most research on the relationship between ecosystem diversity and stability has focused on species richness, the variation in species composition provides the mechanistic basis to explain the relationship between species richness and ecosystem functioning. The abundance of benthic mega-invertebrates and its diversity may indeed influence the amount and diversity of resources consumed by these group within the BAR patches (Tavares et al., 2019); in particular, benthic mega-invertebrates is composed mostly by mobile omnivores (e.g.: sea urchin and starfish) that are able to shift and broaden their diet with prey of different trophic levels affecting the trophic diversity of this group (Agnetta et al., 2013). The trophic diversity of the benthic mega-invertebrates found in the barren system has likely an effect on the efficiency by which these consumers capture resources and convert those into biomass (Hays et al., 2016), giving to this group of consumers a fundamental role in the transfer of energy. Our results evidence an intimate connection between coralline barrens and benthic mega-invertebrates, opposing the common view of coralline barrens as lifeless habitats, with low diversity and productivity. The overlooked benthic mega-invertebrates, which provide key ecosystem functions such as nutrient cycling, organic matter transport, sediment mixing, may substantially contribute to the secondary production in coralline barrens counterbalancing the significant reduction in biomass and biodiversity of meio and macrofauna observed in these ecosystems.

CRediT authorship contribution statement

Davide Agnetta: Conceptualization, Methodology, Writing – review & editing. **Chiara Bonaviri:** Methodology, Writing – review & editing. **Fabio Badalamenti:** Conceptualization, Writing – review & editing. **Francesco Di Trapani:** Data curation. **Paola Gianguzza:** Writing – review & editing.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106579.

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