

Research Article

Benthic megafauna and the functioning of macroalgal forests and urchin barrens

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Two temperate rocky reef food-web models, representing the trophic diversity of the Mediterranean rocky reef communities, were built for the two stable states: macroalgal forests and barren grounds, which are characterized by opposite amounts of erect macroalgal biomass. The food webs described here include 46 functional nodes or groups (comprising auto- and heterotroph species) and elucidate how the loss of erect macroalgal biomass from rocky reefs modifies the trophic roles of the different components of the community and how these changes modify its functioning. Results reveal that both alternative states exhibit a dominance of consumers of low trophic levels (TLs), with most of the energy flow occurring within the first three TLs. Detritus plays a significant role in energy recycling, with a substantial proportion of energy flowing into and from detritus in both alternative states. Transfer efficiency from detritus is higher than from primary producers, emphasizing the importance of recycling in supporting ecosystem stability. Functional group analysis indicates different biomass and production distributions between macroalgal forest and barren states, with corresponding rearrangements in the intensity of biomass flow as well as the roles of the distinct functional groups. Benthic megafauna covers different functional roles in barrens and supports a stable food web, counterbalancing the significant reduction in biomass and biodiversity of meio- and macro-fauna observed in this system. Network flow analysis



reveals similar complexity and meta-stability between the two systems, despite differences in primary production and energy utilization.

Keywords: benthic megafauna, Ecopath, Mediterranean community, rocky reef functioning, seurchins

Introduction

Macroalgal forests are among the most productive and biodiverse ecosystems worldwide (Steneck et al. 2002, Piazzzi et al. 2018, Pinna et al. 2020). They serve as a crucial link between coastal and pelagic systems, sustaining complex food webs (Steneck et al. 2002, Krumhansl and Scheibling 2012, Teagle et al. 2017, Vergés and Campbell 2020). Canopy-forming macroalgal species provide substratum and shelter for organisms, which consume their thallus or associated assemblages (Taylor 1998, Norderhaug et al. 2005, Thiriet et al. 2016), act as nursery grounds for pelagic and benthic organisms (Steneck et al. 2002, Graham 2004, Cheminée et al. 2017) and produce macroalgal detritus which fuels secondary production via the detritivore pathway (Duggins et al. 1989, Yorke et al. 2019). These processes concentrate living biomass, amplify secondary production, and connect shallow and deep ecosystems in coastal areas (Taylor 1998, Steneck et al. 2002, Filbee-Dexter and Scheibling 2014).

Canopy-forming macroalgae perform similar functional roles, despite the variation among species with different growth forms and life strategies (Bustamante et al. 2017, Chemello and Milazzo 2002, Cheminée et al. 2013, Eger et al. 2024, Piazzzi et al. 2018, Pinna et al. 2020). These range from fast-growing giant kelp, dominating temperate and arctic rocky coastlines, to smaller, long-lived *Fucales* (genera *Cystoseira*, *Ericaria* and *Gongolaria*, hereafter *Cystoseira* s.l.) dominating Mediterranean shallow rocky reefs (Steneck et al. 2002, Vergés and Campbell 2020). Irrespective of the dominant species, macroalgal forests face global threats from cumulative local and global anthropogenic stressors (Ling et al. 2015). Overfishing of predators leading to grazer population outbreaks, habitat destruction, water pollution, increases in seawater temperatures and heat waves, as well as consequent changes in species physiology and distribution have resulted in the loss of macroalgal forests across large areas worldwide (Guidetti 2006, Gianguzza et al. 2011, Sala et al. 2011, Bonaviri et al. 2017, Wernberg et al. 2018, Cvitković et al. 2024). Consequently, barren ground systems dominated by encrusting coralline algae and sea urchins develop and persist for years, representing an alternative meta-stable state of rocky reefs (Galasso et al. 2015, Ling et al. 2015, Glasby and Gibson 2020). Barren grounds exhibit relatively low structural complexity, diversity, and productivity, with their formation considered to have unexpected detrimental effects on ecosystem functioning in coastal rocky reefs (Filbee-Dexter and Scheibling 2014, Bianchelli and Danovaro 2020).

Sea urchin barren formation triggers different processes that contribute to their persistence. Sea urchins act as ecosystem engineers: their grazing pressure leads to the replacement

of erect, palatable algal species with encrusting, grazing-resistant species (Bulleri et al. 2002). Once a barren is formed, sea urchins may switch from a cryptic 'wait and sit' to a mobile foraging mode. By grazing on new thalli over large areas, they prevent the re-establishment of erect algae thereby maintaining the barren habitat (Dumont et al. 2004, 2006, MacGregor and Johnson 2022). Sea urchin population persistence is also favored by the reduction of micropredators of urchin recruits – such as crabs and shrimps – associated with erect algal canopies (Bonaviri et al. 2012, Pinna et al. 2024) and by food and shelter resources present in the barren (Agnetta et al. 2013). On Mediterranean rocky reefs, omnivorous scraper sea urchin species (i.e. *Arbacia lixula*) and herbivorous gastropods may establish alongside the original grazers (e.g.: *Paracentrotus lividus*), contributing to the stability of the barren system (Bonaviri et al. 2011, Agnetta et al. 2013, Piazzzi et al. 2016). Interestingly, benthic assemblages – including sponges, hydrozoans, bryozoans, polychaetes, echiurans, sipunculids, mollusks, ophiuroids and ascidians – associated with barren encrusting coralline algae can emerge (Ojeda and Dearborn 1989, Fanelli and Piraino 1998, Tuya et al. 2006, Włodarska-Kowalczyk et al. 2009, Chenelot et al. 2011, Galasso et al. 2015, Agnetta et al. 2024a). Despite the low structural complexity of 'barren' reefs, they host a substantial amount of living biomass, that persists over long periods (Agnetta et al. 2024a). This living component of the barrens may have unforeseen effects on trophic structure, energy flow, nutrient recycling, stability, productivity, as well as ecosystem connectivity in rocky reef systems.

Encrusting coralline algae, abundant in barren systems, are an important food resource for a wide range of grazers, including mollusks and echinoids (Manevelde et al. 2006). Sea urchins consume these algae directly and promote their rapid colonization on bare surfaces (Wai and Williams 2005, Agnetta et al. 2013). In barren areas where sea urchins are abundant, they capture drifting algal fragments and detritus transported by currents. Through grazing, they transform this material into smaller particles and fecal pellets available to benthic detritivores (Yorke et al. 2019). The continuous input of fresh particulate organic matter (POM) supports deposit feeders such as holothurians and sipunculid worms, which are generally more common in barren grounds than in macroalgal forests (Mamelona and Pelletier 2005, Tuya et al. 2006, Chenelot et al. 2011, Pinna et al. 2020, Agnetta et al. 2024a).

Additionally, the smooth surface of encrusting coralline algae sustains an unexpectedly diverse and sometimes abundant cryptic macrofauna, which may constitute food for large invertebrates and fish (Ojeda and Dearborn 1989, Chenelot et al. 2011, Agnetta et al. 2013, 2024a).

Sipunculids and sponges found in barrens (Pinna et al. 2020) may constitute part of the diet of larger benthic consumers, such as urchins and starfish (Agnetta et al. 2013, 2024a, Di Trapani et al. 2020). A rich benthic megafauna assemblage, including starfish, urchins, sponges, holothurians, bryozoans, polychaetes, echiurans, anemones and mollusks has been reported in Mediterranean barren grounds (Agnetta et al. 2024a). Although barren grounds are well-documented as alternative states to macroalgal forests in temperate rocky reefs, a comprehensive understanding of their food web structure and functioning remains limited, particularly concerning the role of organisms inhabiting barrens in mediating energy transfer.

Food web models are useful tools for depicting the properties of marine ecosystems and for studying the effects of community changes on their functioning (Coll and Libralato 2012). In this context, the mass-balance food-web model ECOPATH has been widely used in marine ecosystems to analyze trophic interactions and energy transfer among interconnected functional groups (hereafter FGs, each composed of groups of species with similar ecological and trophic roles). It helps to identify the FGs that have a significant effect on the ecosystem and characterizes the overall activity, size, maturity, energy export, metabolism, efficiency of energy utilization, and complexity of the ecosystem, as well as the effects of disturbance (Agnetta et al. 2022, Keramidas et al. 2023).

To compare the overall functioning of the two meta-stable alternative states of sublittoral rocky reefs systems in the Mediterranean Sea, two ECOPATH food-web models were constructed for barren and macroalgal forest systems, respectively, using field sampling of biomass and reference data from large, mature and shallow rocky systems dominated by either macroalgae forests or barren grounds off the Adriatic coast. This approach allows for a comparison between the two systems based on key network indices, such as production, energy fluxes, system complexity, and keystoneity. We expect higher production and greater system complexity in macroalgal forests compared to barren systems. Furthermore, we anticipate a reconfiguration of biomass flow intensities, potentially altering the functional roles of various groups within each state.

Material and methods

ECOPATH model

The two ECOPATH (www.ecopath.org; Christensen and Walters 2004) food-web models for the Mediterranean rocky reef were built to represent the macroalgal forest and barren stable state. ECOPATH describes yearly biomass and flows among functional groups (FGs) based on a quantitative mass-balance approach (Christensen and Walters 2004). ECOPATH balances energy flows and biomass among FGs, which represent species or groups of species with similar ecological roles and trophic status. FGs represent the studied rocky reef species and were chosen based on previous studies and literature for both forest and barren areas of the region

(Bianchelli et al. 2016, Pinna et al. 2020). The aggregation of species into functional groups was therefore based on a qualitative assessment. Species were aggregated into FGs based on similarities in ecological function, diet, habitat use, and size. In particular, the models include 12 fish groups, 11 groups of benthic megafauna (invertebrates size > 20 mm, Agnetta et al. 2024a), 15 groups of benthic macrofauna (invertebrate size range: 1–20 mm), and 1 group of meiofauna (invertebrate size range: 0.02–1.00 mm). Additionally, 2 plankton groups, 2 detritus groups and 5 benthic primary producer groups were considered. Single species components such as the sea urchins *P. lividus*, *A. lixula*, the bearded fireworm *Hermodice carunculata* and the octopus *Octopus vulgaris* were included on the basis of their abundance and ecological role (Table 1). In the construction of the models, fisheries were not included, as the study area is uniformly subject to heavy fishing pressure (RAC/SPA – UNEP/MAP 2013).

The energy equilibrium within and between FGs is maintained through two linear equations. The first one equates the production of each functional group (P_i) to predator consumption ($M2_i$), export from the system, other forms of mortality ($M0_i = 1 - \text{Ecotrophic efficiency, EE}$), and biomass accumulation (BA_i); the other equates food consumption (Q_i) to the sum of production (P_i), respiration (R_i), and the unassimilated food (UN_i) for each FG. Input parameters for each FG included biomass (B_i), production rate (P/B_i) (equivalent to total mortality rate), consumption rate (Q/B_i), dietary information (represented by the diet matrix DC_{ij} , indicating the fraction of prey i in the diet of predator j), and the unassimilated food ratio (UN_i) for each group. The model typically estimates gross food conversion efficiency (P/Q), respiration rate (R/B), and the proportion of production either consumed within the system by predators or exported (known as ecotrophic efficiency, EE) for each group. This enables an assessment of whether the food web model is well set (PREBAL, Link 2010) and balanced ($EE < 1$ for all groups; with higher values typically observed for top predators and smaller organisms, Christensen and Walters 2004).

In order to better define the functional role of the different FGs we considered four different food-web indicators: 1) total absolute flow, defined as the contribution of each FGs to the sum of all flow in the ecosystem (total flow); 2) relative ascendancy, the contribution of each FG to the ascendancy, which measured the degree of organization of the ecosystem and its ability to cope with perturbations; 3) keystoneity (Libralato et al. 2006), which individuated keystone FGs, i.e. those FGs with low biomass but nevertheless able to induce large change in the biomass of other FGs; 4) overall relative effect, which measures the impact that a small change in the biomass of a FG has on the biomass of all other FGs in the food web. Both keystoneity and overall relative effect were obtained from the mixed trophic impact (Libralato et al. 2006).

Ecological indicators of the entire food webs were calculated based on network analysis. We considered total system throughput (TST) as a measure of size of the system and its

Table 1. Description of the functional groups.

No.	Group name	Short description	Taxon
1	PesUAd	fish preying upon adult sea urchin	<i>Diplodus sargus</i> , <i>Diplodus vulgaris</i>
2	PesUJu	fish preying upon juvenile sea urchin	<i>Coris julis</i> , <i>Thalassoma pavo</i>
3	PesPePL	pelagic planktivore fish	<i>Atherina boyeri</i>
4	PesNO	benthopelagic omnivore fishes	<i>Liza aurata</i> , <i>Mugil cephalus</i>
5	PesNPL	benthopelagic planktivore fish	<i>Boops boops</i>
6	PesNP	benthopelagic piscivore fishes	<i>Dentex dentex</i> , <i>Epinephelus costae</i> , <i>Epinephelus marginatus</i>
7	PesNE	benthopelagic herbivore fishes	<i>Sparisoma cretense</i>
8	PesNC	benthopelagic carnivore fishes	<i>Apogon imberbis</i> , <i>Chromis chromis</i> , <i>Dicentrarchus labrax</i> , <i>Diplodus annularis</i> , <i>Diplodus puntazzo</i> , <i>Labrus merula</i> , <i>Oblada melanura</i> , <i>Seriola dumerilii</i> , <i>Serranus cabrilla</i> , <i>Serranus scriba</i> , <i>Sparus aurata</i> , <i>Spondyllosoma cantharus</i> , <i>Symphodus cinereus</i> , <i>Symphodus doderleini</i> , <i>Symphodus mediterraneus</i> , <i>Symphodus melanocercus</i> , <i>Symphodus ocellatus</i> , <i>Symphodus roissali</i> , <i>Symphodus rostratus</i> , <i>Symphodus tinca</i>
9	PesCrO	cryptic omnivore fishes	<i>Gobius buccichi</i> , <i>P. sanguinolentus</i> , <i>Parablennius rouxi</i> , <i>Parablennius zvonimiri</i>
10	PesBP	benthic piscivore fishes	<i>Muraena helena</i>
11	PesBE	benthic herbivore fishes	<i>Sarpa salpa</i>
12	PesBC	benthic carnivore fishes	<i>Mullus surmuletus</i> , <i>Scorpaena porcus/maderensis</i>
13	Octvu	octopus	<i>Octopus vulgaris</i>
14	Arlix	sea urchin	<i>Arbacia lixula</i>
15	Paliv	sea urchin	<i>Paracentrotus lividus</i>
16	Hermo	fireworm	<i>Hermodice carunculata</i>
17	Ophiu	brittle star	<i>Ophiura</i> spp.
18	MTunF	tunicates	<i>Halocynthia papillosa</i> , <i>Microcosmus</i> spp.
19	MSclF	stony corals	<i>Balanophylla</i> spp.
20	MPorF	sponges	<i>Protula</i> spp., <i>Chondrilla nucula</i> , <i>Chondrosia reniformis</i> , <i>Cliona</i> spp., encrusting red sponge, <i>Ircinia</i> spp., <i>Keratosia</i> , <i>Petrosia</i> spp.
21	MPolF	polychaetes, filter feeders (>2cm)	<i>Protula</i> spp., <i>Sabella spallanzani</i> , <i>Terebellidae</i>
22	MOloD	sea cucumber	<i>Holothuria forskali</i> , <i>Holothuria tubulosa</i> , <i>Holothuria polii</i>
23	MMolS	whelk	<i>Hexaplex trunculus</i>
24	MMolF	bivalves	<i>Arcidae</i> , <i>Gastrochaena</i> spp., <i>Ostrea edulis</i>
25	MBriF	bryozoans	<i>Schizoporellidae</i>
26	MAstO	omnivore starfish	<i>Echinaster sepositus</i> , <i>Hacelia attenuata</i> , <i>Ophidiaster ophidianus</i>
27	MAstC	carnivorous starfish	<i>Marthasterias glacialis</i>
28	meiof	meiofauna	<i>Nematodes</i> , <i>Priapulida</i> , <i>Gnathostomulida</i> , <i>Gastrotricha</i> , <i>Holothuroidea</i> and <i>Thermosbanacea</i> , <i>Copepoda</i> , <i>Gastropoda</i> , <i>Halacaroidea</i> , <i>Cnidaria</i>
29	mSipD	Sipuncula	
30	mPolFf	filter feeder polychaetes	
31	mPolE	herbivore polychaetes	
32	mPolD	detritivore polychaetes	
33	mPolC	carnivore polychaetes	
34	mMolLO	omnivore gastropods	
35	mMolIF	filter feeder molluscs	
36	mMolIE	herbivore molluscs	
37	mMolIC	carnivore molluscs	
38	mDecO	omnivore decapods	
39	mAmpO	omnivore amphipods	
40	mAmpF	filter feeder amphipods	
41	mAmpD	detritivore amphipods	
42	mAmpC	carnivore amphipods	
43	ZooPL	zooplankton	
44	PhytoPL	phytoplankton	
45	Encr	encrusting coralline algae	
46	Turf	turf algae	
47	EA	corticated algae	
48	Cys	leathery macrophyte	
49	Mphyto	microphytobenthos	

metabolism (Ortiz-Zayas et al. 2005). TST consists of total consumption (TC), total exports (TEX), total respiration (TR), and total flows into detritus (TDET). To characterize the overall activity of the ecosystem, we considered total primary production (TPP) and total biomass (TB) (Ortiz-Zayas et al. 2005). Net system production (NSP), which consists in the value of the difference between TPP and TR, represents the sum of the productivity of all producers. The ratio TPP/TR quantifies system maturity (Odum 1969, Christensen 1995). The connectance index (CI) and system omnivory index (SOI) reflect the complexity of the internal connections within the system (Christensen and Walters 2004).

The initial ECOPATH model, constructed on the input parameters outlined in the Supporting information, underwent an evaluation through a pre-balancing analysis (PREBAL) (Link 2010, Heymans et al. 2016), which assesses the coherence of data with fundamental ecological principles. Several diagnostics were employed in this study to examine: biomass variation across taxa/trophic levels (with biomass ideally spanning 5–7 orders of magnitude and exhibiting a slope of 5–10% decline on a logarithmic scale), vital rates across taxa/trophic levels (expected to generally decline with increasing trophic level), the growth efficiency rate P/Q (ideally < 0.5), the respiration/assimilation rate (expected to be < 1), and the ecotrophic efficiency (EE) (expected to be < 1). Moreover, ECOPATH can provide an instantaneous estimate of trophic flow for a given reference season/year averaging window. The calculations assumed mass balance; however, in several cases, biomasses may have changed over the period for which reference data (B, P/B, Q/B, diet composition) were collected. In these cases, assuming equilibrium during the reference period could lead to overly optimistic model outputs estimates. To address this uncertainty and assess whether differences in key outputs, such as total production between the two systems, were consistent, an ensemble of balanced models was built for each State (BAR versus FOR) by randomly resampling the main parameters (Supporting information).

Data source

The estimation of the mean biomass of each benthic organisms in barren grounds and macroalgal forest models was based on data collected during two sampling campaigns conducted in June 2014 and June 2015. Sampling was conducted at two sites, (Molunat) Croatia and Tivat (Montenegro), approximately 100 km apart. At each site, two areas characterized by mature barren grounds and macroalgal forests – both of which have been present for over a decade (Bonaviri et al. unpubl.) – were randomly selected, approximately 100 meters apart, at a depth of 6 meters (Fig. 1).

During the sampling campaigns, benthic organisms were collected within surfaces of 400 cm² integrating air-lift sample and scraping (Piazzi et al. 2018, Pinna et al. 2020). Visual censuses of megafauna and fishes were conducted along strip transects of 50 × 5 m (250 m²) (Harmelin-Vivien and Harmelin 1975, Agnetta et al. 2024a). Mean macroalgal biomass was measured as dry weight, while microphytobenthos biomass was estimated in relation to macroalgal biomass. Macrofauna biomass was measured either as dry weight (for mollusks with exoskeleton and polychaetes) or based on experimental measures of abundance and average body mass of the species collected (crustaceans). Megafauna and fish biomass were calculated using abundance data and published length–weight relationships. Biomass for lower trophic levels, such as zooplankton, phytoplankton, as well as detritus groups, was estimated from outputs of the Adriatic Sea ECOPATH models (Piroddi et al. 2015). All biomass values were expressed as dry weight, with conversion factors applied where appropriate (Ricciardi and Bourget 1998, Reed et al. 2016). Species-specific parameters and dietary data were compiled mainly from both published and unpublished information, as detailed in the Supporting information.

Input of the models such as biomass, parameters (i.e. production per unit of biomass, P/B; and consumption per unit biomass, Q/B, were estimated from empirical parameters) and diet of each FG were obtained as the weighted average of the values available for the species in that group (Table 2),

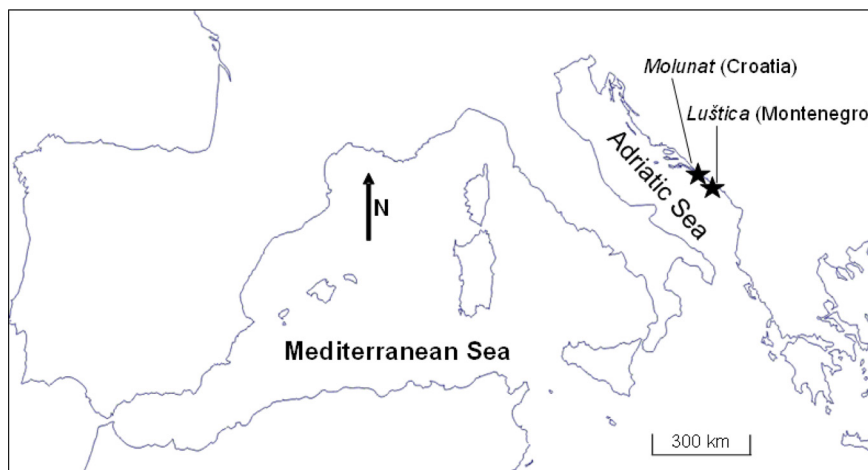


Figure 1. Map of the study sites.

Table 2. Final parameters for ECOPATH models representing the macroalgal forest and barren ground alternative states of the Mediterranean rocky subtidal ecosystem. TL stands for trophic level, B stands for biomass [as tons per km², in dry weight], P/B for turnover rate [as year⁻¹], Q/B for consumption rate [as year⁻¹], EE for ecotrophic efficiency, and P/Q for gross food conversion efficiency.

No. and group name	Forest	Barren	Forest	Barren	P/B	Q/B	Forest	Barren	Forest	Barren
	TL		B				EE		P/Q	
1.PesUAd	2.7	2.7	0.5	0.5	1.7	5.4	0.0000	0.0000	0.3148	0.3148
2.PesUJu	2.4	2.5	0.1	0.2	1.7	5.4	0.0000	0.0000	0.3148	0.3148
3.PesPePL	2.7	2.7	0.0	0.0	0.9	10.3	0.9439	0.3490	0.0913	0.0913
4.PesNO	2.9	2.9	0.0	0.1	1.1	10.8	0.7366	0.7920	0.0991	0.0991
5.PesNPL	3.0	3.0	0.0	0.0	1.4	5.0	0.9494	0.6074	0.2700	0.2700
6.PesNPL	2.9	2.9	0.1	0.0	0.6	2.6	0.5213	0.4288	0.2190	0.2192
7.PesNPL	2.0	2.0	0.1	0.0	0.8	12.0	0.3204	0.2440	0.0648	0.0648
8.PesNC	2.5	2.6	0.7	0.4	1.6	5.3	0.4961	0.8247	0.2996	0.3047
9.PesCrO	2.3	2.3	0.0	0.0	0.7	5.7	0.5199	0.9333	0.1272	0.1272
10.PesBP	3.3	3.3	0.0	0.0	0.7	3.2	0.6363	0.8070	0.2200	0.2188
11.PesBE	2.0	2.0	0.1	0.0	0.8	3.9	0.1019	0.9202	0.2000	0.2000
12.PesBC	2.9	3.0	0.0	0.1	1.0	4.3	0.8534	0.2156	0.2188	0.2194
13.Octvu	2.1	2.9	0.3	0.1	1.8	12.0	0.0726	0.1895	0.1477	0.1477
14.Arlx	2.2	2.0	2.4	30.6	0.5	2.9	0.1335	0.0124	0.1742	0.1742
15.Paliv	2.0	2.0	9.8	54.2	0.4	1.5	0.0615	0.0120	0.2397	0.2403
16.Hermo	2.3	2.2	0.0	0.1	6.2	31.1	0.0000	0.0000	0.2000	0.2000
17.Ophiu	2.6	2.5	0.1	0.0	2.7	12.2	0.4791	0.9360	0.2182	0.2181
18.MTunF	2.0	2.0	1.2	1.4	0.4	3.6	0.0397	0.2724	0.1052	0.1050
19.MScIF	2.0	2.0	0.0	0.1	1.4	6.0	0.0106	0.0724	0.2383	0.2383
20.MPorF	2.0	2.0	37.3	32.4	0.02	0.8	0.8838	0.7328	0.0225	0.0250
21.MPolF	2.0	2.0	0.0	0.0	6.2	15.5	0.8205	0.1874	0.4016	0.4015
22.MOlD	2.0	2.0	0.2	0.4	0.4	3.3	0.0346	0.2352	0.1310	0.1317
23.MMolS	2.2	2.2	0.0	0.4	4.0	22.2	0.0036	0.0471	0.1800	0.1800
24.MMolF	2.0	2.0	0.0	1.0	6.3	29.9	0.6388	0.2688	0.2100	0.2100
25.MBrIF	2.0	2.0	0.0	0.1	0.2	0.8	0.7256	0.8559	0.2500	0.2500
26.MAstO	2.2	2.3	0.6	0.5	0.5	3.2	0.0311	0.2182	0.1512	0.1512
27.MAstC	3.1	3.1	0.0	0.1	0.3	1.3	0.0000	0.0000	0.1970	0.1970
28.meiof	2.0	2.0	0.2	0.0	9.0	36.0	0.5908	0.6571	0.2500	0.2500
29.mSipD	2.0	2.0	3.3	2.6	8.0	32.0	0.2400	0.2482	0.2500	0.2501
30.mPolFf	2.0	2.0	0.7	0.1	6.2	15.5	0.0684	0.4781	0.4016	0.4015
31.mPolE	2.0	2.0	0.6	0.0	6.2	15.5	0.0269	0.7771	0.4016	0.4015
32.mPolD	2.0	2.0	1.1	0.1	6.2	15.5	0.0340	0.8818	0.4016	0.4015
33.mPolC	2.1	2.1	2.6	0.4	6.2	15.5	0.0578	0.6549	0.4016	0.4015
34.mMolO	2.0	2.0	0.0	0.0	6.8	29.5	0.0984	0.9755	0.2298	0.2297
35.mMolF	2.0	2.0	0.1	0.1	6.3	29.9	0.8246	0.8836	0.2100	0.2100
36.mMolE	2.0	2.0	0.0	0.0	0.3	11.7	0.1998	0.8526	0.0291	0.0291
37.mMolC	2.5	2.5	0.0	0.0	6.8	37.2	0.7123	0.9097	0.1824	0.1823
38.mDecO	2.1	2.1	0.1	0.0	2.1	11.2	0.2128	0.7510	0.1851	0.1848
39.mAmpO	2.0	2.2	0.5	0.0	6.0	27.8	0.0353	0.9402	0.2156	0.2157
40.mAmpF	2.0	2.0	0.0	0.0	6.0	27.8	0.6690	0.6987	0.2156	0.2157
41.mAmpD	2.0	2.1	0.7	0.0	6.0	27.8	0.0238	0.8728	0.2156	0.2157
42.mAmpC	3.0	3.0	0.0	0.0	6.0	27.8	0.1664	0.8146	0.2156	0.2157
43.ZooPL	2.0	2.0	0.1	0.1	34.7	115.8	0.3150	0.1870	0.3000	0.3000
44.PhytoPL	1.0	1.0	0.3	0.3	115.8		0.2930	0.2930		
45.Encr	1.0	1.0	19.3	361.8	0.9		0.1596	0.2332		
46.Turf	1.0	1.0	260.9	23.0	2.0		0.0362	0.8028		
47.EA	1.0	1.0	117.6	3.7	1.9		0.0403	0.9127		
48.Cys	1.0	1.0	190.0	12.2	1.5		0.0238	0.0161		
49.Mphyto	1.0	1.0	0.1	0.1	210.0		0.2749	0.1239		
50.POM	1.0	1.0	0.2	0.2			0.2108	0.9975		
51.Detritus	1.0	1.0	0.2965	0.297			0.1863	0.3862		

with the proportion of local species biomass (or prey weight for diet) within the group used as the weighting factor.

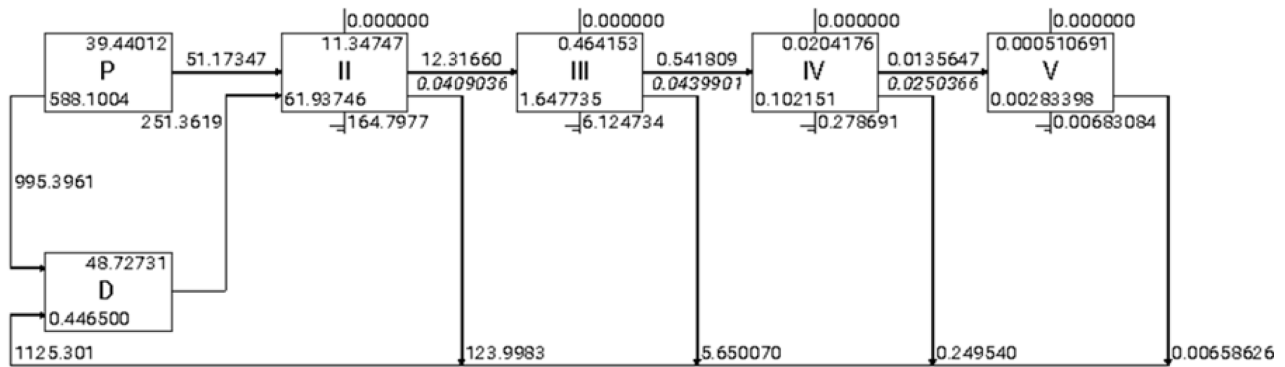
Results

Energy flow in in forest and barren states

According to the two balanced models, barren and macroalgal forest states of Mediterranean sublittoral rocky ecosystems include seven and six discrete trophic levels, respectively. Most energy transfer occurs within the first three levels, accounting for over 99% of total system throughput (TST)

in both alternative states (Fig. 2). Biomass decreases with increasing trophic levels, aligning with the vertex-up (apex-down) Eltonian pyramid model (Fig. 2). TL 1 includes detritus, macroalgae, phytoplankton and microphytobenthos, while the higher TLs include macrofauna, megafauna, and fish. Carnivorous amphipods, the benthopelagic planktivorous fish *Boops boops*, the carnivorous starfish *Marthasterias glacialis*, and the benthic piscivorous *Muraena helena* exhibit higher values at TL 3 or above in both food webs. Energy flows in both models either derive directly from detritus or indirectly from primary production through detritus- and grazing-based food chains (Fig. 2). The Lindemann spine

FOREST



BARREN

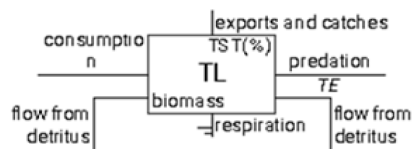
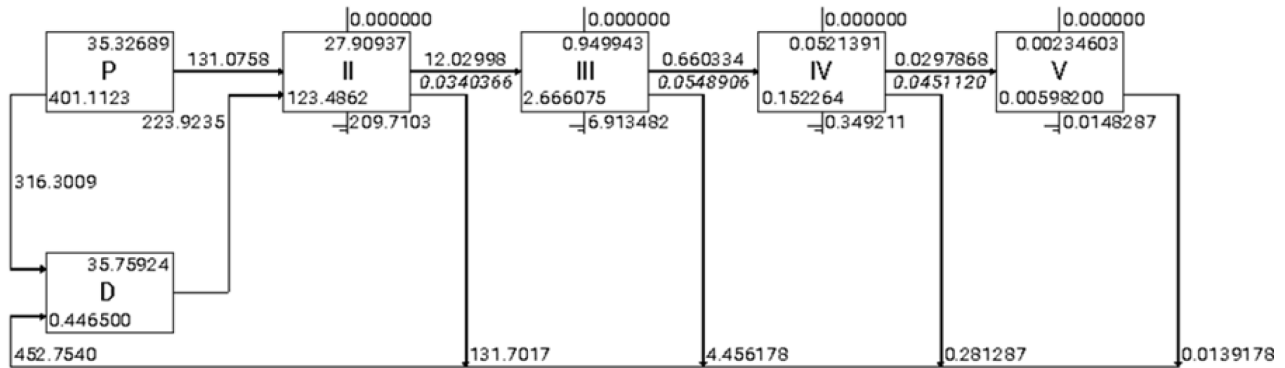


Figure 2. Lindeman spine diagram of macroalgal forest and barren grounds ecosystems of Mediterranean rocky reef, only the first five levels are presented.

illustrates a significant proportion of energy flow from the first to the second level and into the detritus pool. The total energy input into the detritus pool amounts to 452.75 and 1125.30 t km⁻² year⁻¹ in barren and forest ecosystems, respectively, with primary producers contributing 88.45% in forests and 69.86% in barren ecosystems, and TL II taxa contributing 11.02% and 28.92%, respectively. The total primary production (TPP) in macroalgal forest and barren ground ecosystems was 1046.09 and 446.98 t km⁻² year⁻¹, respectively, with 95.15% and 70.76% of this production flowing into detritus (Fig. 2). A total of 224 and 251 t km⁻² year⁻¹ of detritus was consumed by TL II, with 123 and 131 t km⁻² year⁻¹ returning to the detritus pool in barren and forest states, respectively.

Overall, the mean trophic efficiency (MTE) in the forest ecosystem (3.56%) was slightly lower than in the barren state (4.38%). These values are below the generally expected Lindeman efficiency of 10%, indicating low MTE values consistent with findings from extensive meta-analyses of marine ecosystem models (Heymans et al. 2014). The MTE from detritus was higher than that from primary producers in both ecosystems. Moreover, the MTE from detritus was higher in the barren than in the forest state (4.98% versus 3.70%), while the MTE from primary producers showed low values in both ecosystems (2.52% and 2.54% in forest and barren models, respectively). Based on the Lindeman spine, the highest transfer efficiency was observed in TL II for both systems.

Biomass and production distribution in forest and barren states

Macroalgal forest and barren grounds were characterized by distinct distributions of biomass and production among the groups considered: high amounts of erect algae in the forest state correlate with increased biomass and production of meiofauna and macrofauna, while large amounts of crustose coralline algae in the barren state correspond to high biomass and production of megafauna (Table 2, Fig. 3). Despite both states feature the same trophic links, the different biomass allocation between them indicates a reconfiguration of biomass-flow intensities, affecting the potential roles of various functional groups within each state.

Total flow (TF) and flow to detritus from encrusting algae, microphytobenthos and megafauna are higher in the barren ground food web than in the macroalgal forest food web. In contrast, erect algae, meiofauna and macrofauna show higher values of TF in the forest state (Fig. 4, 5). In the barren state, encrusting coralline algae (FG 45) exhibit the highest values of both total flow (TF) and relative ascendancy. Conversely, in the forest state, the highest values are observed for corticated algae (FG 47), leathery macrophytes (FG 48) and turf (FG 46) (Fig. 3).

Regarding metazoans, the omnivorous sea urchins *A. lixula* (FG 14) and *P. lividus* (FG 15), along with carnivorous starfish (FG 27), show a notable difference in total flow (TF) and relative ascendancy from the forest to the barren state. Conversely, polychaetes (FGs 30, 31, 32, 33) and amphipods

(FGs 39, 41, 42) showed higher values in the macroalgal forest state (Fig. 3). Sipunculid worms (FG 29) and sponges (FG 20) maintain consistently high values of TF and relative ascendancy in both states.

These trends influence the overall relative effects and keystone indices for the two alternative states. For example, megafauna such as omnivorous sea urchins (FGs 14 and 15), omnivorous and carnivorous starfish (FGs 26 and 27), the scavengers *Hermodice carunculata* and *Hexaplex trunculus* (FGs 16 and 23), and bivalves (FG 24) exhibited higher values of overall relative effects in the barren state than in forest state (Fig. 3). In contrast, macrofauna groups comprising omnivores, herbivores and detritivores – show an opposite trend (Fig. 3).

Among invertebrate groups, the fireworm *H. carunculata* (FG 16) and the sea urchin *P. lividus* (FG 15) showed the highest values of keystone indices in the barren ground food web, whereas brittle stars (FG 17) held that distinction in the macroalgal forest web (Fig. 3). Regarding fish, predators of adult sea urchins and benthopelagic carnivorous fish (FGs 1 and 8) showed high values of overall effect and keystone index in both food web models (Fig. 3).

Network flow indicators

Summary statistics and indicators of network flow and ecosystem structure for the food webs of each alternative state of Mediterranean rocky sublittoral communities are presented in Table 3. In the barren ground state, the total system throughput (TST) was 1266.42 t km⁻² year⁻¹, with total consumption (TC) contributing 29.04%, total exports (TEX) 18.07%, total respiration (TR) 17.13%, and total flow into detritus (TDET) 35.76%. Conversely, in the macroalgal forest state, TST reached 2616.86 t km⁻² year⁻¹, with TC accounting for 12.05%, exports for 32.76%, respiration for 6.54%, and flow to detritus for 48.65%.

Although both food webs exhibited high TDET values, it was notably higher in the macroalgal forest state, indicating that recycling was the primary means of energy utilization in both states, with energy underutilization observed in both cases. The total production (see also the Supporting information) and total primary production/total respiration ratio (TPP/TR) was higher in the macroalgal forest than in the barren ground food web, while the connectance index (CI) and omnivory index were similar in both systems.

Discussion

The two food-web models constructed for each of the two alternative states of the Mediterranean rocky sublittoral community, showed that the algal assemblages significantly influenced the total primary production, which was twice as large in the macroalgal forest state compared to the barren ground state, consequently impacting the structure and functioning of the entire community.

Both food webs were characterized by a predominance of consumers with low trophic levels (TLs). This pattern

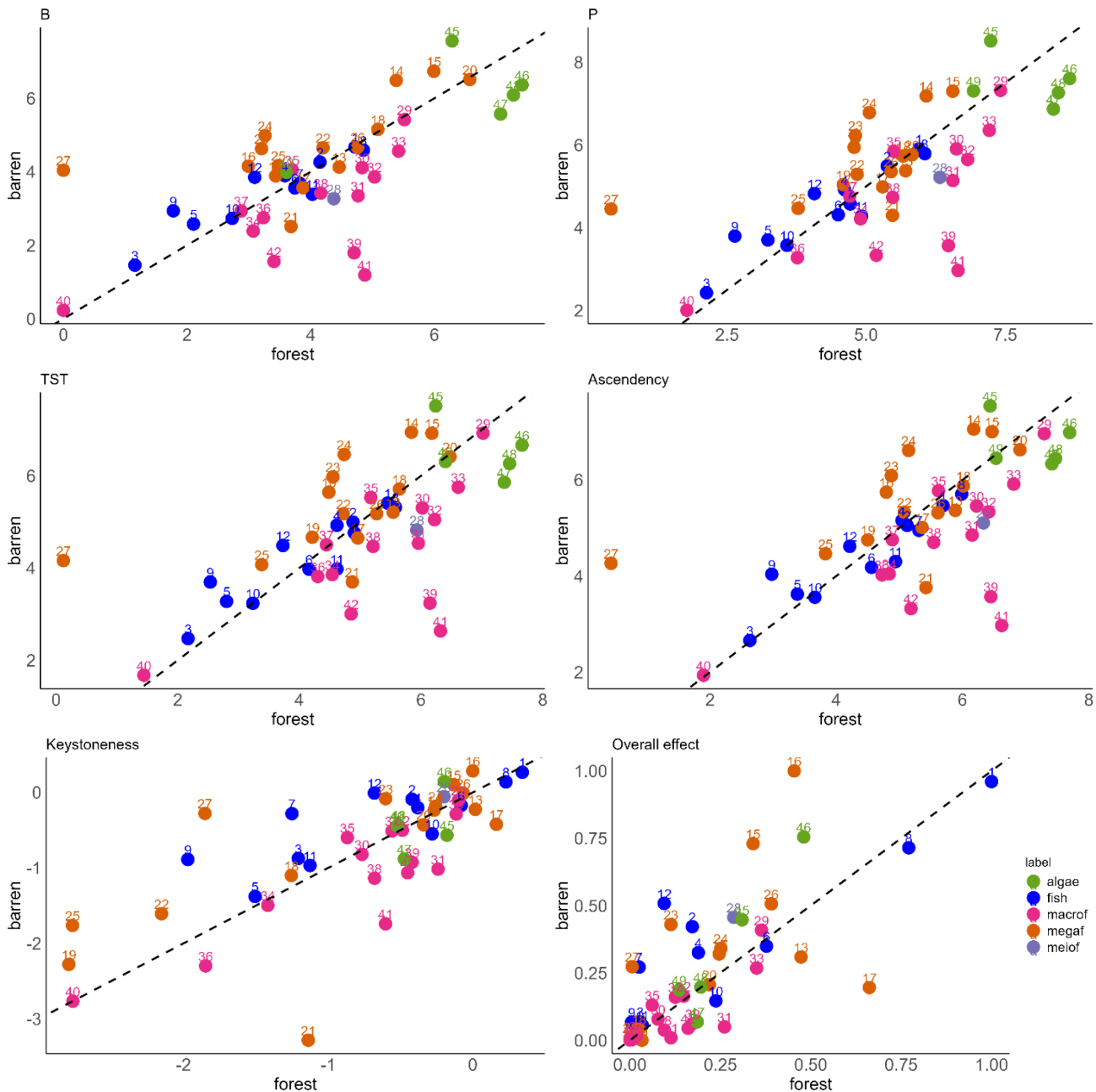


Figure 3. Comparison of six food-web indicators between the two systems. Numbers refer to functional groups (FGs) codes. Biomass (B), throughput (TST) and ascendency are in $\log_{10} + 5$, production (P) is in $\log_{10} + 6$. Dashed black line of equality.

may be attributed to the specific local characteristic of the studied systems (i.e. small benthic system subjected to high fishing pressure) (Heymans et al. 2014, Pipitone et al. 2023, Agnetta et al. 2024b) as well as the relatively high standing crop of benthic macroalgae observed in both states (erect macroalgae in the forest state and encrusting macroalgae in the barren state) (Wu et al. 2016). The Lindemann spine analysis showed a large proportion of energy flowing into detritus from TL I in both food webs, although this proportion was higher in the macroalgal forest state by approximately 18%. In the macroalgal forest, a significant portion of the algae

likely decays and settles on the seafloor, where it is decomposed by bacteria, providing energy to TL II through the detritus-based pathway (Schaal et al. 2010). Approximately half of the detritus consumed by TL II returned to the detritus pool in both models, indicating the significant role of TL II in system recycling. The mean transfer efficiency from detritus confirmed the importance of recycling in supporting the stability of both food webs (Vasconcellos et al. 1997).

Indicators revealed that the two food web models were supported by different functional groups: mega- and macrofauna in the barren ground and macroalgal forest food web

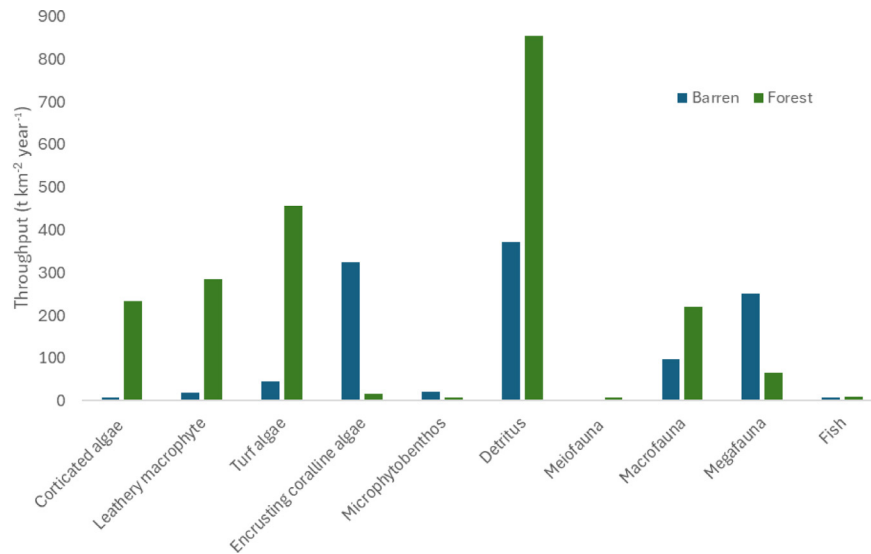


Figure 4. Total flow in macroalgal forest and barren grounds in rocky sublittoral ecosystems of the Mediterranean Sea.

models, respectively. In the barren ground food web, sea urchins exhibited high values of biomass, system throughput (ST), ascendancy and overall effect. Omnivorous sea urchins may play a pivotal role in organic matter recycling, feeding on encrusting organisms, detritus and microphytobenthos, and producing feces that, when degraded by bacteria, contribute to the detritus-based pathway (Mamelona and Pelletier 2005, Krumhansl and Scheibling 2012). Similarly, sea urchins such as *A. lixula* and *P. lividus* can exploit resources present in the barren by grazing on coralline algae and consuming benthic organisms (*A. lixula*) or feeding on drift algae and detritus (*P. lividus*) (Agnetta et al. 2013), acting as energy hubs by providing food to suspension and deposit feeders in the barren

ground web. In our study, the spiny starfish *M. glacialis* showed a high value of overall relative effect in the barren ground food web, indicating its potential role in controlling sea urchin populations there (Galasso et al. 2015). Other groups of benthic megafauna, such as omnivorous starfish (e.g.: *Echinaster sepositus*, *Hacelia attenuata*, *Ophidiaster ophidianus*), filter feeders (e.g. bivalves), and scavengers (e.g. *H. carunculata* and *H. trunculus*), exhibited higher values of overall relative effects in the barren ground food web compared to the macroalgal forest food web. Conversely, the opposite trend was observed for benthic macrofauna groups, indicating their role in the functioning of the macroalgal forest food web. Exceptions to this trend were sipunculids

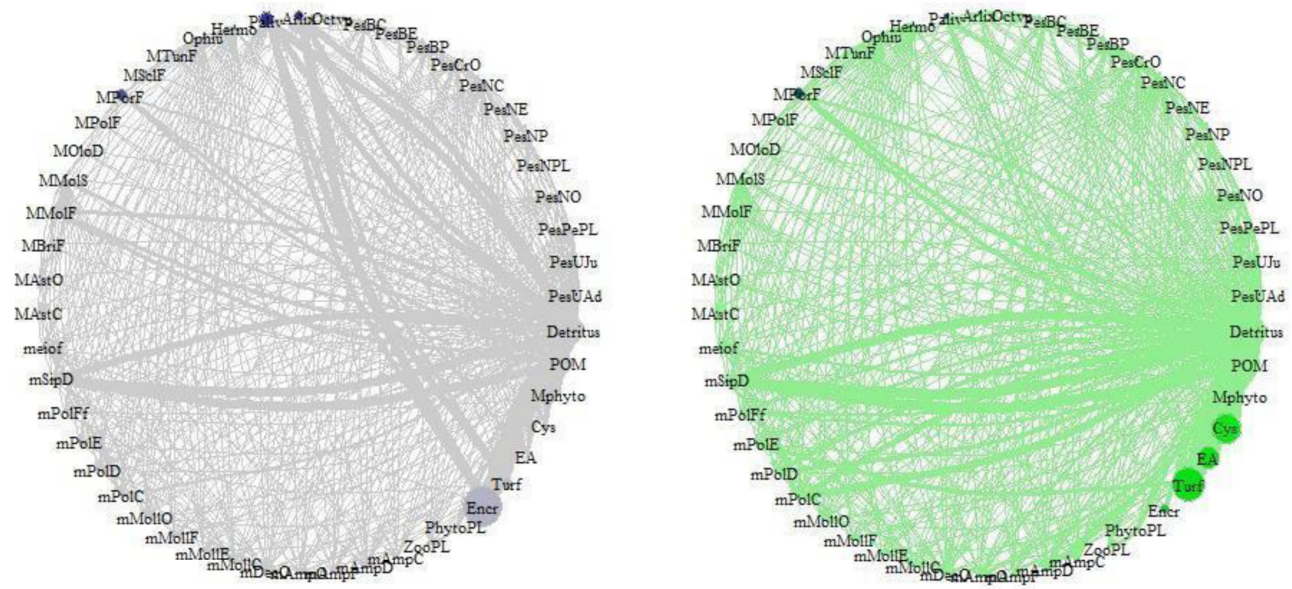


Figure 5. Comparison between biomass flows in the food webs of macroalgal forest and barren ground states of the Mediterranean subtidal rocky community.

Table 3. Indicators of network flow and ecosystem structure for the food webs of the alternative states (either barren grounds or macroalgal forests) of the Mediterranean rocky sublittoral community.

Flow indicators	Barren	Forest
Total consumption, TC (t km ⁻² year ⁻¹)	367.74	315.44
Total export, TEX (t km ⁻² year ⁻¹)	228.83	857.23
Total respiration, TR (t km ⁻² year ⁻¹)	216.99	171.21
Total flows into detritus, TDET (t km ⁻² year ⁻¹)	452.85	1272.98
Total system throughput, TST (t km ⁻² year ⁻¹)	1266.42	2616.86
Total production, TP (t km ⁻² year ⁻¹)	524.58	1111.02
Net system production, NSP (t km ⁻² year ⁻¹)	447.38	1029.87
Total primary production/total respiration, TPP/TR	2.06	6.02
Total biomass (excluding detritus) (t km ⁻² year ⁻¹)	527.42	651.71
Connectance index	0.16	0.16
System omnivory index	0.09	0.09

and sponges, whose indicators (ST, overall relative effects, and ascendancy) were high in both models. Sipunculids are worm-like invertebrates present in both alternative reef states and are important detritivores in rocky reefs, contributing to the diet of many fishes and invertebrates (Hansen 1978, Murina 1984). Sponges are key components of rocky reef communities and potentially play significant ecological roles (e.g. benthopelagic coupling, food sources and habitat provision for other organisms) in both macroalgal forest and barren ground states of rocky sublittoral communities (Bell 2008, Costa et al. 2018, Di Trapani et al. 2020). Regarding the keystone roles of benthic organisms, we found high values for both turf algae and the fireworm *H. carunculata* in the barren ground food web model. The key role of turf algae is likely linked to that of *P. lividus*; erect macrophytes are an important component of *P. lividus*' diet (Agnetta et al. 2013), and turf algae plausibly represent a significant resource for *P. lividus* within barren grounds. Interestingly, *H. carunculata* was the main invertebrate keystone predator in the barren web model. *Hermodice carunculata* is an amphinomid polychaete capable of consuming a wide range of marine invertebrates, exploiting dorsal stinging chaetae and their eversible pharynx to capture even large, shielded prey (Simonini et al. 2017, 2018). The diet of *H. carunculata* includes sea urchins, starfish, tube worms, sea cucumbers and sponges (Righi et al. 2020) and its predatory activity likely affects the functioning of barren grounds.

In the forest food web, a high keystone value for brittle stars was found. It has been shown that brittle star biomass is positively correlated with the abundance of macrofauna and the percentage of sediment organic matter, indicating that brittle stars could enhance rates of benthopelagic coupling and play a key role in reef system functioning (Gerald et al. 2017). Regarding fish, they are characterized by low values of biomass, productivity, ST and ascendancy, likely since the present study was conducted in a heavily fished area with similar fishing pressure across sites (RAC/SPA - UNEP/MAP 2013).

Nevertheless, benthopelagic carnivorous fish and predators of adult sea urchins (i.e. *Diplodus vulgaris* and *D. sargus*)

exhibited high values of overall effect and keystone values in both food webs, suggesting that these fish may impact on the biomass of other functional groups, contributing to the stability of both food webs. In particular, the presented results confirm that seabreams play a role in the top-down control of the sublittoral communities in Mediterranean rocky reefs (Guidetti 2006).

As expected from the total primary production (TPP) data, the total production (TP) of the macroalgal forest food web was about twice as high as that of the barren ground food web. This trend remained consistent even when input parameters were randomly varied within plausible ranges (Supporting information). Moreover, the results show a higher percentage of flows into detritus and exports in the forest state than in the barren state, while the opposite trend was observed in respiration and consumption flows, with higher percentages in the barren food web. We found a high value of TPP/TR, which is regarded as an indicator of ecosystem maturity (Odum 1969), in both state webs. When TPP/TR is close to one, all primary production is used for respiration, thereby leaving no residual production and indicating a mature system. In our study, we found values of TPP/TR higher than one, indicating that the two-food web models are incomplete, and the primary production cannot be fully utilized. This finding likely depends on the low biomass of key components of the food web such as fish predators of sea urchins and macrofaunal organisms, resulting from the heavy impact of fishing in the studied area (V. Macic pers. comm.). Notably, TPP/TR was even higher in the macroalgal forest food web, possibly due to the age of the barrens studied (several decades) and the different energy pathways characterizing the two states. Similar values for the connectance index (CI) and system omnivory index (SOI), suggest that barren grounds and macroalgal forest systems are characterized by similar complexity of interspecies relationships and, consequently, stability.

Similar to what observed in kelp forests (Eger et al. 2024), our study confirms that the productivity of macroalgal forests is greater than that of barren grounds, with higher energy export from the macroalgal forests to surrounding systems. However, we also found that barren grounds effectively store energy and may support a diverse megafauna that performs various functional roles within a stable food web. This stability is likely enhanced by certain external drivers (most probably heavy fishing pressure in this case), which allows them to mitigate the negative impacts of the significant reduction in biomass and biodiversity of meio- and macrofauna observed in this system compared to macroalgal forests. While benthic megafauna thrives in the barren grounds, benefiting from increased resource availability, macrofauna may also rely on the structural complexity and higher productivity provided by macroalgal forests. These differences highlight the ecological significance of the rocky reef alternative states in supporting diverse faunal communities. Furthermore, the variations between the two states highlight the need for targeted conservation efforts – such as restoring key functional groups of organisms, including both consumers (e.g. fish

predators) and foundation species (e.g. erect algae) – as shifts in these communities could profoundly impact ecosystem stability and function. Overall, this study provides valuable insights into the structure and functioning of rocky reef communities under alternative meta-stable states, emphasizing the importance of understanding ecosystem functioning to identify disturbance thresholds leading to abrupt changes. Such information is critical for the effective management and conservation of subtidal rocky reefs. Although both the macroalgal forest and the barren ground examined in the present study represent mature states – given their persistence over decades and their typical features, such as relatively stable biomass pools and well-structured energy pathways (this study, Uribe et al. 2021) – and although the sensitivity analysis supports the robustness of our results, some limitations must be acknowledged. In particular, the food-web models are based on data collected during a single sampling period and at limited spatial scales. Therefore, the models should be interpreted as ecological meaningful, but not definitive, representation of the two alternative states. Additional multi-seasonal sampling would be necessary to assess the temporal dynamics and functioning of these systems.

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Author contributions

Davide Agnetta and **Paola Gianguzza** share last authorship. **Chiara Bonaviri**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Davide Agnetta**: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (lead); Software (lead); Supervision (lead); Validation (lead); Visualization (equal); Writing – review and editing (lead). **Stefania Pinna**: Conceptualization (equal); Investigation (equal); Writing – review and editing (equal). **Luigi Piazzini**: Investigation (equal); Writing – review and editing (equal). **Fabio Badalamenti**: Conceptualization (equal); Investigation (supporting); Writing – review and editing (equal). **Giulia Ceccherelli**: Investigation (supporting); Writing – review and editing (equal). **Davide Iacofano**: Investigation (equal). **Manfredi Di Lorenzo**: Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Francesco Di Trapani**: Investigation (equal). **Sabrina Lo Brutto**: Investigation (equal); Writing – review and editing (equal). **Vesna Mačić**: Investigation (equal); Writing – review and editing (equal). **Anna Maria Mannino**: Investigation (equal); Writing – review and editing (equal). **Francesco Mura**: Investigation (equal). **Luigi**

Musco: Investigation (equal); Writing – review and editing (equal). **Laura Tamburello**: Investigation (supporting); Writing – review and editing (equal). **Tomas Vega Fernandez**: Investigation (equal); Writing – review and editing (equal). **Salvatrice Vizzini**: Investigation (supporting); Writing – review and editing (equal). **Trevor Willis**: Writing – review and editing (equal). **Paola Gianguzza**: Conceptualization (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.b5mkkwhth> (Bonaviri et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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