

Capturing ecological complexity: OCI, a novel combination of ecological indices as applied to benthic marine habitats



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ABSTRACT

The novel Overall Complexity Index (OCI) is proposed to measure ecological complexity, incorporating four complexity indices: (1) exergy and (2) throughput as extensive metrics, (3) specific exergy and (4) information as intensive metrics. Exergy and specific exergy estimate structural complexity while throughput and information functional complexity. OCI was applied to benthic habitats in a coastal marine tract encompassing a Marine Protected Area (MPA) in north-western Italy. The four individual indices did not always show homogeneous results in assigning complexity to different habitats. On the contrary, the additive measure provided by OCI showed that seagrass meadows and coralligenous reefs are in all the most complex habitats. Applying OCI provided results consistent with traditional approaches based on expert judgement, which usually attach more interest to seagrass meadows and hard bottoms with respect to soft bottoms, but expressed a synthetic, objective and quantitative approach. OCI can be mapped for management purposes, resolving the discordances evidenced by the individual indices. Ecological complexity in the study area is concentrated in some hot spots, as mapped by OCI, while the greatest part of the seafloor is occupied by low complexity habitats. Only some of these complexity hotspots are included within the Marine Protected Area, while this study suggests that high complexity areas, adjacent to the existing MPA, should be considered for protection possibly reshaping MPA's limits.

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1. Introduction

The concept of complexity applied to ecological communities concerns at its basis the existence of groups of species usually occurring together in combinations (Nesis, 1977; Giller, 1984; Greig-Smith, 1986; Burkovsky, 1992). From these combinations, interactions between species arise from evolutionary reasons or similarities in their environmental requirements. Ecological complexity is then generated by the web of interactions (interpreted in the wider perspective, as for example competition, facilitation, parasitism, predation, trophic or feeding interactions) within a community. The web of interactions is characterised by the number, nature, strengths, and structural patterns of biotic links among species (Zobel and Zobel, 1988; Laska and Wootton, 1998; Casti, 2008).

Ecosystems are open systems combining living organisms together with their physical environment, containing feedback loops, and having a history. Thus, they change over time, and prior states exert influence on present states, which, in turn, will affect future states. Ecosystems are nested and encompass various

organisational levels and this is why they are complex. Ecosystems employ energy and matter to move further from the thermodynamic equilibrium and maintain a state of low-entropy compared with the surrounding. This is made by growing and developing, which means that ecosystems increase their physical structure, and then their size, as well as the embodied information, and then their network (Jørgensen and Fath, 2004). The more ecosystems move through self-organisation, specialising their ordered hierarchical structure, the more they become complex (Nielsen and Jørgensen, 2013). At each system level, some features not predictable from the composing subsystems arise: these characteristics are named emergent properties (Goldstein, 1999).

Complexity is then an emergent property related to the size and organisation of ecosystems, linked to the necessity of maintaining a state far from thermodynamic equilibrium through growth and development and realised by means of the creation of a hierarchical organised structure.

Complexity is a multifactor phenomenon, extraordinarily difficult to measure, but its appraisal is fundamental to obtain a full understanding of the system analysed.

As a consequence, valid complexity indicator needs to be able to capture these features with a holistic approach and then considering the study object as an independent whole, since a system cannot be described and understood if emergent properties are

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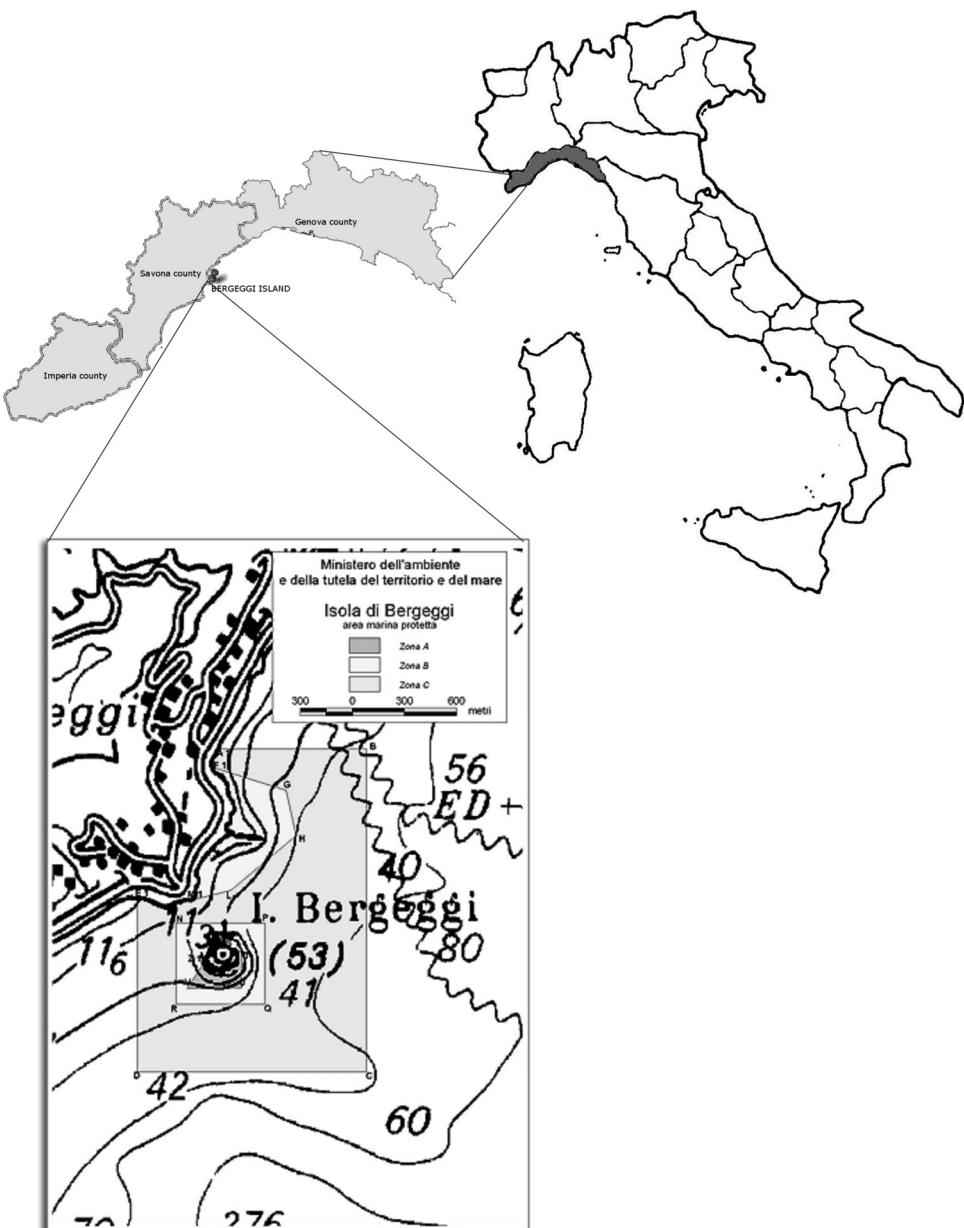


Fig. 1. Study area and its location. Grey shadow represents "Isola di Bergeggi" Marine Protected Area.

not analysed. A number of approaches have been adopted to measure ecological complexity (Morin, 1984; Bennett, 1990; Edmonds, 1995; Loehle, 2004).

The term is often associated with other concepts such as diversity or resilience. Actually, diversity is a component of ecological complexity while resilience is further emergent property of complex systems (Morin, 1999; Kay, 2002; Naeem, 2013). Since diversity seems to be easily measurable, it represents the most frequently adopted measure of complexity in ecology. On the contrary, the link between complexity itself and other system properties such as resilience or stability is still a debated issue (Logofet, 2008; Arreguín-Sánchez, 2014; Meerow and Newell, 2015). Some other indicators have been suggested as complexity proxies such as: spatial, temporal, geometric and functional, phylogenetic variety, connectivity and connectance or interaction strength. All these approaches, however, have shown limitations (May, 1973, 1981; Mikhailovsky, 1978, 1988; Pimm, 1982, 1984, 1991; McShea, 1991; Emmeche, 1997; Clarke and Warwick, 1998; Loehle, 2004; Parrot, 2010; Naeem, 2013).

The main objective of this study is to introduce a novel and practical measure of ecological complexity (complexity hereinafter). To this purpose, a thermodynamic analysis and a network analysis were employed, tested on and applied to a case study, and then combined. The thermodynamic analysis, based on exergy and specific exergy, is aimed at measuring structural complexity while the network analysis, based on throughput and information, is aimed at quantifying functional complexity.

Structural complexity is related with compartments of the system and their inner architecture whereas a function is represented as a scheme characterised by typical preconditions and postconditions and then functional complexity is linked to relations within compartments (Goel et al., 2009). Structural complexity refers to different physical parts in the system, functional complexity relates with how they interact.

For example, in an organism, organs can refer to structural complexity while metabolism to functional complexity (McShea, 1996).

Both analyses quantify the complexity in a system perspective and in extensive and intensive terms alike as size and organisation

Table 1

Conversion factors employed. DW (dry weight), WW (wet weight), AF (Ash free dry weight). a: Palmerini, 1991; b: Ricciardi and Bourget, 1998; c: Toussaint and Schneider, 1998; d: Jørgensen et al., 2005.

Group	DW/WW	AF/WW	AF/DW	Reference
Algae	0.281	0.119	0.528	a
<i>Cymodocea nodosa</i>	0.251	0.199	0.791	a
<i>Posidonia oceanica</i>	0.251	0.199	0.791	a
Foraminifera	0.670	0.010		b
Porifera	0.168	0.107	0.471	c and d
Cnidaria	0.312	0.132	0.491	a
Mollusca	0.323	0.072	0.176	a
Annelida	0.183	0.115	0.653	a
Sipuncula	0.178	0.112	0.643	b
Crustacea	0.286	0.111	0.440	a
Bryozoa	0.635	0.050	0.102	a
Echinodermata	0.511	0.103	0.237	a
Tunicata	0.063		0.399	a and b
Others	0.275	0.110	0.502	a and b

Table 2

Values of the complexity of the biomass expressed by the weighing factors used in this study (Jørgensen et al., 2010).

Organisms	Weighting factor
Algae	20
<i>Cymodocea nodosa</i>	393
<i>Posidonia oceanica</i>	393
Foraminifera	21
Porifera	98
Cnidaria	91
Mollusca	310
Annelida	133
Sipuncula	133
Crustacea	232
Bryozoa	91
Echinodermata	144
Tunicata	246
Others	177

of the system. Exergy and specific exergy are based on storage and components, and then they relate to structural complexity, since they are able to describe how different elements of the systems are established. Structural complexity is measured as the thermodynamic distance from the equilibrium in genetic and evolutionary terms. Throughput and information are based upon flows and relationships, and then they refer to functional complexity since they are able to describe how elements mutually interact (Jørgensen, 2002). Functional complexity is evaluated as quantity and efficiency of energy exchanges among different compartments (Toussaint and Schneider, 1998; Jørgensen, 2000; Jørgensen et al., 2005).

Table 3

Adjacency matrix for organisms occurring in the benthic habitats considered.

	Algae	<i>C. nodosa</i>	<i>P. oceanica</i>	Foraminifera	Porifera	Cnidaria	Mollusca	Annelida	Sipuncula	Crustacea	Bryozoa	Echinodermata	Tunicata	Others
Algae	0	0	0	0	0	0	1	1	1	1	0	1	0	1
<i>C. nodosa</i>	0	0	0	0	0	0	1	1	1	1	0	1	0	1
<i>P. oceanica</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Foraminifera	0	0	0	0	0	0	1	1	1	1	0	1	0	1
Porifera	0	0	0	0	0	0	0	0	0	1	0	1	0	1
Cnidaria	0	0	0	0	0	0	0	0	0	1	0	1	0	1
Mollusca	0	0	0	0	0	0	1	0	0	0	0	1	0	1
Annelida	0	0	0	0	0	0	0	1	1	1	0	0	0	1
Sipuncula	0	0	0	0	0	0	0	1	1	0	0	0	0	1
Crustacea	0	0	0	0	0	0	1	1	1	1	0	1	0	1
Bryozoa	0	0	0	0	0	0	0	0	0	1	0	1	0	1
Echinodermata	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Tunicata	0	0	0	0	0	0	0	0	0	1	0	1	0	1
Others	0	0	0	0	0	0	1	1	1	1	0	1	0	1

These complexity measures were applied to and tested on a coastal marine benthic system in North West Mediterranean Sea.

The benthic system is here viewed as a key subsystem of the larger marine system. The benthic system exerts a regulatory effect on the total system metabolism and controls water column biomass converting it into macrofauna biomass with lower respiration rates. It represents a storage compartment containing sizeable part of the systems energy content and nutrients able to face fluctuations. It has been recognised that the benthic compartment is characterised by stable energy flows since it responds to changes smoothly than the pelagic compartment, thus representing a sort of “memory block” of the ecosystem (Ott and Fedra, 1977; Herman and Scholten, 1990; Ozolin'sh, 2002).

In the first decade of the 2000s, the implementation of the European Water Framework Directive and the Marine Strategy Framework Directive to define the Ecological Quality Status of marine environments highlighted the need to acquire better information about the structure and functioning of benthic communities, since seafloor habitats were recognised as good indicators of human pressure on marine ecosystems (Dauvin, 2015).

Fabiano et al. (2004) proposed employing the benthic subsystem to apply thermodynamic and network measures. The rationale behind this approach is that an analysis of this target sub-systems within the ecosystem as a whole represents an efficient way to investigate specific topics such as disturbance, health state or, exactly, complexity on which the selected systems are more sensitive (Vassallo et al., 2006).

The main goals of the present study were: (1) measuring structural complexity by means of exergy and specific exergy; (2) assessing functional complexity by means of throughput and information; (3) developing and applying a practical and synthetic measure of complexity to apply to ecosystems, natural sub-systems and their compartments; (4) characterising different habitats according to complexity; (5) suggesting management practices for the area analysed.

In particular, differences among habitats through a holistic view have been considered in a management perspective. This should allow verifying whether the habitats usually listed as important (in terms of conservation practices) also show high levels of complexity. Finally, to make results explicit, the spatial patterns of benthic habitats complexity have been mapped.

2. Materials and methods

2.1. Study area

The area of interest occupies a surface of 451 ha, is located the Liguria Region (an administrative region of Northwest Italy) and

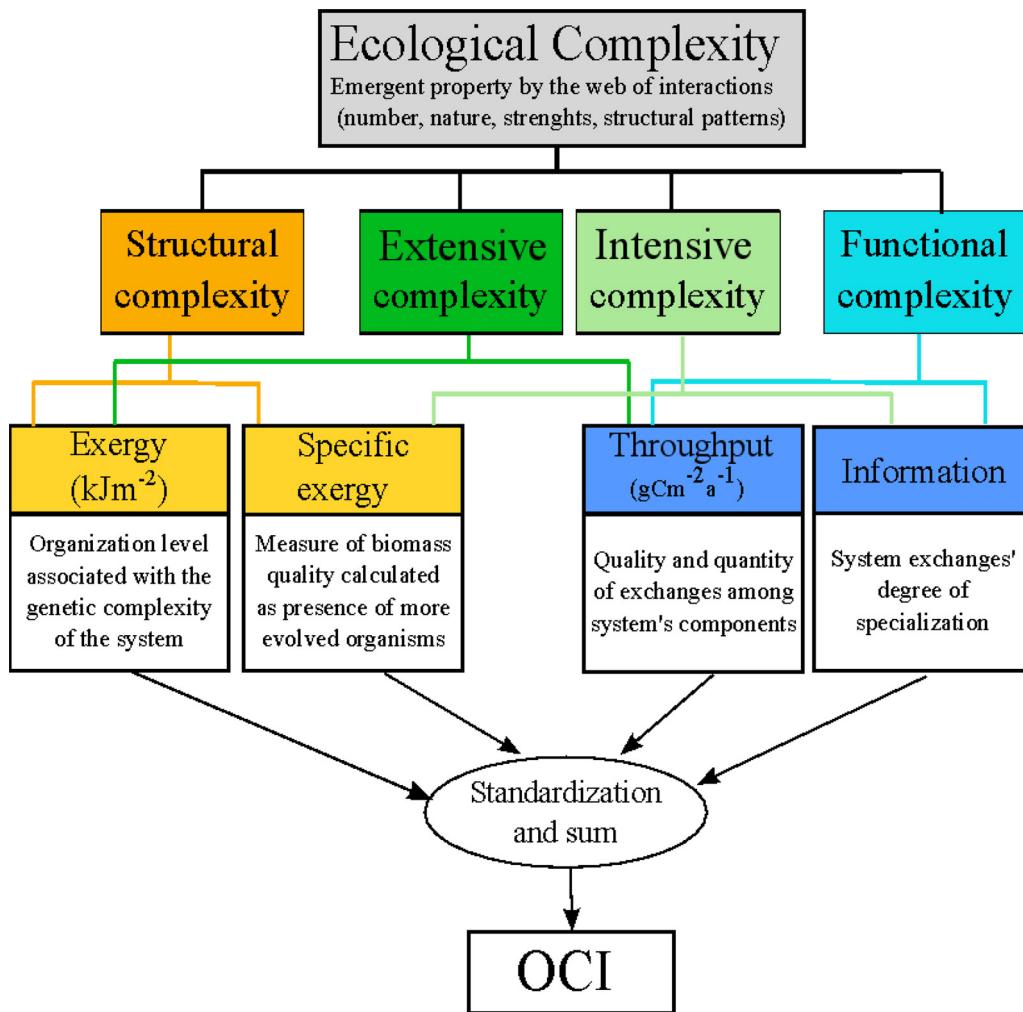


Fig. 2. Schematic flow chart of the logical process leading to OCI with main concepts explained.

Table 4

Theoretical framework synthesis and main concepts employed in the paper. Reported definitions concern this specific study and relate to the ecology field.

Concept	Definition	Indices
<i>Structural complexity</i>	It is related with compartments of the system and their inner architecture; it refers to different physical parts in the system.	Exergy and specific exergy
<i>Functional complexity</i>	It is related with how the components of the system interact since a function is represented as a scheme characterised by typical preconditions and postconditions	Throughput and information
<i>Extensive complexity</i>	It is related with system's size in term of biomass or entity of overall activity between compartments	Exergy and throughput
<i>Intensive complexity</i>	It is not dependent on system size, it is an intrinsic characteristic of components or fluxes	Specific exergy and information
<i>Overall complexity</i>	Emergent property related to the size and organisation of ecosystems, linked to the necessity of maintaining a state far from thermodynamic equilibrium through growth and development and realised by means of the creation of a hierarchical organised structure	OCI

completely envelops the MPA named “Isola di Bergeggi” (215 ha) (Fig. 1).

The MPA, established in 2007, includes the marine seafloor facing the promontory that hosts Bergeggi municipality and encircling the island bearing the same name. The coastline of Bergeggi municipality is jagged with caves, cliffs of dolomitic limestones, and pocket beaches and, together with the island, is part of Bergeggi Regional Nature Reserve since 1985 (Rovere et al., 2010, 2011b). The island of Bergeggi is composed of calcareous rocks; it occupies a surface of 364 m² with a coastline of almost 260 m, with steep cliffs on the eastern part and a gentle slope in the western part. It is separated from the land by a shallow-water channel 250 m wide and 12 m maximum deep.

The knowledge on the marine habitats of Bergeggi is inhomogeneous. Most studies deal with the Marine Cave of Bergeggi, where information has been collected since the 1970s (Parravicini et al., 2010), and seagrass meadows, investigated since the 1980s (Montefalcone et al., 2007). Soft bottoms have been the object of a single large-scale investigation in the 1990s (Somashini et al., 1998). A series of surveys, especially on hard bottoms, was carried out in the 2000s in view of the institution of the MPA: for shallow algal reefs, which showed degraded by the impact of date-mussel harvesting (Rovere et al., 2009), a list of conspicuous species is available (Parravicini et al., 2009); a preliminary study typified coralligenous reefs at various depths (Parravicini et al., 2007). The foreseen institution of the MPA also fostered investigations on fish

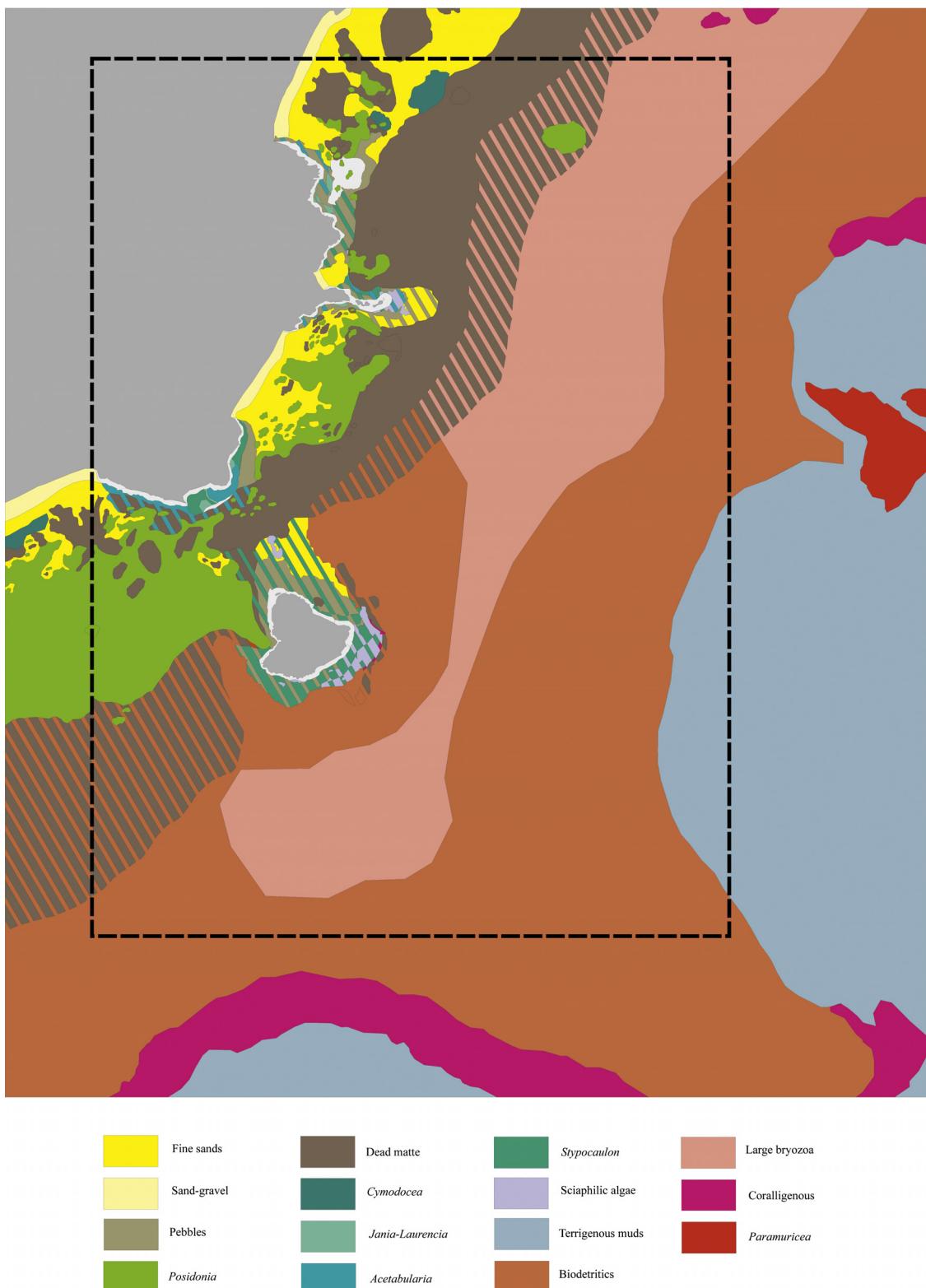


Fig. 3. Spatial distribution of Bergeggi benthic habitats, according to EUNIS classification. In dashed lines MPA boundaries.

communities (Molinari and Tunesi, 2003a, 2003b; Parravicini et al., 2008). Based on all the above information, recent studies tackled management aspects, such as environmental quality appraisal (Rovere et al., 2007, 2011a) habitat mapping (Rovere et al., 2010), marine spatial planning (Parravicini et al., 2012), and natural capital assessment (Vassallo et al., 2013a).

For the purposes of the present work, the main habitats recognised through the analysis of the above-mentioned literature have been equated, whenever possible, to the benthic habitats codified by both the UNEP Regional Activity Centre for Specially Protected Areas (RAC-SPA) and the European Union Nature Information System (EUNIS). RAC-SPA classification was expressly established for

Table 5

Benthic habitats identified in Bergeggi area together with the seafloor extent they occupy. Habitats are coded according to RAC SPA (which also provides indication of conservation importance) and EUNIS classifications. ¹ = name not as such in RAC-SPA classification.

Shortened names	RAC SPA	Habitat types	Code	Importance	EUNIS	Surface area (ha)	Percentage (%)
Fine sands		Biocenosis of well sorted fine sands	III.2.2.	Remarkable habitat	A5.236	10.9	2.42
Sand-gravel		Biocenosis of coarse sands and fine gravels	III.3.1.	Other habitat	A5.13	2.5	0.55
Pebbles		Facies with encrusting bryozoa on infralittoral pebbles ¹	III.4.1.	Other habitat	A5.131	2.9	0.65
<i>Posidonia</i>		<i>Posidonia oceanica</i> meadows	III.5.1.	Priority habitat	A5.535	20.2	4.48
Dead matte		Facies of dead "mattes" of <i>Posidonia oceanica</i>	III.5.1.3.	Remarkable habitat	A5.5353	46.9	10.41
<i>Cymodocea</i>		Association with <i>Cymodocea nodosa</i>	III.2.3.4.	Priority habitat	A5.53132	0.9	0.19
<i>Jania-Laurencia</i>		Association with <i>Jania rubens</i> and <i>Laurencia obtusa</i> ¹	III.6.1.	Remarkable habitat	A3.33	0.1	0.02
<i>Acetabularia</i>		Association with <i>Acetabularia acetabulum</i> ¹	III.6.1.	Remarkable habitat	A3.23	0.9	0.20
<i>Stylocaulon</i>		Association with <i>Stylocaulon scoparium</i>	III.6.1.23.	Other habitat	A3.331	2.6	0.57
Sciaphilic algae		Association with emiphophilic and sciaphilic infralittoral algae in sheltered waters ¹	III.6.1.32.	Other habitat	A3.23J	0.7	0.15
Terrigenous muds		Biocenosis of coastal terrigenous muds	IV.1.1.	Other habitat	A5.39	118.0	26.10
Biodetratics		Biocenosis of the coastal detritic bottoms	IV.2.2.	Other habitat	A5.46	141.0	31.36
Large bryozoa		Facies with large bryozoa	IV.2.2.10.	Priority habitat	A5.463	76.2	16.91
Coralligenous		Coralligenous biocenosis	IV.3.1.	Priority habitat	A4.32	23.6	5.24
<i>Paramuricea</i>		Facies with <i>Paramuricea clavata</i>	IV.3.1.13.	Priority habitat	A4.26B	3.3	0.74

the Mediterranean Sea (Bellan-Santini et al., 2002) and also provides an indication of the conservation importance of each habitat type (Relini, 2000). In particular, a 'priority habitat' absolutely requires conservation; a 'remarkable habitat' deserves special management measures; while an 'other habitat' is freely available for sustainable use (Bianchi et al., 2012). EUNIS classification has a major interest since it covers all the European marine habitats in an unambiguous single frame, but has been shown not perfectly adequate for the Mediterranean Sea (Mo et al., 2012). RAC-SPA and EUNIS classifications are both hierarchical. As a consequence, in the absence of an exact correspondence with the habitats occurring in the area of study the code of the habitat-type immediately superior was adopted.

2.2. Quantitative analysis

The main taxonomic groups found in each habitat were listed (Table 1). Groups have been chosen and aggregated in order to make different habitats comparable and according to available data. Information regarding biomass per unit area of each taxonomic group has been obtained from the literature (Table S1). The total biomass of each habitat was obtained by multiplying the biomass per unit area for the surface occupied by the habitat. Biomasses in different units were converted to the corresponding carbon content: wet and dry weights have been first turned into ash free dry weight (AFDW) using conversion factors from the literature (Palmerini, 1991; Ricciardi and Bourget, 1998) (Table 1) and then in carbon content assuming a 0.45 gC/gAFDW ratio (Berger et al., 1996).

2.3. Thermodynamic analysis

Meyer and Jørgensen (1979) proposed a couple of thermodynamic metrics (exergy and specific exergy) to identify the distance of ecosystems from the thermodynamic equilibrium, thus considered as suitable ecological quality indicators (Marques et al., 1997; Jørgensen, 2000).

The thermodynamic definition of exergy is the amount of work the system can perform when brought into equilibrium with its environment (Jørgensen, 1995).

This method is considered the best candidate for exergy calculations of ecosystems, because it takes into account the overall organisational level of organisms (Pusceddu and Danovaro, 2009). Exergy links the chemical energy of the various groups of the ecosystem to the genetic structure according to the following equation:

$$Ex = \sum_{i=1}^n \beta_i * X_i$$

where X_i is the concentration (biomass per unit area) of each group (species or group of species with similar genetic information) in the system and β_i represents the weighting factors based on exergy detritus equivalent (Fonseca et al., 2000; Jørgensen et al., 2010) (Table 2). Detritus is considered as the reference level for the exergy calculation being the simplest form of organic matter in ecosystems (Jørgensen et al., 2010); that is, the complexity of each organism is measured as thermodynamic distance (the DNA complexity has been suggested as a proxy of this distance) from the same amount of organic matter at thermodynamic equilibrium, namely detritus (Jørgensen, 2008).

Exergy detritus equivalents are expressed in $g m^{-2}$ and can be converted into $kJ m^{-2}$ by a factor of $18.7E-03$, corresponding to the approximate average energy content of 1 g of detritus (Jørgensen, 2000). Variations in exergy values could be due to variations of biomass or to variations of the genetic structure of biomass, which is identified by the specific exergy (Jørgensen, 2008). Specific exergy (Ex_{sp}) is given by:

$$Ex_{sp} = \frac{Ex}{\text{total biomass}} = \frac{Ex}{\sum_{i=1}^n X_i}$$

Exergy and specific exergy are here respectively intended as the extensive (i.e., which depend on the amount of matter) and intensive (i.e., which do not depend on the amount of matter) measures of ecosystem complexity. Exergy is driven both by the quantity and

Table 6Data of biomass per unit area ($\text{gC}\cdot\text{m}^{-2}$) of different groups in the habitats analysed.

Habitat	Algae	<i>Cymodocea nodosa</i>	<i>Posidonia oceanica</i>	Foraminifera	Porifera	Cnidaria	Mollusca	Annelida	Sipuncula	Crustacea	Bryozoa	Echinodermata	Tunicata	Others	
Fine sands							2.45E-01	5.75E+00		5.96E-01		3.12E-02		1.87E-01	
Sand-gravel							2.45E-02	1.44E+00		5.96E-02		3.12E-03		1.87E-02	
Pebbles	4.48E+00				2.41E-04		4.29E-01	7.49E-02	3.15E-04	6.78E-02	1.55E+00	2.65E-03	3.99E-02	1.71E+00	
<i>Posidonia</i>	3.25E+01		7.83E+02		1.17E+00		2.23E+01	3.66E+00		7.94E+00	1.90E-01	4.42E-01	3.18E+01		
Dead matte	1.31E+02						2.03E-01	5.93E+00	7.59E-01	2.40E-01		6.42E-01		1.30E+00	
<i>Cymodocea</i>		2.61E+02					1.59E-02			2.51E-02				1.93E-03	
<i>Jania-Laurencia</i>	5.10E+01			1.05E-02	7.22E-03	1.49E-02	1.23E+00	8.05E-01	6.03E-03	9.12E-02	3.34E-03	6.00E-02		2.31E+01	
<i>Acetabularia</i>	2.53E+01						4.29E+00	7.49E-01	3.15E-03	6.78E-01		2.65E-02	3.99E-01	1.71E+01	
<i>Stylocaulon</i>	9.99E+02						4.29E+00	7.49E-01	3.15E-03	6.78E-01		2.65E-02	3.99E-01	1.71E+01	
Sciaphilic algae	1.92E+02						1.07E+01	2.13E-01	4.51E-03	3.72E-01		4.15E-02		4.68E-01	
Terrigenous muds							2.81E-01	4.81E-01		7.50E-02		1.56E-01		1.61E-01	
Biodetratics							1.72E-02	6.33E-01		1.72E-02		1.31E-01		6.22E-02	
Large bryozoa							3.45E-02	7.33E-01		2.77E-02	3.50E+00	1.51E-01		3.34E-01	
Coralligenous	1.03E+01		6.10E-03	4.83E+01	2.63E+02	1.04E+01	1.28E+02			1.78E+02	1.81E+01		1.67E+01	1.37E+02	
<i>Paramuricea</i>			3.94E-03	4.44E+01	3.16E+02	1.92E+00	1.32E+02			3.70E-02	1.28E+01		1.54E+00	1.79E+02	

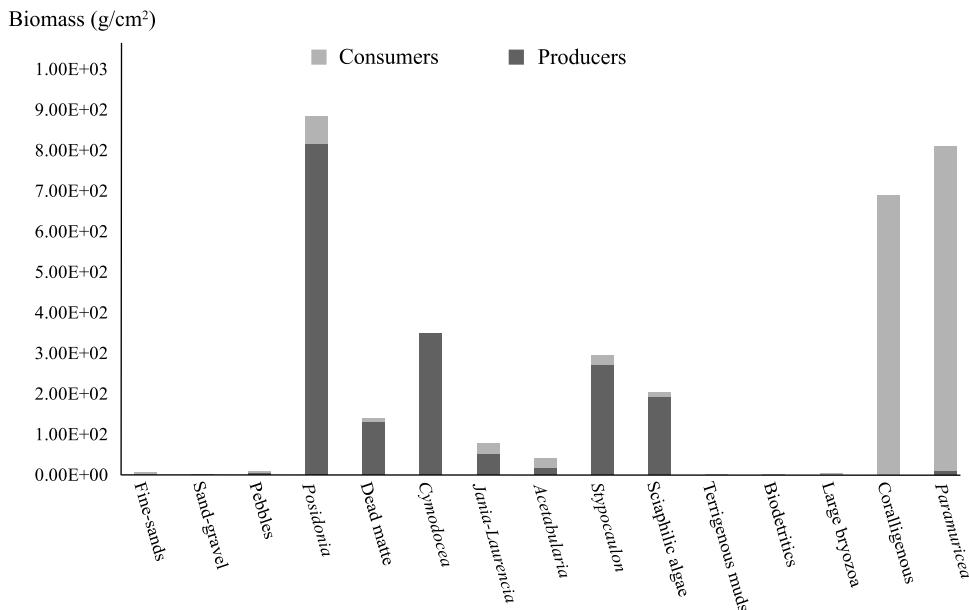


Fig. 4. Total biomass of each habitat split among primary producers and consumers.

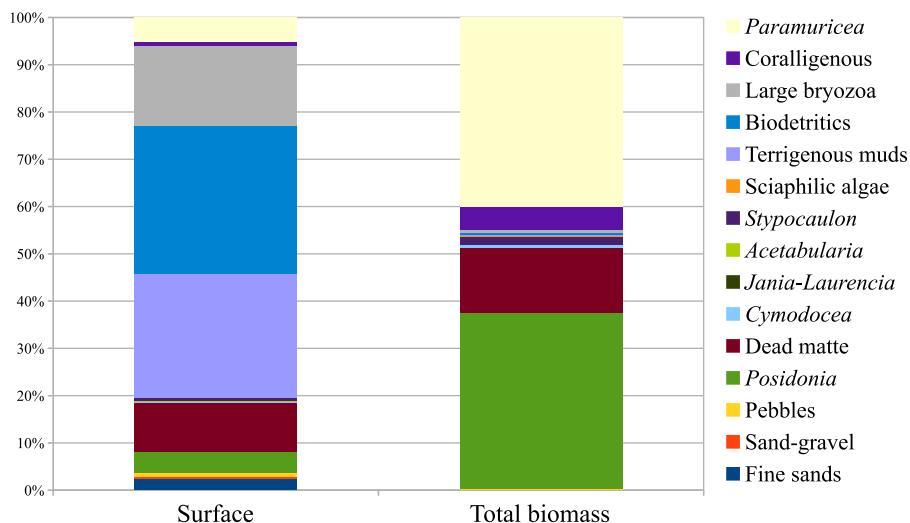


Fig. 5. Percentage contribution of habitats' surface and habitats' biomass to Bergeggi area.

quality of the biomasses embedded in the system examined, and thus is here considered as a measure of the overall structure of the system. On the contrary, specific exergy is merely a measure of the quality of the biomasses of the system and therefore represents the efficiency of the system (Fabiano et al., 2004; Vassallo et al., 2013a).

Both exergy and specific exergy relate to the genetic complexity stored in organisms' biomass: they are measured as thermodynamic distance from the same amount of organic matter at thermodynamic equilibrium. The more a system and its organisms are organised, the more they are exergetic and structurally complex. Exergy measures the level of organisation associated with the genetic complexity of the system, specific exergy is a good expression for the presence of more evolved organisms (Jørgensen, 2000; Libralato et al., 2006a).

Exergy and specific exergy have been already applied to the benthic system in a holistic perspective as, for instance, health conditions and environmental quality indicators (Fabiano et al., 2004; Libralato et al., 2006b; Park et al., 2006; Vassallo et al., 2012)

2.4. Network analysis

Ecosystem functionality, efficiency and ability to exploit, move and convey energy and matter are emergent properties of a complex living system. Their identification needs a whole system approach able to recognise, measure and combine the web of fluxes within the ecosystem (Vassallo et al., 2006, 2013b). Ulanowicz (1986) proposed a set of metrics (here identified as network analysis) based on a statistical approach to the study of ecosystem fluxes. Network analysis is able to measure key signals of ecosystem functioning. Among these signals, average mutual information (AMI in formulas) and total system throughput (T in formulas) have been chosen.

The average mutual information (information, hereinafter) is based on the statistical evaluation of how much each biomass flux in the food web is forced to enter a specific compartment (*j*) when released by another one (*i*). In this way, information is able to measure the level of organisation by with the exchanges among

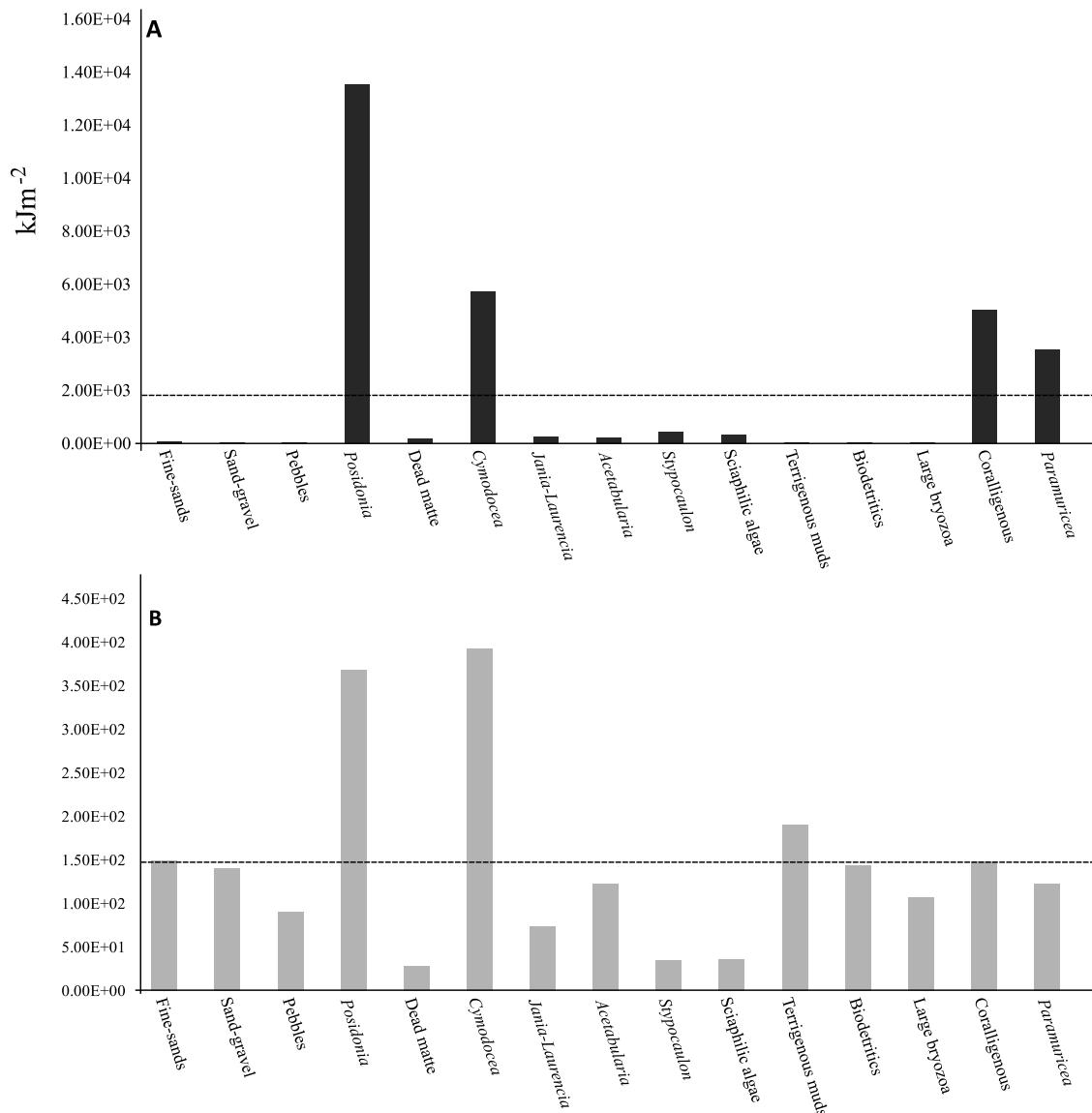


Fig. 6. Exergy (A) and specific exergy (B) of habitats. Average values in dashed lines.

components of the system are transacted. Ulanowicz (1986) suggested the formulation for its calculation as follows:

$$\text{AMI} = \sum_{i=1}^n \sum_{j=1}^n \frac{T_{ij}}{T} * \log \left[\frac{T_{ij} * T}{T_i T_j} \right],$$

where T_{ij} is the flux of biomass leaving compartment i and entering compartment j , T_i is the total flow out compartment i , T_j the total flow out compartment j and T is the sum of all the fluxes of biomass in the system, that is, the total system throughput. Total system throughput can rise due to an increase of system extent (more species, or by extending ecosystem borders), or due to a greater system activity (e.g., during phytoplankton blooms) (Scharler, 2008). The computation of throughput, measured in $\text{gC m}^{-2} \text{a}^{-1}$, used the following equation:

$$T = \sum_{i=1}^n \sum_{j=1}^n T_{ij}$$

The overall system activity is expressed as the sum of all transfer processes occurring in the system T ; the degree of organisation is measured by information (Ulanowicz and Abarca-Arenas, 1997;

Jørgensen and Svirezhev, 2004). As a consequence, information and throughput can be considered as intensive and extensive measures of functional complexity, respectively. Functional complexity is here identified as the ability of the system to perform work and exchange matter and energy efficiently. Throughput counts the quantity of exchanges while information measures the degree of specialisation of these exchanges.

Throughput and information have been calculated by means of Ecopath with Ecosim, a free ecological/ecosystem modelling software suite (Christensen and Walters, 2004).

Ecopath with Ecosim is widely employed when calculating model-derived indicators in marine environments (Piroddi et al., 2015).

For a basic parameterisation, the simulation's routine uses a system of linear equations, which can be expressed for an arbitrary time period by:

$$\frac{Bi * P}{B * EE_i} = C_i + \sum_{j=1}^n \left[B_j * \left(\frac{Q}{B} \right)_j * DC_{ij} \right]$$

Software needs five parameters for each group: biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B),

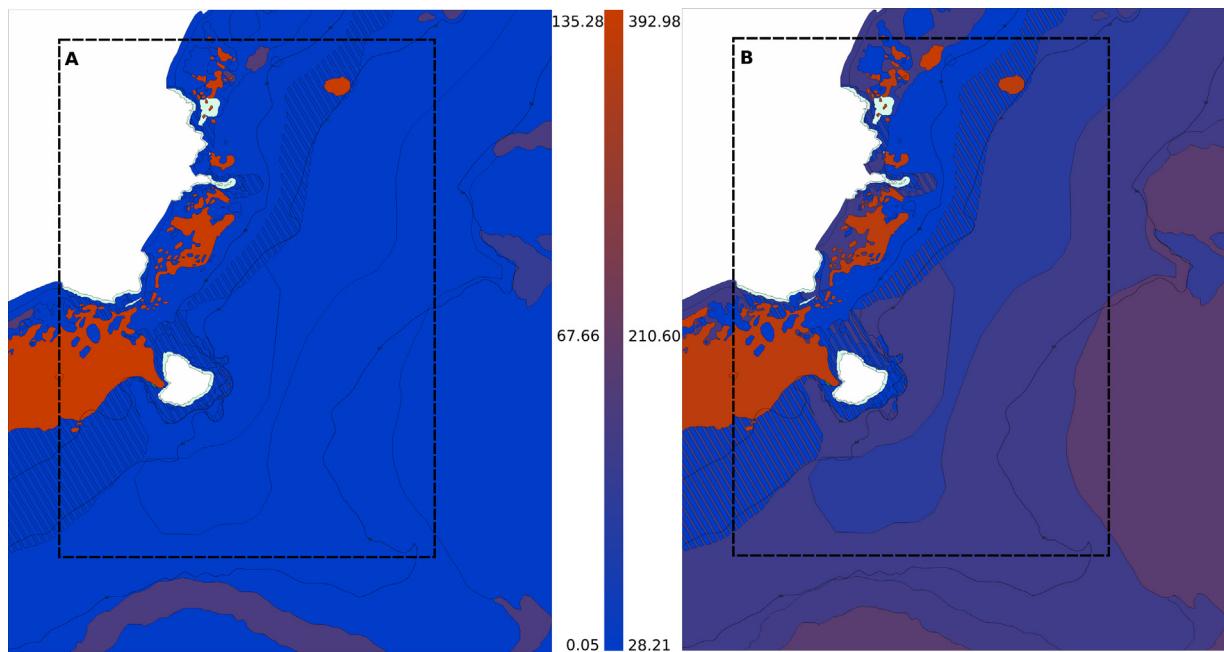


Fig. 7. Spatial distribution of Exergy (A) and Specific exergy (B); boundaries of MPA in dashed lines; in legend minimum, central and maximum values of Exergy are reported at left of the chromatic scale in 1E02 while minimum, central and maximum values of Specific exergy are reported at right.

ecotrophic efficiency (*EE*), and diet composition (*DC*). If one of these parameters is not available, it could be calculated knowing four further parameters: unassimilated/consumption ratio (*U/Q*), net migration rate (*NM*), biomass accumulation (*BA*), catch mortality (*Y*).

The simulation compartments consist of the 14 different taxonomic groups listed in Table 1. *P/B*, *Q/B*, *U/Q* values for the organisms considered and the respective literature sources are reported in Supplementary Material Table S2. Detritus fate has been addressed to detritus compartment and total export has been fixed to 0.

Ecotrophic efficiency is defined as the part of biomass that goes to predation and catches. As a consequence, its value ranges between 0 and 1. Information on ecotrophic efficiency was always lacking and was therefore estimated applying the following equation.

$$EE_i = \frac{[Y_i + NM_i + BA_i + \sum_{j=1}^n B_j + (Q_j/B_j) * D_i]}{[B_i * (P_i/B_i)]}$$

Steady-state was assumed for the Ecopath model parameterisation, with both *BA* and *NM* rates null for each simulation (Tecchio et al., 2013).

The software routine gives an error message if the ecological efficiency results > 1 for each compartment. If inconsistencies (*EE* > 1) were detected the diet matrix was adjusted by reducing the predation pressure on the group displaying *EE* > 1 (Christensen and Walters, 2004).

For the accounting of energy and matter coming from other compartments of the ecosystem (i.e. relationship with water column), we included an “import” flow in the diet matrix parameterisation for each group.

Diet composition expressed as diet matrix is a key factor for a realistic simulation. The quantitative assessment of prey/predation relationships is often difficult and normally shows large variance that may lead to errors. In this study, the diet matrix was obtained according to MATBLD method (Ulanowicz and Scharler, 2008). The method is based on the recognition of predation path by means of an adjacency matrix (Table 3). Adjacency matrix is a way of presenting the direct relationships between predators and prey and it is a binary matrix with direct links shown as 1s and non direct

links shown as 0s. The diet fluxes are assigned according to the joint proportion of predator demand and prey availability.

The matrix was compiled through the analysis of the relevant literature (Brusca and Brusca, 2003; Araújo and Bundy, 2011; Navarro-Barranco et al., 2013).

The model outputs all the information about trophic flows between compartments required to calculate information and throughput (Ulanowicz, 1986).

Similarly to thermodynamic analysis, network analysis has been already applied to benthic systems (Arregui-Sánchez et al., 2002; Fabiano et al., 2004; Vassallo et al., 2013b)

2.5. OCI (Overall Complexity Index)

In order to ascribe a single quantitative value to habitat complexity, able to comprise all the information emerged from previous appraisals, a novel index, named Overall Complexity Index (OCI), was constructed. OCI is an additive combination of four system indices that examine and assess complexity.

A highly developed and organised system, complex for the four types of complexity identified, is expected to exhibit high values of all the indices utilised here: exergy, specific exergy, throughput, and information. Then, standardised values of the four indices were summed up to obtain an aggregate estimate of each habitat complexity in a 0–4 range. At this purpose the following formula for each index and each habitat was applied:

$$OCI = \sum_{i=1}^4 SI_i = \sum_{i=1}^4 \frac{V_i - \text{Min}_i}{\text{Max}_i - \text{Min}_i} \text{ where, } SI_i = \text{standardised value of}$$

the index; V_i = original value of the index; Min_i = minimum value of the index among considered habitat; Max_i = maximum value of the index among considered habitat.

The index thus calculated is able to provide a wide view about the system complexity properties.

2.6. Summary of theoretical background

The concepts and process leading to OCI calculation are summarised in Fig. 2.

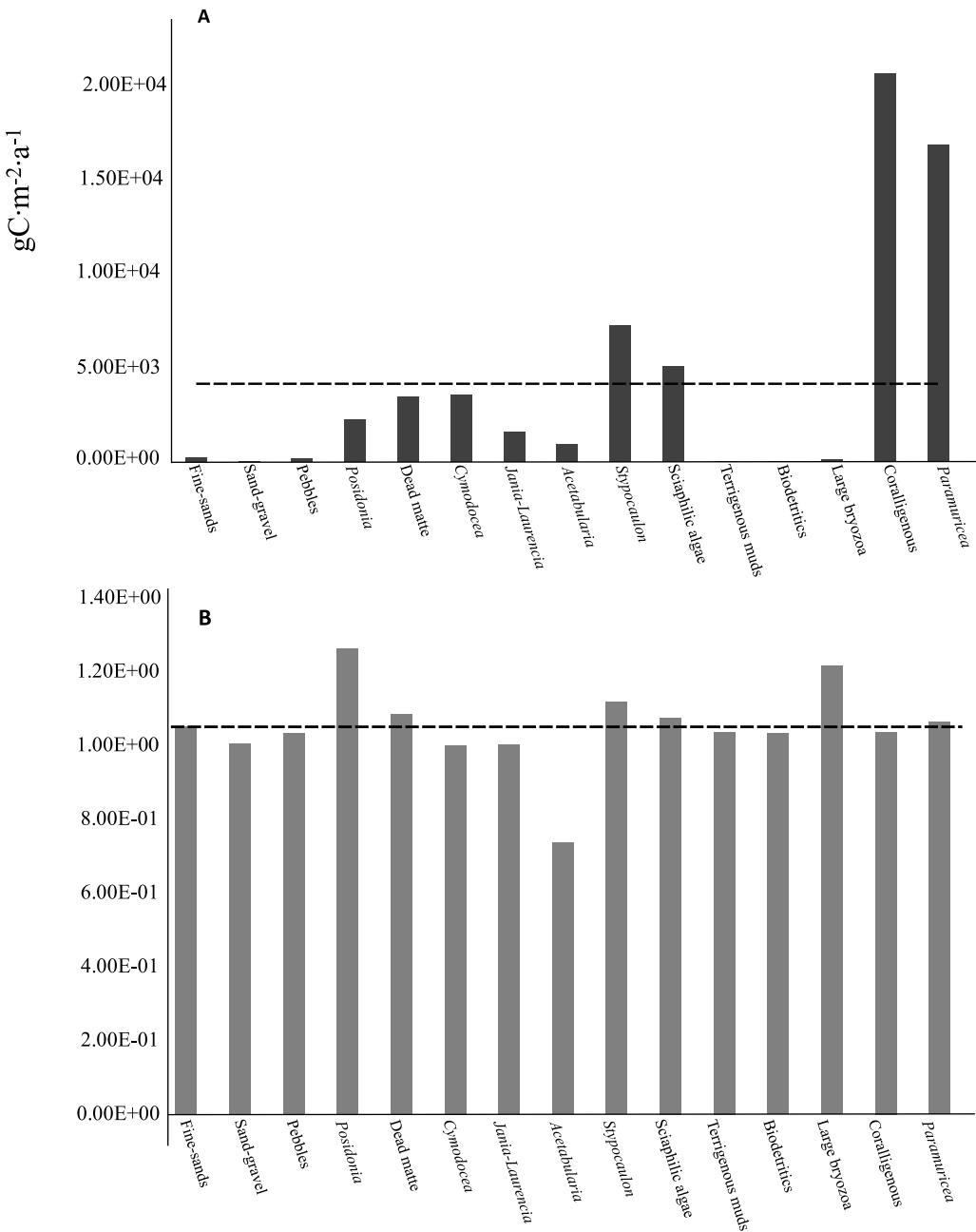


Fig. 8. Throughput (A) and information (B) in different habitats. Average values in dashed lines.

In order to clarify the theoretical design followed in the paper, the main concepts about complexity have been synthesised in Table 4. Different indices combinations provide various pieces of information about complexity.

3. Results

A total of 15 habitats, here named according to RAC-SPA and coded according to both RAC-SPA and EUNIS to facilitate comparison with other areas, was retained and mapped (Fig. 3); the map allowed computing the seafloor surface they occupy (Table 5).

The biomass of the different groups in the 15 habitats is shown in Table 6. Among the habitats considered, *Paramuricea*, coralligenous and *Posidonia* show the greatest biomass per unit area. This biomass is almost completely composed by primary producers in *Posidonia*, while it is due to consumers in *Paramuricea* and coralligenous (Fig. 4).

The seafloor of Bergeggi area is occupied for over 50% by biodetrities and terrigenous muds, while the biomass in the area is mainly due to coralligenous and *Posidonia* (over 70%) (Fig. 5).

3.1. Thermodynamic analysis for structural complexity

Exergy values range from 5.12 to 1.35E+04 kJ m⁻², with an average equal to 1.95E+03 ± 3.75E+03 kJ m⁻². The lowest value is associated to biodetrities, the highest to *Posidonia*. Very low values are also associated with terrigenous muds and sand-gravel. Only *Posidonia*, *Cymodocea*, coralligenous and *Paramuricea* show exergy values greater than the average (Fig. 6).

Specific exergy ranges between 2.82E+01 and 3.93E+02, with an average value equal to 1.43E+02 ± 1.07E+02. The lowest value is ascribed to dead matte, the greatest to *Cymodocea*. *Cymodocea* and *Posidonia* show values of specific exergy over 2.5 times greater than

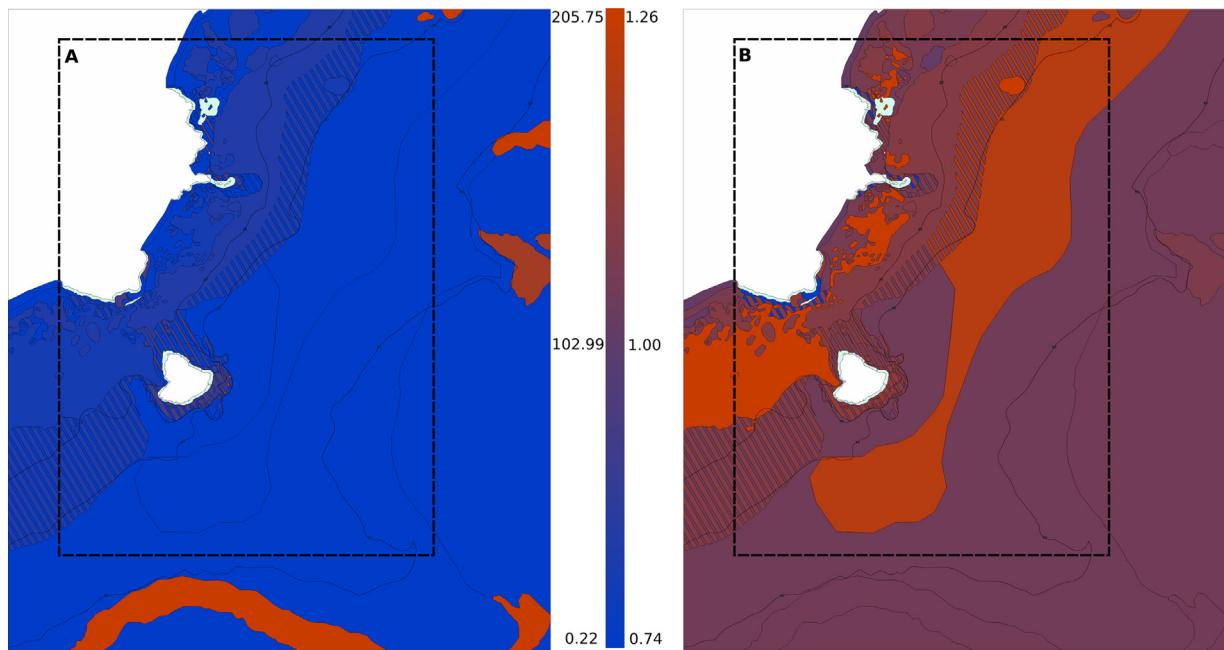


Fig. 9. Spatial distribution of Throughput (A) and Information (B), boundaries of MPA in dashed lines; in legend minimum, central and maximum values of Throughput are reported at left of the chromatic scale in 1E02 while minimum, central and maximum values of Information are reported at right.

the average. Fine sands, coralligenous and biodetritics show values very close to the average (Fig. 6).

If spatial distribution is considered (Fig. 7), high exergy values are all located within 30 m depth, mostly in correspondence of *Posidonia*. Similarly, the habitats showing higher values of specific exergy are located within 30 m depth, thus excluding terrigenous mud that is the habitat located farthest from the coast.

3.2. Network analysis for functional complexity

Throughput ranges between $2.23\text{E+}01 \text{ gCm}^{-2} \text{ a}^{-1}$ (biodetritics) and $2.06\text{E+}04 \text{ gCm}^{-2} \text{ a}^{-1}$ (coralligenous). Average value is $4.13\text{E+}03 \pm 6.33\text{E+}03 \text{ gCm}^{-2} \text{ a}^{-1}$, and only four habitat types exceed this value: coralligenous, *Paramuricea*, *Stylocaulon* and sciophilic algae (Fig. 8). Biodetritics and terrigenous muds also display very low values.

Information ranges from $73.73\text{E-}01$ (*Acetabularia*) to $1.26\text{E+}00$ (*Posidonia*). The average value of $1.05 \pm 1.15\text{E-}01$ is exceeded by six habitat types: *Posidonia*, large bryozoa, *Stylocaulon*, dead matte, sciophilic algae, and *Paramuricea* (Fig. 8).

Considering the spatial distribution of throughput (Fig. 8), wide areas with high values are all located deeper than 50 m and correspond to the coralligenous. As far as information is concerned, wide areas with higher values occur at various depths. Areas covered with *Acetabularia*, which exhibits the lowest value, are concentrated near the coast (Fig. 9).

4. Discussion

In order to (1) synthesise information from the four calculated indices (exergy, specific exergy, throughput and information) and (2) better assess habitats' characteristics in complexity terms adopting a system perspective, radial plots of different habitats were drawn. To make indices comparable, values were standardised on a 0–1 scale, where 0 corresponds to the minimum value recorded and 1 to the maximum one. Plots are shown in Fig. 10.

Different quarters of the plots identify different facets of complexity:

- the first quarter characterises the extensive quantitative complexity since it is identified by the extensive measures influenced by the system size (exergy and throughput): if a habitat shows high values of these indices its degree of complexity is principally due to its ability to store great quantity of matter and to establish a wide number of huge exchanges among compartments.
- the second quarter characterises structural complexity since it is identified by thermodynamic measures (exergy and specific exergy) that relate with storages and the nature of matter that compose them in evolutionary terms.
- the third quarter characterises the intensive complexity since it is identified by measures not dependent on size but only from the intrinsic nature of the system (specific exergy and information): if a habitat shows great values of these indices its degree of complexity is principally due to the quality of the matter it stores and to the specialisation degree of exchanges.
- the fourth quarter characterises functional complexity, identified by the network analysis measures (throughput and information) that estimate the ability to make the system working through the exchanges' network.

The greater the area occupied in each quarter, the greater the corresponding typology of complexity.

Seagrass meadows, and in particular those of *Posidonia*, demonstrate to be structurally and intensively complex, while coralligenous and *Paramuricea* facies emerge as functionally and extensively complex. *Acetabularia* proves to be the lowest complexity habitat. The remaining habitats show a moderate degree of intensive and functional complexity while structural and extensive seem to be very low.

4.1. OCI (Overall Complexity Index) evaluation

OCI is an additive combination of the four system indices considered, which examines and assesses overall ecosystem complexity. The numerical values of the indices from standardisation procedure and measure of overall complexity are reported in Fig. 11.

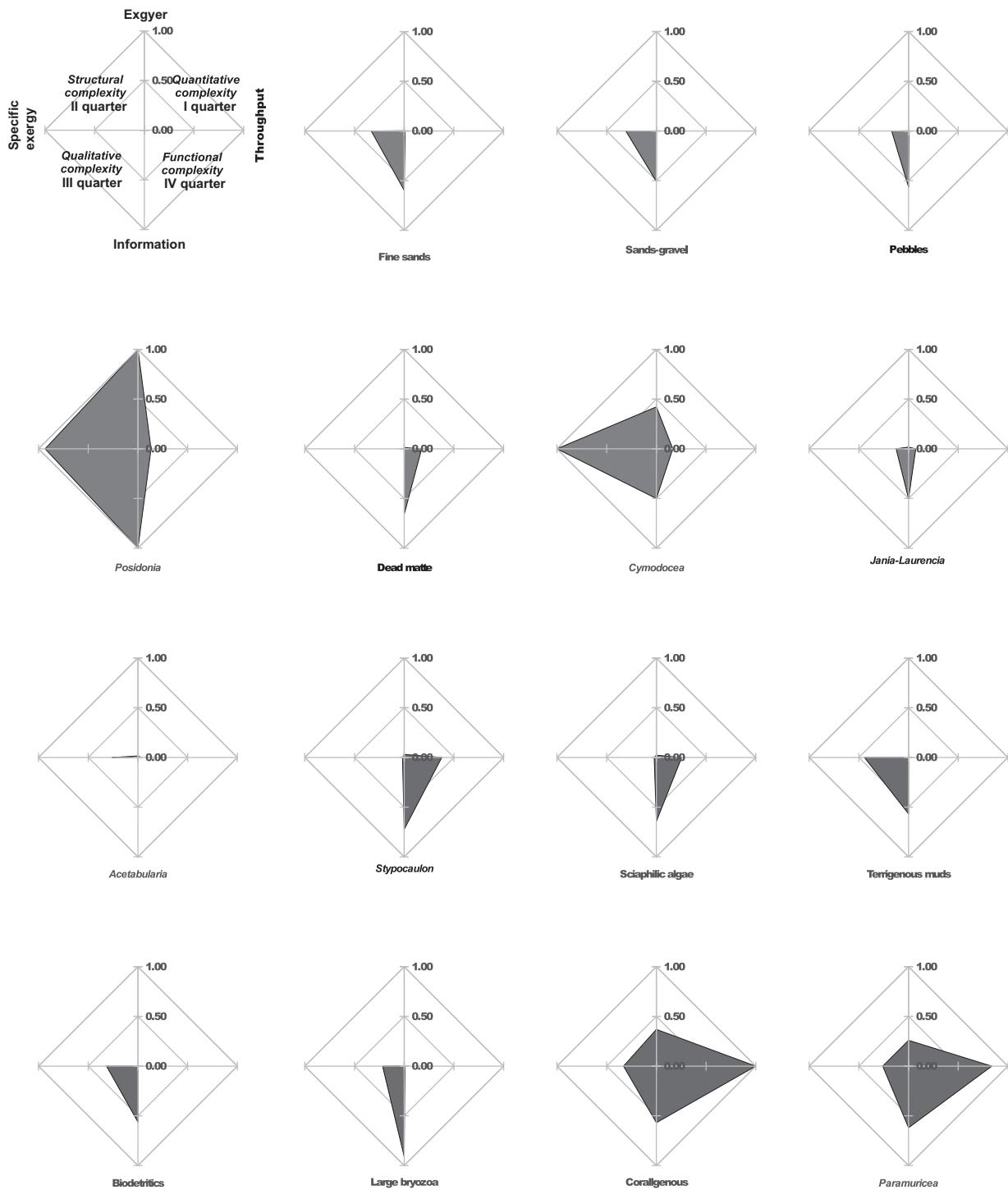


Fig. 10. Radial plots of the habitats analysed.

Minimum and maximum OCI potential scores, equal to 0 and 4 respectively, are not present. This means that the habitats considered never display the minimum or the maximum values for the four complexity indices contemporaneously.

The minimum OCI value is shown by *Acetabularia*, as expected. Four habitats show an OCI value higher than the average: *Posidonia* shows the greatest one, followed by coralligenous, *Cymodocea*, and finally *Paramuricea*.

Some main characteristics can be found analysing Fig. 11.

- The majority of habitats show the same level of intensive functional complexity since information varies in a restricted

range of values (if *Acetabularia*, *Posidonia* and large bryozoa are excluded).

- In hard bottom habitats, coralligenous excluded, complexity is mainly functional since thermodynamic parameters, in *Stylocaulon* and *sciaphilic algae*, are very low.
- Soft bottom habitats show very low levels of extensive complexity since throughput and exergy are almost scarce, in relative terms, in fine sands, sand-gravel, pebbles, terrigenous muds and biotritrics; here, complexity can be ascribed to the inner and intrinsic organisation of the habitat.
- Dead matte and large bryozoa habitats show particular patterns if compared with other soft and hard bottoms, showing

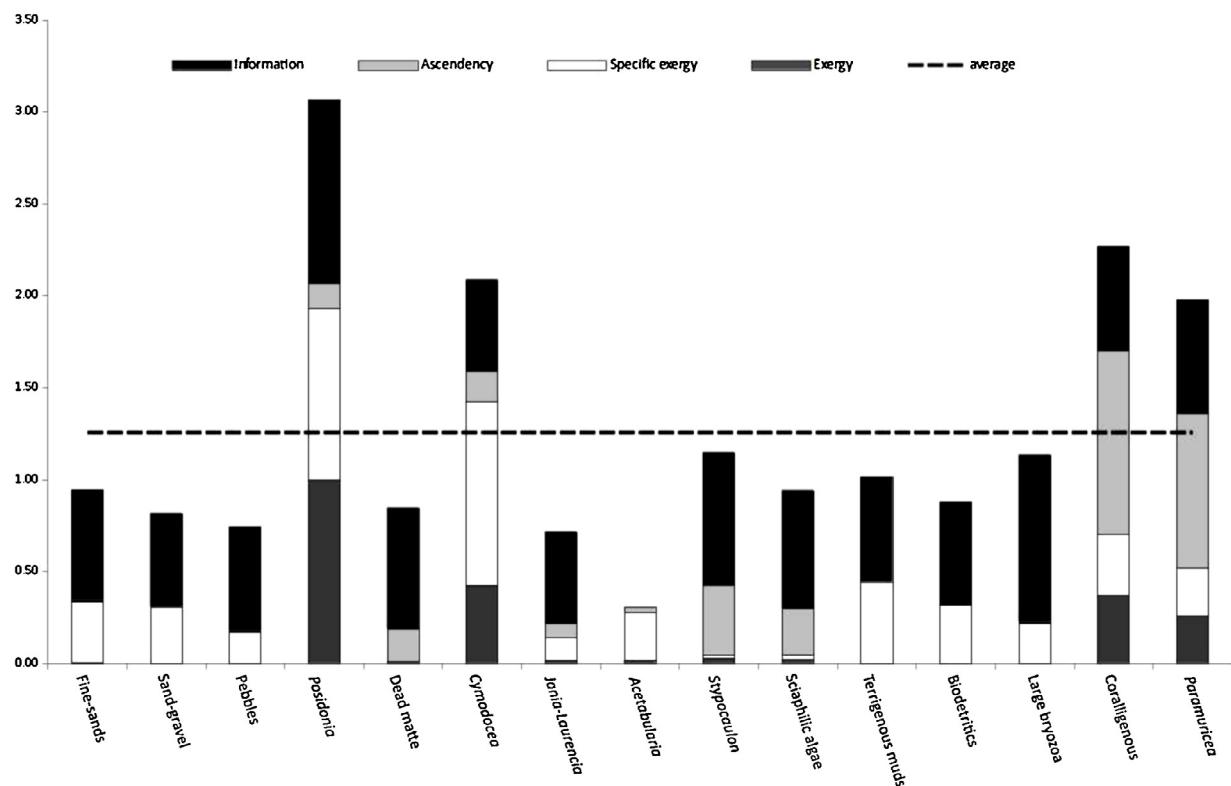


Fig. 11. OCI of different habitats. The dashed line depicts the average value for Bergeggi area.

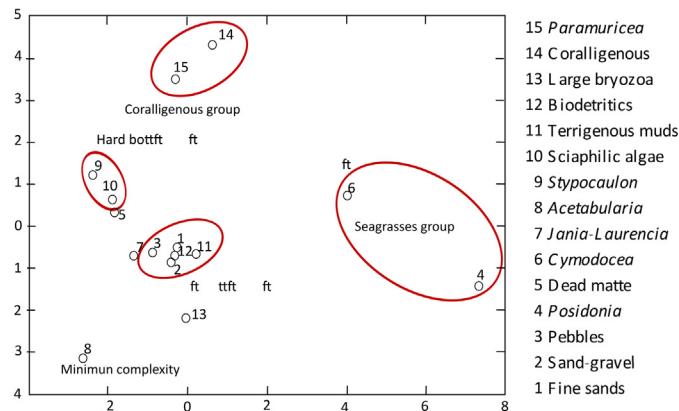


Fig. 12. MDS and main complexity clusters.

respectively high functional complexity in absence of structural and low extensive complexity.

As a consequence, habitats seem to group in specific clusters and, in order to verify this hypothesis, an MDS (MultiDimensional Scaling) has been produced employing calculated habitats' values for exergy, specific exergy, throughput and information.

From MDS (Fig. 12), the previous groups can be identified and characterised as follows.

- Seagrass group: high level of complexity, mainly structural.
- Coralligenous group: high level of complexity, mainly functional.
- Soft bottoms group: low extensive complexity.
- Hard bottoms groups: low structural complexity.
- Minimum complexity value: *Acetabularia*.

Results obtained are consistent with traditional floral and faunal studies and seascape approaches. These traditional 'naturalistic' approaches usually attach more interest to seagrass meadows and hard bottoms with respects to soft bottoms (Bianchi et al., 2005). Seagrasses and the coralligenous are priority habitats according to RAC-SPA criteria, being characterised by high vulnerability, rarity, and heritage, aesthetic and economic values. OCI indicates they also own a high complexity level, thus confirming the compulsionness of their conservation. Seagrass meadows are widely recognised as key ecosystems in shallow coastal waters because of their ability to support a complex trophic food web and a detritus-based food chain (Pergent et al., 2014). Coralligenous is a habitat unique to the Mediterranean Sea, and a hotspot of biodiversity in the subtidal (Ballesteros, 2006). The great complexity in seagrass meadows arise from their ability to efficiently convert solar radiation into organic matter; in the coralligenous, complexity level is associated with the highly functional trophic network, based on suspension feeders, able to convey the particulate organic matter suspended in the water column to the benthic system (Ott and Fedra, 1977). Naturalists also attain priority importance to the large bryozoa habitat (Bianchi, 2009), which nonetheless exhibits an OCI value lower than the average. Current naturalist evaluations rely upon expert judgement. The inherent risk of ambiguity and biased opinions may be partially avoided using converging consensus techniques such as the so-called Delphi method (Worrell et al., 2013) and others (Kontogianni et al., 2015). However, expert judgement remains somewhat prone to subjectivity, while OCI represents a synthetic, objective and quantitative approach that can be repeated over time and compared through different areas. The two methods should be employed in synergy and may reciprocally feed each other with information (Guidetti et al., 2014). The European Union Marine Strategy Framework Directive (MSFD) and similar marine legislations worldwide recommend the combined use of expert judgement and biotic indices to assess the quality of marine environments (Borja et al., 2012).

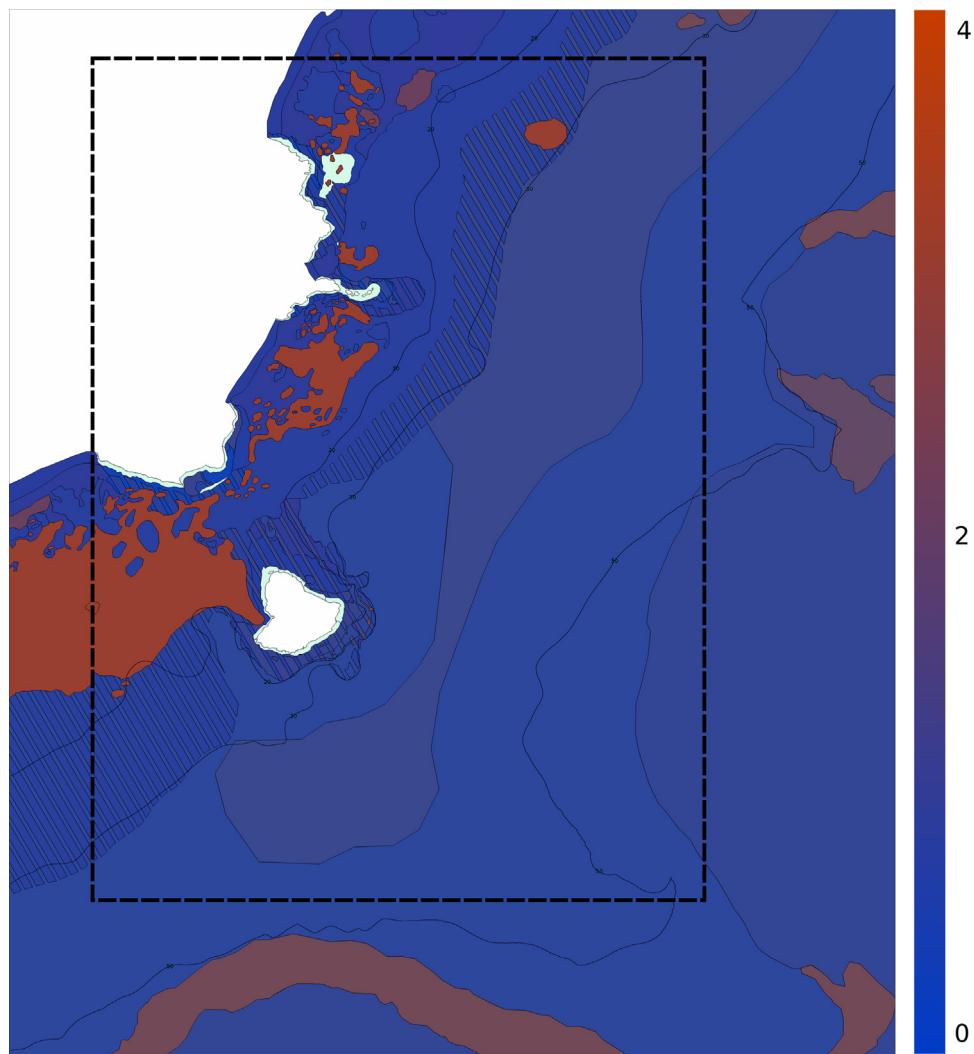


Fig. 13. Spatial distribution of OCI, boundaries of MPA in dashed lines.

4.2. Complexity mapping

OCI provides an objective and synthetic quantitative measure of complexity. This allows mapping complexity for management purposes.

As a consequence and as final elaboration, the spatial distribution of complexity in the area has been obtained and it is shown in Fig. 13. Complexity is concentrated in some hot spots located within 30 m or beyond 50 m, due to the presence of seagrasses (*Posidonia* and/or *Cymodocea*) and coralligenous habitats, respectively. The greatest part of the Bergeggi seafloor surface is occupied by habitats with low complexity values in relative terms and in particular soft bottoms with low quantitative complexity occupy over the 50% of total surface

While the MPA hosts both *Posidonia* and *Cymodocea*, most coralligenous habitats are located outside the MPA. Therefore, these high complexity areas adjacent to the existing MPA should be considered for protection: their conservation importance (UNEP-MAP-RAC/SPA, 2008) is here fully supported by the high complexity value. We recommend that the current MPA administration addresses its efforts to envisage the feasibility of enlarging its extent to include those coralligenous habitats that presently lay unprotected outside its boundaries.

5. Conclusions

A total of 15 benthic habitats in the Bergeggi area, partially comprised in a Marine Protected Area, have been analysed in order to investigate the issue of ecological complexity and provide a synthetic, objective and quantitative measure. To this purpose, a thermodynamic analysis based on exergy and specific exergy and a network analysis based on throughput and information were employed. This allowed estimating 4 components of complexity: structural, functional, extensive and intensive.

Seagrass meadows and coralligenous resulted extremely important in the context of the studied area, being able to contribute to over the 70% of total biomass in the area, to show the greatest biomass per unit area and to record the highest values of complexity. In particular, *Posidonia* demonstrated to be structurally and intensively complex, while coralligenous and *Paramuricea* facies emerge as functionally and extensively complex. *Acetabularia* proves to be the habitat with lowest complexity. The remaining habitats show a moderate degree of intensive and functional complexity associated with low values of structural and extensive components. Soft bottom habitats, which occupy over the 50% of the Bergeggi area, show very low levels of extensive complexity. In hard bottom habitats, coralligenous excluded, complexity is mainly

functional since thermodynamic parameters, in *Stylocaulon* and *Sciaphilic* algae, are very low.

In order to synthesise information from the four components, the additive index OCI was created. The minimum OCI value is shown by *Acetabularia*, as expected. Four habitats show an OCI value higher than the average: *Posidonia* shows the greatest one, followed by coralligenous, *Cymodocea*, and finally *Paramuricea*.

Habitats can be then grouped in five clusters: (1) seagrass group (high level of complexity, mainly structural); (2) coralligenous group (high level of complexity, mainly functional); (3) soft bottoms group (low extensive complexity); (4) hard bottoms groups (low structural complexity); (5) *Acetabularia* (minimum complexity value).

OCI provided a quantitative support to studies previously performed, attaching interest to seagrass meadows and hard bottoms with respects to soft bottoms and identifying seagrasses and the coralligenous as priority habitats. Being quantitative and obtained by means of a defined and repeatable procedure, OCI not only gives an objective evidence of the importance of these habitats but also allows mapping and monitoring them through time, facilitating their management. Finally, even if OCI has been here applied to a sub-system, the benthic compartment of the larger marine ecosystem, it is a very versatile tool, being applicable to whole ecosystems, either marine or terrestrial, and ecosystem compartments at whatever scale: opportunities arise for becoming a shared approach to evaluate complexity.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.01.029>.

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