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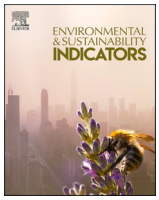

Ericaria amentacea natural capital: the hidden treasure of Mediterranean midlittoral environments

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ABSTRACT

In Italy, the "Environmental Accounting in Italian Marine Protected Areas" (EAMPA) research program assessed the natural capital within Marine Protected Areas (MPAs). The program did not include the midlittoral rocky habitats, where several brown algae of the complex *Cystoseira sensu lato* thrive, representing ecosystem engineers. Among these, *Ericaria amentacea* is a sensitive species undergoing decline across the Mediterranean. In this study, the value of *E. amentacea* stands was assessed in two MPAs (Portofino MPA-PFN and Ciclopi Islands MPA-CIC) during two phenological stages: (quiescent and vegetative). Results showed no significant differences between MPAs, while temporal differences were significant. Indeed, integrating the separate contributions of the perennial cauloid and deciduous fronds allowed a more refined assessment of the effective value of *E. amentacea* canopies and an estimate of their flows. During the vegetative phase, when branch grow (flows), the value concentrates in the canopy (PFN: quiescent phase 1.64E+12 sej/m^2, vegetative phase 6.21E+12 sej/m^2; CIC: quiescent phase 1.28E+12 sej/m^2, vegetative phase 2.96E+12 sej/m^2). These findings highlight the role of this habitat as a biodiversity hotspot.

1. Introduction

Natural capital is defined as the totality of natural assets, both renewable and non-renewable (e.g., geology, soil, air, water, living organisms) (de Groot et al., 2010). Hence, it is a stock that generates resource flows (Ekins et al., 2003) which are required to support ecosystem functions. Among these functions, some provide direct or indirect benefits humans, representing the so-called 'ecosystem services' (Natural Capital Committee, 2021). The concept of natural capital is therefore intrinsically anthropocentric, emphasizing how nature supports human well-being and is central to sustainable development (Bateman and Mace, 2020). In this perspective, several innovative advances have been done in the last decades to unravel the relationship between decision-making and natural capital accounting. For instance, international bodies such as the World Bank and the United Nations Environment Programme (UNEP) have proposed metrics to assess the physical and monetary value of natural capital (Bateman and Mace, 2020). In Europe, natural capital accounting is recognized within the EU Biodiversity Strategy to 2020 (European Commission, 2011) as well as in the EU's Seventh Environmental Action Programme (7th EAP) (European Commission, 2013), while key institutions (DG Environment, Eurostat and the European Environment Agency) have promoted

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ecosystem accounting initiatives (Capriolo et al., 2020; Vigerstol and Aukema, 2011; Nedkov and Burkhard, 2012; Zulian et al., 2013; Burkhard and Maes, 2017; La Notte et al., 2017).

In Italy, the Ministry of the Environment and Energy Security (formerly the Ministry of the Environment and the Safeguard of the Territory and the Sea) launched and implemented the research program "Environmental Accounting in Italian Marine Protected Areas" (EAMPA). The aim of EAMPA was to develop a framework for assessing the stock of natural capital and ecosystem services provided by Marine Protected Areas (MPAs) using a multidisciplinary (ecological and economic) approach (Franzese et al., 2017; Picone et al., 2017; Vassallo et al., 2017; Paoli et al., 2018, 2020; Buonocore et al., 2020a, 2020b, 2021; Rigo et al., 2021; Dapueto et al., 2022; Bordoni et al., 2023, Silva et al., 2024). This framework was applied to the coastal ecosystems in the Italian MPAs, but the intertidal habitats were not included. The omission of the intertidal (defined as, the transitional zone between low and high tide) likely reflect the microtidal nature of the Mediterranean, where the mean tidal range is about 0.20–0.30 m (Lozano and Candela, 1995; Tsimplis et al., 1995; Marra et al., 2017). This zone is particularly sensitive, as it is exposed to strong fluctuations in environmental conditions (Helmuth et al., 2006; Blanchette et al., 2008) and is highly vulnerable to anthropogenic pressures (Verlaque and Tiné, 1979; Benedetti-Cecchi et al., 2001; Soltan et al., 2001; Mancuso et al., 2018). In the Mediterranean midlittoral zone, some fucoid within the *Cystoseira sensu lato* (hereinafter *Cystoseira* s.l.) complex play a crucial role as habitat-formers. *Cystoseira s.l.* comprise c three distinct genera: *Cystoseira, Ericaria*, and *Gongolaria* (Novoa and Guiry, 2019). These taxa play a crucial role as ecosystem engineers, establishing and maintaining a species-rich assemblages (Ballesteros, 1990a,b; 1998, 2009; Sales and Ballesteros, 2009; Cheminée et al., 2013; Blanfuné et al., 2016; Thibaut et al., 2016; Cannarozzi et al., 2023a,b; Mancuso et al., 2023). Intertidal *Cystoseira s.l.* species are recognized as indicators of water and ecosystem quality by the Water Framework Directive (WFD, 2000/60/EC). Indeed, their presence and continuity are used in the calculation of the CARLIT index (CARtography of LITtoral and upper-sublittoral benthic communities) (Ballesteros et al., 2007; Mangialajo et al., 2007), which describe the ecological status of a water body based of the composition and structure of midlittoral rocky fringe communities.

These macroalgae are listed as priority species under the Barcelona Convention, protected by the Bern Convention and recognized as endangered by international organizations such as RAC/SPA, MedPan. Specifically, *Ericaria amentacea* (C. Agardh) Molinari & Guiry, endemic to the Mediterranean, is one of the most vulnerable and its loss and degradation due to direct and indirect human impacts are reported along the Mediterranean coasts (Benedetti-Cecchi et al., 2001; Thibaut et al., 2005, 2014; Mangialajo et al., 2007; Mangialajo et al., 2008a,b; Strain et al., 2014; Mineur et al., 2015; Falace et al., 2018; Mancuso et al., 2018; Blanfuné et al., 2019; De La Fuente et al., 2019; Bordoni et al., 2025).

Ericaria amentacea is constituted by a caespitose thallus made by a perennial basal short cauloid (Figure_1) and numerous deciduous annual branches (Figure_1) (Gómez Garreta et al., 2002; Mangialajo et al., 2008a,b; Giaccone, 2009; Mannino et al., 2009; Cormaci et al., 2012; Taşkin et al., 2012). Like all the *Cystoseria s.l.* complex species, *E. amentacea* exhibits marked seasonal phenology: new branches emerge from the cauloid in spring, and fully develop in summer, reaching up to 40–50 cm (Gómez Garreta et al., 2002; Mangialajo et al., 2008a,b; Giaccone, 2009; Cormaci et al., 2012; Rendina et al., 2023). From August to October, the branches are shed, and only the cauloid remains (Gómez Garreta et al., 2002; Mangialajo et al., 2008a,b; Giaccone, 2009). From a natural capital theory perspective, the cauloid represents the stock while the branches are the annual flows generated by the stock itself.

The aim of this study is to fill the current knowledge gap on the natural capital of *E. amentacea* canopies within two MPAs, focusing on

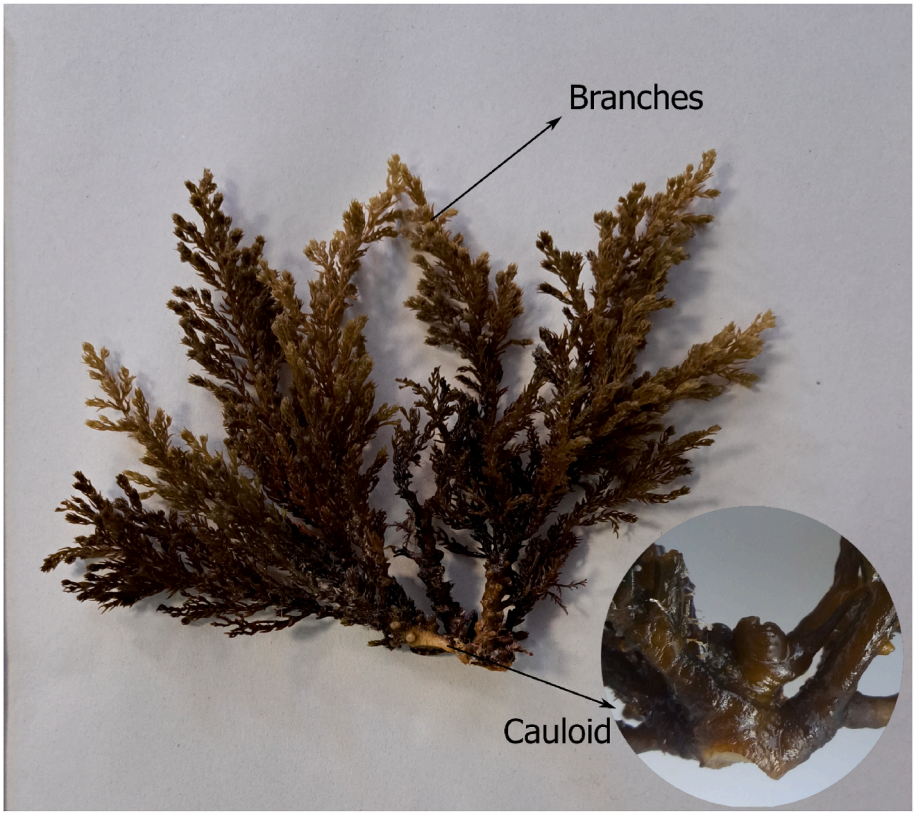

Fig. 1. Ericaria amentacea *thallus showing the perennial cauloid and annual branches.*

their spatial and phenological dynamics. To this end, both natural capital and annual flows components were assessed at different times and in different sites. Surveys of *E. amentacea* were carried out in two Mediterranean Marine Protected Areas (Portofino MPA in the northwest and Ciclopi Islands MPA in the south centre) characterised by different climate and interannual variability.

2. Materials e methods

2.1. Study area

The sampling was performed in two sites, around 1000 km apart: the Portofino MPA (Ligurian Sea, NW Mediterranean Sea; hereinafter PFN) and the Ciclopi Islands MPA (Ionian Sea, hereinafter CIC) (Figure_2) (Giakoumi et al., 2013). The experimental sites were located within MPAs where most human activities are regulated or excluded (Venturini et al., 2016; Paoli et al., 2017), thereby reducing the potential influence of cumulative anthropogenic pressure on natural capital estimates.

Both MPAs are located in the Temperate Division, Tyrrhenian Province (Blasi et al., 2014), but PFN is located in the Northern and Central Tyrrhenian Ecoregional section, characterized by average summer temperature of 24 °C, winters average temperature of 11 °C, and annual rainfall of 1300 mm/y (Brandolini et al., 2006; Faccini et al., 2008; Sacchini et al., 2012). CIC, instead, is located in the Sicilia Ecoregional section, where average summer and winter temperatures are 27 °C and 10 °C respectively, and annual precipitation average 680 mm/y (Brandimarte et al., 2011; Colonese et al., 2011; Sciandrello et al., 2017).

PFN, established in 1998, covers 346 ha and encompasses three small coastal municipalities. Its recognized for the high natural value of terrestrial and marine landscape and rich biodiversity (Paoli et al., 2017; Vassallo et al., 2021a). PFN MPA has been included as a Site of Community Importance in the European Natura 2000 Network and since 2005 has been designated a Specially Protected Area of Mediterranean Interest (SPAMI) according to RAC/SPA Office (Venturini et al., 2016; Paoli et al., 2017).

The area surrounding PFN has the characteristics of a tourist resort with an economy mainly linked to the tertiary sector (Paoli et al., 2017). PFN is surrounded by ports and marinas: from the western part more than 5000 recreational boats can reach the MPA in a few hours, while in the eastern part there are a total of 2000 recreational boats (Venturini et al., 2021).

CIC, established in 1989, covers a surface of 623 ha. In the north, the coastline is characterized by four islets with vertical slopes and small pebble beaches, while the coasts in the west and south are flat and intersected by dune systems. This MPA includes three marinas, the largest of which accommodates about 380 boats in summer. In both MPAs, the following activities are allowed for licenced users: sunbathing, diving, professional fishing, recreational fishing, and recreational boating (Costanzo et al., 2021).

2.2. Assemblage modelling

At both locations, *Ericaria amentacea* was sampled at two phenological stages: the quiescent phase (October 2020) and the vegetative phase (July 2021) (Figure_3), the latter corresponding to the peak of frond development (Cannarozzi et al., 2023a,b).

During each sampling campaign, 15 random samples were taken from sub-horizontal rocky reefs in the swash zone (0–0.5 m depth) at each site, for a total of 60 samples. Each experimental site (~3 km long rocky coast stretch) was divided into three random sampling stations, with five replicate samples per station (n = 5), to obtain representative samples set of *E. amentacea* assemblages. For sampling, a PVC cylinder (160 cm^2) was placed over the algal stands and a spatula was slid under the cylinder to scrape off *E. amentacea* and any associated organisms, following Cannarozzi et al. (2023a,b). Samples were then preserved in 4

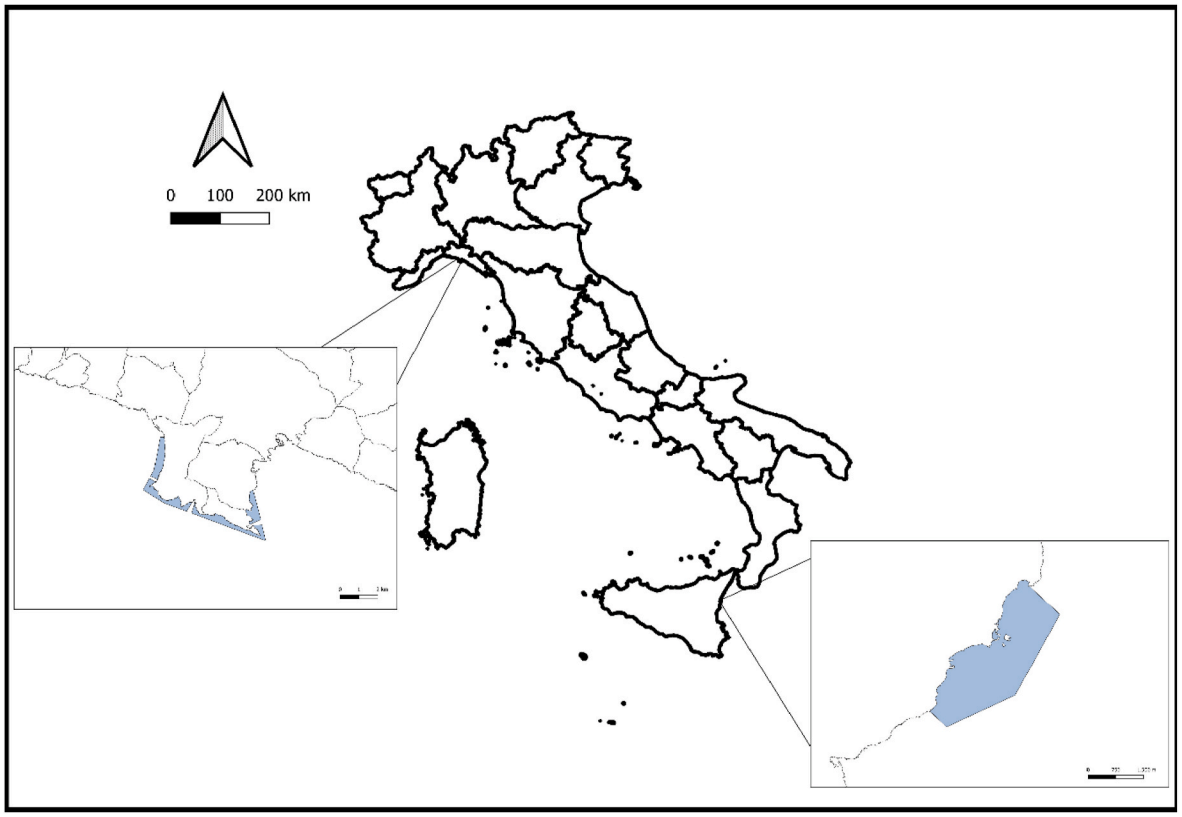

Fig. 2. study sites.

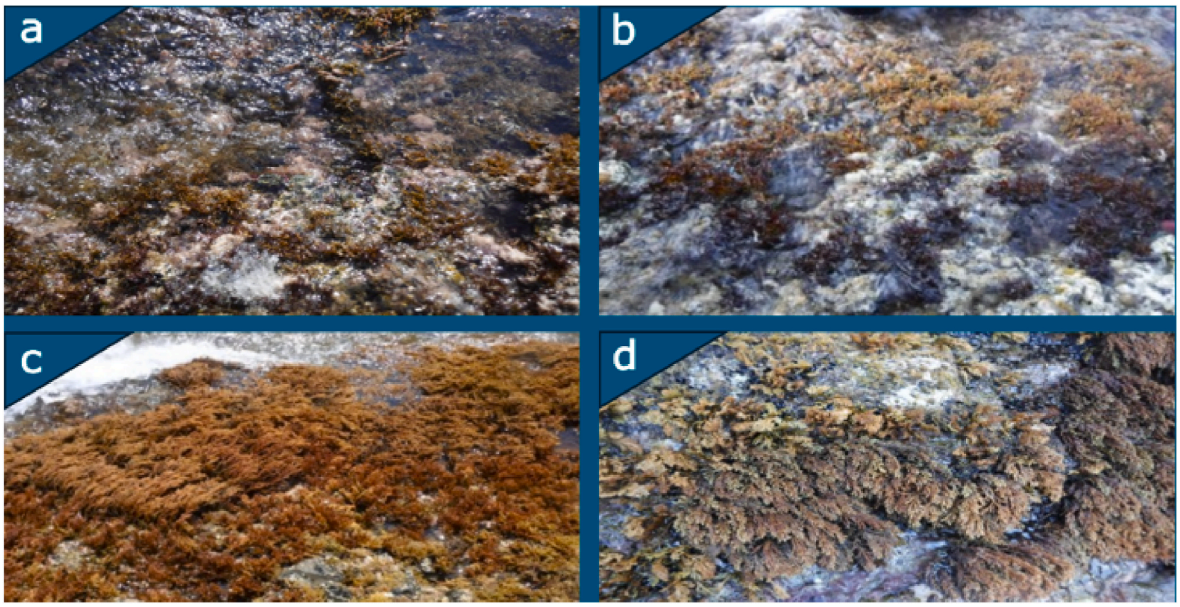

Fig. 3. Ericaria amentacea sampled during the a, b) quiescent phase in October and c, d) the vegetative phase in July.

% buffered formaldehyde-seawater solution and brought to the laboratory for subsequent processing. Samples were sieved through a 1-mm mesh and soaked in sea water for 24 h to remove formaldehyde residues. Samples were sorted by separating the organisms from the inorganic debris and carefully detaching epibionts (i.e., other algae and invertebrates). Macroalgae other than *E. amentacea* were pooled, whereas the invertebrates were classified according to major taxonomic groups (phylum or subphylum) and trophic guilds (i.e., predators, suspension-feeders, grazers, detritivores) (hereinafter referred to as groups). *E. amentacea* and the associated assemblage were then dried at 80 °C for 48 h, weighed and then burned at 500 °C for 4 h (*E. amentacea* and other algae) or at 550 °C for 1 h (macrozoobenthos). Samples were weighed to determine the total inorganic content and obtain as difference the ash-free dry weight (AFDW) and the amount of carbon contained in the organisms (gC) using conversion factors (Brey, 1990). Trophic levels were assessed using trophic web simulations according to Paoli et al. (2016), with biomasses calculated in gC. Results are expressed as biomass per unit area (gC/m^2) to ensure comparability with other studies and systems.

2.3. Natural capital evaluation

The emergy method (Odum, 1988, 1996) has recently been used to estimate the value of natural capital (Tilley, 1999; Tilley and Swank, 2003; Brown et al., 2006; Turcato et al., 2015; Vassallo et al., 2021b). Vassallo et al. (2017) developed a dedicated protocol for assessing natural capital in marine coastal environments, which has been widely adopted in subsequent research applications (Franzese et al., 2017; Picone et al., 2017; Paoli et al., 2018; De La Fuente et al., 2019; Buonocore et al., 2021; Rigo et al., 2021; Bordoni et al., 2023; Dapueto et al., 2020; Rigo et al., 2020; Rigo et al., 2024). Emergy measures natural capital through accounting for the natural resources used (directly and indirectly) to build up and maintain the biomass of all the organisms within the considered habitat (Buonocore et al., 2020). For this reason, this method is defined a "donor-side" approach (Ulgiati et al., 2011; Vassallo et al., 2017). Emergy is a thermodynamic methodology, in which all inputs supporting a system are expressed in terms of solar emergy Joule (sej), that equals the total amount of available solar energy used, directly or indirectly, to generate and maintain a product or a service (Odum, 1996). The solar emergy required to generate one unit of a product or a service is referred to as Unit Emergy Value (UEV, e.g. sej J^{-1} or sej g^{-1}). The emergy content of a system or a flow can be translated into currency equivalent values using the "emergy-to-money ratio" (EMR) (Lou and Ulgiati, 2013). The EMR represents the average amount of emergy needed to generate one unit of money in the national economy (Odum, 1996). This conversion translates the values of biosphere's investment in equivalents of a specific currency, and it allows to clarify the importance of natural capital to policy makers and other stakeholders, granting an effective communication in socio-economic contexts (Turcato et al., 2015, 2015a).

The natural capital stocked in *E. amentacea* canopies was assessed through the emergy analysis, following the procedure described by Vassallo et al. (2017) and Paoli et al. (2018, 2022). First, a system diagram of the *E. amentacea* assemblage is depicted by: 1) using the symbology proposed by Odum (1996), 2) considering all the information gathered about the system inputs and 3) identifying the components that characterize the system itself. According to Odum's symbology the boundaries of the system under study are represented by a main rectangle; the inputs are indicated on the left side and at the top of the rectangle. Within the rectangle, the components are arranged and represented according to their role: the producers as bullets and the consumers as hexagons. All these flows converge in the heat sink, indicating the heat losses that occur during each energy conversion according to the second law of thermodynamics.

Once the diagram has been sketched and then the system under study and its functioning have been depicted, it can be used as a basis to perform natural capital calculation. Natural capital assessment is based on the modelling of the trophic network composed by all the organism depicted in the diagram. To model the trophic network two basic information are required: the amount of stocked biomass and the trophic levels (TL) of the different groups. These data are used to calculate the primary production (PP) needed in space and time to initiate and maintain the studied trophic web. PP is then the quantity of autotrophs that, being the first basic component that fuels the trophic web, allows natural capital to be stocked and renewed in a defined surface for a certain number of years (Vassallo et al., 2017; Paoli et al., 2018). PP was calculated using the following equations (Pauly and Christensen, 1995; Vassallo et al., 2017):

$$PP = Ba + Be \quad (1)$$

where Ba is the biomass of primary producers (i.e. *E. amentacea* and other algae) and Be is the autotrophic biomass necessary to sustain consumers. In according to (Pauly and Christensen, 1995), Be is calculated as follows:

$$Be = \sum B_i * 7^{(TL_i - 1)} \; i = 1, 2, 3, \ldots n \quad (2)$$

where B_i and TL_i are respectively the biomass and trophic level of each group of heterotrophs occurring in the system.

In particular, the TL are calculated as 1 added to the mean trophic level of the preys (Lindeman, 1942; Rigler, 1975; Pauly et al., 2000).

The second step involved valuing all environmental inputs that support PP. The list of inputs, along with their calculation formulas is reported in Table 1, following Vassallo et al. (2017). Wave energy, although sometimes included in emergy assessments of oceanic intertidal environments (Berrios et al., 2021), was not accounted in this study. In the microtidal Mediterranean system under investigation, the study sites are located in the swash zone (0–0.5 m depth), where incoming wave energy has largely dissipated after passing through the breaker zone. Under these conditions, wave action functions primarily as a disturbance rather than a supporting factor, as it removes biomass and nutrients, facilitating the export of locally produced organic matter. This contrasts with high-energy oceanic intertidal systems, where wave energy can contribute positively to ecosystem functioning. Moreover, wave energy is generally excluded from natural capital assessments conducted under the protocol adopted here.

Once the value of each input is obtained in common units the matching emergy value of each input is obtained by multiplying common units by the corresponding UEV (Table 2). The reported UEVs consistent with those used in previous natural capital assessments (Buonocore et al., 2020a; b; De la Fuente et al., 2019; Franzese et al., 2017; Picone et al., 2017; Paoli et al., 2018; Rigo et al., 2021) ensuring comparability and potential integration with other studies. For the same reason, the baseline adopted was that of Brown and Ulgiati (2010). Brown et al. (2016) recently updated the emergy baseline to 1.20 E+25 sej yr^{-1}: a scaling factor of 0.79, obtained as ratio between the two baselines, can be applied to update all the results of this study and of previous ones.

The natural capital value of the whole system is obtained from the sum of the emergy values of the inputs through the following algorithm:

$$\text{Maximum (carbon, nitrogen, phosphorus)} + \text{Maximum (solar radiation, rain, wind, currents)} + \text{runoff} + \text{tides} + \text{geothermal heat} \quad (3)$$

Carbon, nitrogen and phosphorus as well as solar radiation, rain, wind, and currents are considered co-product groups (nutrients and environmental resources respectively), i.e., resulting from the same processes at the biosphere level. For this reason, only the largest values within each group is included in the calculation of the emergy associated with *E. amentacea* assemblages (Odum, 1996; Vassallo et al., 2017; Paoli et al., 2018; De La Fuente et al., 2019). As with biomass values calculated for assemblage modeling, assemblage emergy results are expressed per unit area (sej/m^2). To convert biophysical values (sej/m^2) into monetary equivalents (em€/m^2), the emergy results are divided by the Emergy Money Ratio (EMR). According to Pereira et al. (2013) and to previous studies regarding natural capital and in order to compare results the 9.60E+11 sej/€ EMR value is here applied (Buonocore et al., 2020a; b; De la Fuente et al., 2019; Franzese et al., 2017; Picone et al., 2017; Paoli et al., 2018; Rigo et al., 2021).

Table 2
employed UEVs (baseline Brown and Ulgiati, 2010).

Inputs	UEVs	Unit	Reference
Carbon	1.02E+08	sej/g	Campbell et al. (2014)
Nitrogen	7.40E+09	sej/g	Odum (1996)
Phosphorus	2.86E+10	sej/g	Odum (1996)
Solar radiation	1.00E+00	sej/J	By definition
Rain	2.93E+04	sej/J	Odum (1996)
Wind	2.41E+03	sej/J	Odum (1996)
Geothermal heat	5.53E+04	sej/J	Brown and Ulgiati (2010)
Marine current (kinetic energy)	1.77E+07	sej/J	Odum (1996)
Marine current (geopotential energy)	3.80E+04	sej/J	Campbell et al. (2005)
Tides	2.71E+04	sej/J	Brown and Ulgiati (2010)
Runoff	6.61E+04	sej/J	Odum (1996)

2.4. Statistical analysis

Analysis of variance (ANOVA) was performed to test for variations in the total natural capital (sej/m^2) of *E. amentacea* stands between sites and sampling times. The design for the analysis consisted of three factors, Time (Ti, fixed, two levels, quiescent phase and vegetative phase), Site (Si, fixed, two levels, PFN and CIC) and Station (St(Si), random, with three levels, nested in Si) with $n = 5$ replicates. The same analysis was performed separately for autotrophic and heterotrophic natural capital (sej/m^2), to test for spatial and temporal variations in these two

Table 1
calculation formulas for the natural capital emergy inputs of marine habitats.

Inputs	Formula	Unit	References
Carbon	Benthic biomass	g	Vassallo et al. (2017)
Nitrogen	Benthic biomass ·7/41	g	Vassallo et al. (2017)
Phosphorus	Benthic biomass/41	g	Vassallo et al. (2017)
Solar radiation	annual solar radiation per unit area · (1-albedo) · area · time for stocks formation	J	Vassallo et al. (2017)
Rain (chemical energy)	annual rainfall · Gibbs free energy · water density · area · time for stocks formation	J	Odum (1996)
Wind	air density · drag coeff. · (wind speed · geostrophic wind velocity)^3 · area · seconds per year · time for stocks formation	J	Odum (1996)
Geothermal heat	area · geothermal flux · time for stocks formation	J	Odum, 1988
Marine current (kinetic energy)	1⁄2 · height water evaporated per year · (current velocity)^2 · supporting time · water sea density	J	Campbell et al. (2005)
Marine current (geopotential energy)	1⁄2 · height of water evaporated on average in the Mediterranean due to currents^2 · water sea density · gravity · supporting time	J	Odum (1996)
Tide	1⁄2 · tides per year · (height)^2 · density sea water · supporting time ·gravity	J	Odum (1996)
Runoff	(annual rainfall – evaporation – aquifer infiltration) · water density · Gibbs free energy · catchment area	J	Odum (1996)

components contributing to the total natural capital of *Ericaria amentacea* assemblages.

Prior to analysis, normal distribution of sample means and variance homogeneity were checked through the Shapiro-Wilk test and the Cochran's *C*-test, respectively. In all cases, logarithmic data transformation was necessary to stabilize variance. Although data transformation to meet ANOVA's assumptions may be not always recommended due to potential issues related to result interpretation and power of analysis (O'Hara and Kotze, 2010; Stroup, 2015), it still represents a valid strategy to address heterogeneous variances in the data (Ribeiro-Oliveira et al., 2018). Logarithmic transformation of data remains a suitable option when mean values are always large and dispersion around means relatively small, as in our case (O'Hara and Kotze, 2010). However, as log-transformed data may lead to excessive conservative tests and loss of power (Stroup, 2015), results should be interpreted with caution.

3. Results

3.1. Assemblage modelling

Autotrophic components were distinguished in *Ericaria amentacea* and "other algae", while heterotrophic components were subdivided into Porifera suspension-feeders, Cnidaria suspension-feeders, Mollusca suspension-feeders, Mollusca grazers, Crustacea grazers, Crustacea predators, Crustacea detritivores, Crustacea suspension-feeders, Annelida detritivores, Annelida predators, Annelida suspension-feeders, Nematoda mix, Echinodermata suspension-feeders, Echinodermata detritivores, Bryozoa suspension-feeders, Platyhelminthes predators and Tunicata suspension-feeders. Biomass values for each group, expressed as gC/m^2, are reported in Table 3. At each site, Mollusca suspension-feeders accounted for the highest biomass in sampling periods. Trophic levels (TLs) for all groups are reported in Table 4.

3.2. Natural capital evaluation

The functioning of *E. amentacea* stands is shown in Figure_4. To create the emergy diagram, the Odum symbols were employed as described in section 2.3. Thus, the inputs are outside the system represented on the left and above, and the outputs are located outside the system on the right. Instead, inside the system the *E. amentacea* canopies components (producers and consumers) are represented.

The natural resources (inputs) associated with *E. amentacea,* canopies expressed in common units, are reported in Table 5 for autotrophs (auto) and heterotrophs (heter) at both sites and in the quiescent and vegetative phase.

The inputs converted in emergy units are shown in Figure_5.

According to Section 2.3, the most important inputs among co-product groups for both the autotrophic and heterotrophic components were nitrogen within the nutrients group (on average 45.01 % of the total natural capital value in PFN and 64.06 % in CIC) and rain within the environmental resources group (on average 12.11 % and 19.27 % respectively) (Figure_6).

Applying equation (3), the final natural capital values are presented in Figure_7 as monetary equivalent values. In both MPAs, *E. amentacea* recorded higher value in the vegetative phenological phase. In PFN, the vegetative phase value was 6.47 em€/m^2 (equal to 6.21E+12 sej/m^2) compared with 1.71 em€ m^2 (1.64E+12 sej/m^2) in the quiescent phase, a 3.79 fold increase. In CIC, the vegetative-phase value was 3.08 em€/m^2 (2.95E+12 sej/m^2) compared with 1.33 em€/m^2 (1.28E+12 sej/m^2) in the quiescent phase, a 2.31 fold increase.

Based on the total natural capital values reported in Figure_7, Figure_8 shows the percentage contribution of autotrophs (*E. amentacea* and other algae) and heterotrophs to the natural capital of the ecosystem. Across all sites and sampling times, *E. amentacea* contributed more than other algae to the autotrophic component.

On average, heterotrophs provided the largest share of total natural capital (mean = 51.54 %). However, patterns differed between sites: in PFN, the heterotrophic contribution was, on average, 2.19 times greater than that of autotrophs, whereas in CIC the autotrophic contribution was approximately three fold that of heterotrophs.

3.3. Statistical analysis

Statistical analysis of natural capital values (in emergy units) were performed to assess significant differences in space and time.

On average, the total natural capital of *E. amentacea* did not differ significantly between the two investigated MPAs (Table 6, Figure_7). ANOVA detected significant temporal variations consistent between the two sites, with significantly higher natural capital in the vegetative phase than in the quiescent phase (Table 6, Figure_7). A significant Ti × St(Si) interaction, indicated marked spatio-temporal variability in total natural capital at small scales (stations within sites). Results of ANOVA on the separate contribution of autotrophic and heterotrophic natural capital were consistent with those obtained analysing the natural capital of the *E. amentacea* canopy as a whole. In both cases, significant

Table 3
biomass values for taxonomic functional groups of Ericaria amentacea assemblage: susp = suspension-feeders, graz = grazers, pred = predators, det = detritivores, mix = omnivores.

	Site	PFN quiescent phase	PFN vegetative phase	CIC quiescent phase	CIC vegetative phase
	Groups	Biomass (gC/m^2)			
Autotrophs	*Ericaria amentacea*	1.56E+02	5.14E+02	3.04E+02	6.74E+02
	Other algae	2.48E+01	3.59E+00	1.56E+02	3.18E+01
Heterotrophs	Porifera susp	0.00E+00	0.00E+00	6.15E-01	0.00E+00
	Cnidaria susp	5.11E-02	2.18E-01	9.61E-02	9.81E-02
	Mollusca susp	4.24E+01	2.24E+02	1.68E+01	4.10E+01
	Mollusca graz	2.16E-01	7.61E-01	8.36E-01	7.55E-01
	Crustacea graz	5.35E-01	1.50E+00	2.67E+00	2.03E+01
	Crustacea pred	1.54E-01	4.32E-01	6.79E-03	9.96E-01
	Crustacea det	2.98E-01	8.39E-01	1.62E+00	1.24E+01
	Crustacea susp	1.31E+01	3.68E+01	1.55E+00	1.18E+01
	Annelida det	3.53E-02	2.96E-02	7.06E-02	1.27E-01
	Annelida pred	1.48E-01	1.24E-01	2.96E-01	5.32E-01
	Annelida susp	1.29E-01	1.08E-01	2.58E-01	4.64E-01
	Nematoda mix	7.01E-02	2.27E-03	0.00E+00	0.00E+00
	Echinodermata susp	0.00E+00	0.00E+00	1.75E-01	4.01E-01
	Echinodermata det	5.71E-02	4.84E-02	0.00E+00	0.00E+00
	Bryozoa susp	4.37E-01	2.65E-01	5.24E-01	3.02E-01
	Platyhelminthes pred	1.52E-02	0.00E+00	0.00E+00	0.00E+00
	Tunicata susp	5.22E-02	0.00E+00	1.53E-02	1.38E-01

Table 4
trophic levels for taxonomic functional groups of Ericaria amentacea *assemblage: susp=suspension-feeders, graz = grazer, pred = predator, det = detritivores, mix=omnivores.*

	Site	PFN quiescent phase	PFN vegetative phase	CIC quiescent phase	CIC vegetative phase
	Groups	TL			
Autotrophs	*Ericaria amentacea*	1.00	1.00	1.00	1.00
	Other algae	1.00	1.00	1.00	1.00
Heterotrophs	Porifera susp	–	–	2.00	–
	Cnidaria susp	2.00	2.00	2.00	2.00
	Mollusca susp	2.00	2.00	2.00	2.00
	Mollusca graz	2.00	2.00	2.00	2.00
	Crustacea graz	2.00	2.00	2.00	2.00
	Crustacea pred	3.00	3.00	3.02	3.02
	Crustacea det	2.00	2.00	2.00	2.00
	Crustacea susp	2.00	2.00	2.00	2.00
	Annelida det	2.00	2.00	2.00	2.00
	Annelida pred	3.02	3.00	3.05	3.02
	Annelida susp	2.00	2.00	2.00	2.00
	Nematoda mix	2.43	2.28	–	–
	Echinodermata susp	–	–	2.00	2.00
	Echinodermata det	2.00	2.00	–	–
	Bryozoa susp	2.00	2.00	2.00	2.00
	Platyhelminthes pred	3.00	–	–	–
	Tunicata susp	2.00	–	2.00	2.00

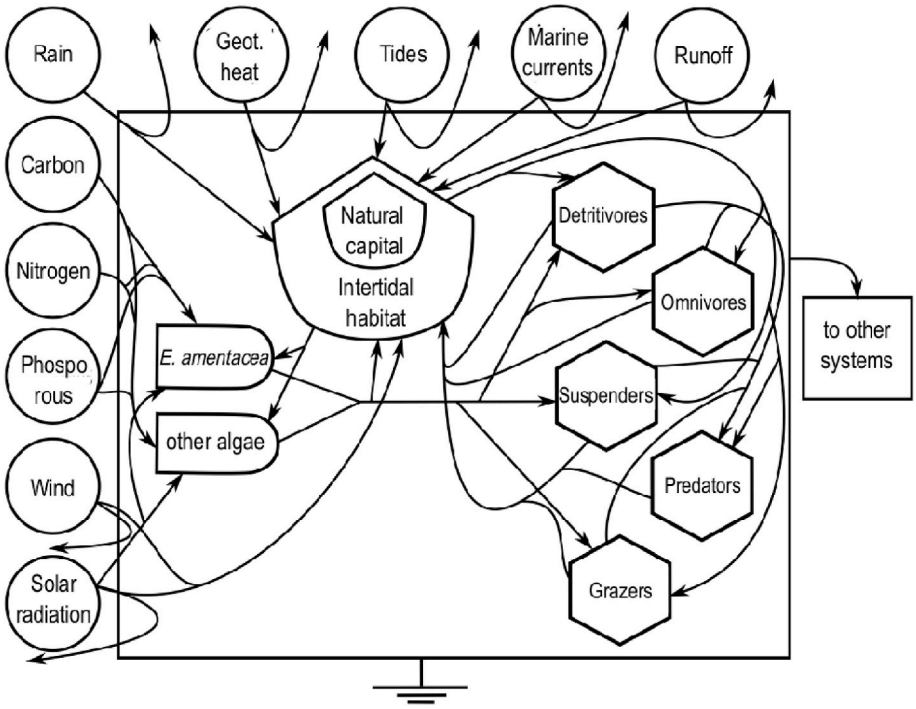

Fig. 4. emergy *diagram of* Ericaria amentacea *canopies*.

Table 5
Ericaria amentacea *stands input values in common units for emergy calculation.*

Input (per m^2)	PFN quiescent phase		PFN vegetative phase		CIC quiescent phase		CIC vegetative phase	
	Auto	Heter	Auto	Heter	Auto	Heter	Auto	Heter
Carbon (g)	1.81E+02	4.18E+02	5.17E+02	1.88E+03	4.59E+02	1.93E+02	7.06E+02	6.95E+02
Nitrogen (g)	3.08E+01	7.14E+01	8.84E+01	3.20E+02	7.84E+01	3.30E+01	1.20E+02	1.19E+02
Phosphorus (g)	4.40E+00	1.02E+01	1.26E+01	4.57E+01	1.12E+01	4.71E+00	1.72E+01	1.69E+01
Solar radiation (J)	8.31E+08	1.11E+09	2.38E+09	4.98E+09	2.44E+09	5.93E+08	3.75E+09	2.13E+09
Rain (J)	2.85E+06	3.81E+06	7.72E+06	1.61E+07	5.70E+06	1.38E+06	1.55E+07	8.79E+06
Wind (J)	1.95E+07	2.61E+07	5.00E+07	1.05E+08	5.06E+06	1.23E+06	9.84E+06	5.59E+06
Geothermal heat (J)	9.11E+05	1.22E+06	2.61E+06	5.46E+06	3.09E+06	7.50E+05	4.75E+06	2.709E+06
Marine current (kinetic energy) (J)	1.23E+01	1.64E+01	3.52E+01	7.36E+01	4.87E+00	1.18E+00	7.48E+00	4.25E+00
Marine current (geopotential energy) (J)	4.67E+03	6.24E+03	1.34E+04	2.80E+04	1.19E+04	2.88E+03	1.83E+04	1.04E+04
Tides (J)	4.90E+05	6.56E+05	1.43E+06	2.98E+06	9.05E+05	2.20E+05	1.40E+06	7.98E+05
Runoff (J)	3.48E+06	4.65E+06	9.42E+06	1.97E+07	1.33E+04	3.34E+03	3.30E+04	1.87E+04

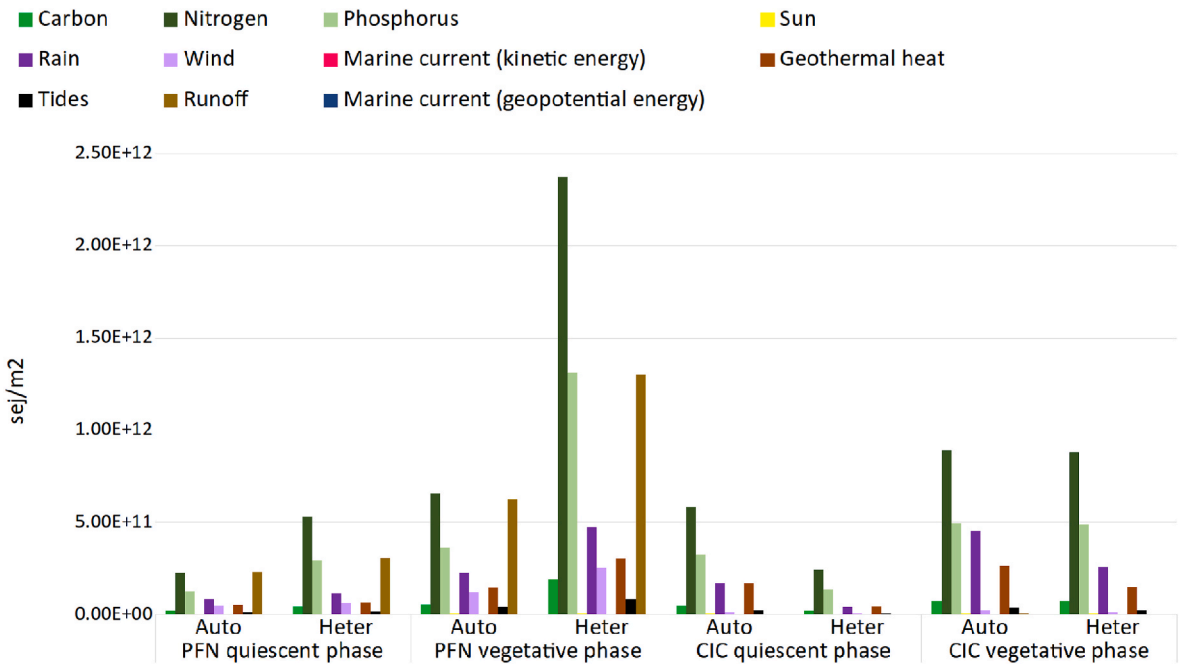

Fig. 5. emergy values of different *inputs to* Ericaria amentacea *stands*.

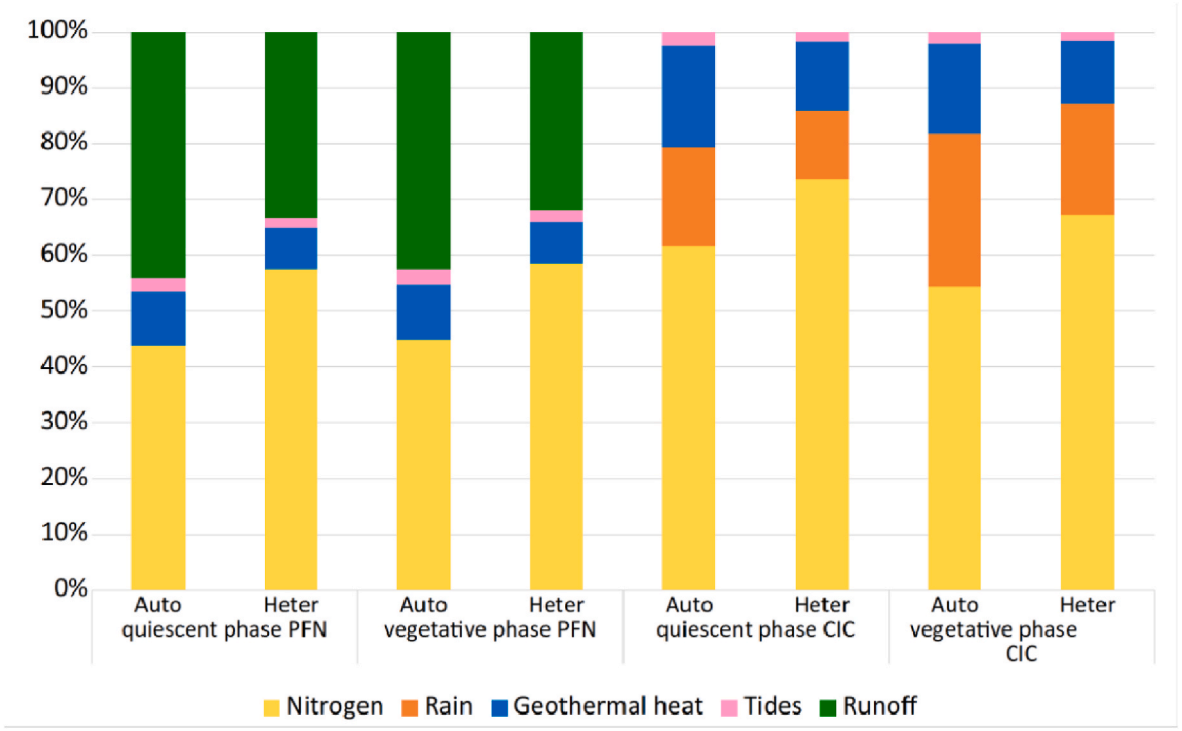

Fig. 6. percent contribution of different emergy inputs (the higher between co-products) to total budget.

temporal variations were found for the two MPAs, along with significant variation at the scale of stations within sites, but not between the two investigated sites (Table 7). However, inspection of graphs in Figure_8 suggested a higher contribution of autotrophic natural capital in CIC than in PFN, whereas the opposite concerned the heterotrophic component. In both cases, statistically significant differences between sites could have remained undetected due to the potential conservativeness of the analysis on log-transformed data.

4. Discussion and conclusions

The average natural capital of *E. amentacea* stands did not differ significantly between PFN (4.08 ± 0.78 em€/m^2) and CIC (2.20 ± 0.25 em€/m^2), nor when autotrophic and heterotrophic components were considered separately.

Nonetheless the relative distribution of autotrophs and heterotrophs in PFN and CIC seems to be opposite, with a greater contribution of

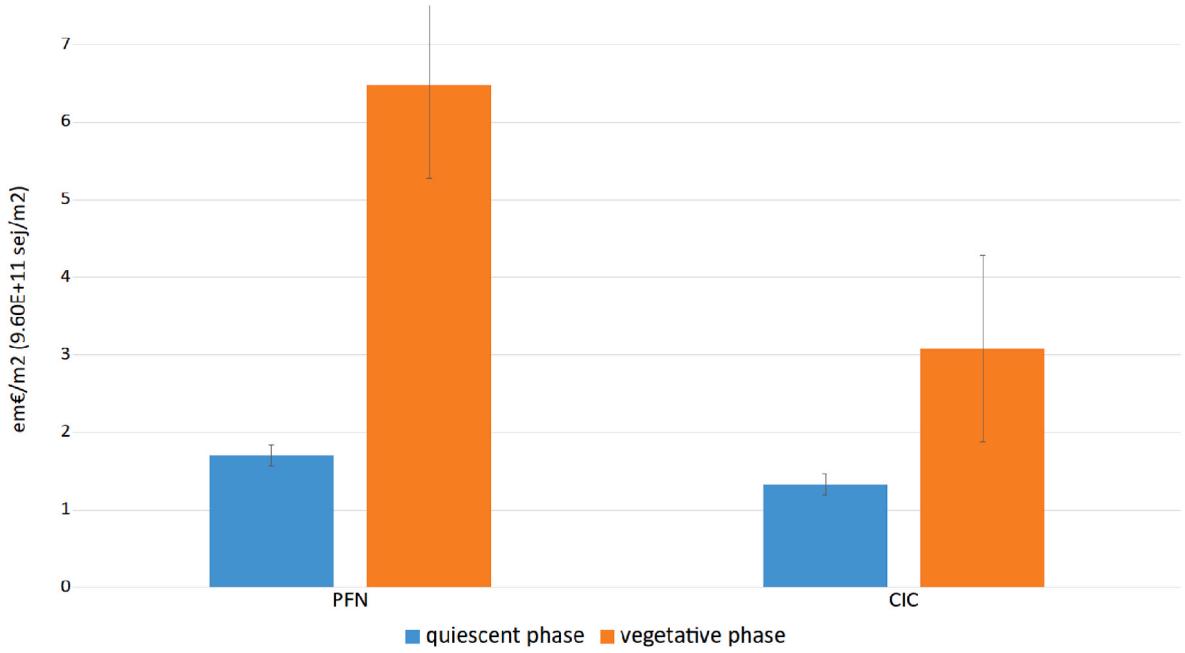

Fig. 7. value of Ericaria amentacea expressed in monetary equivalents.

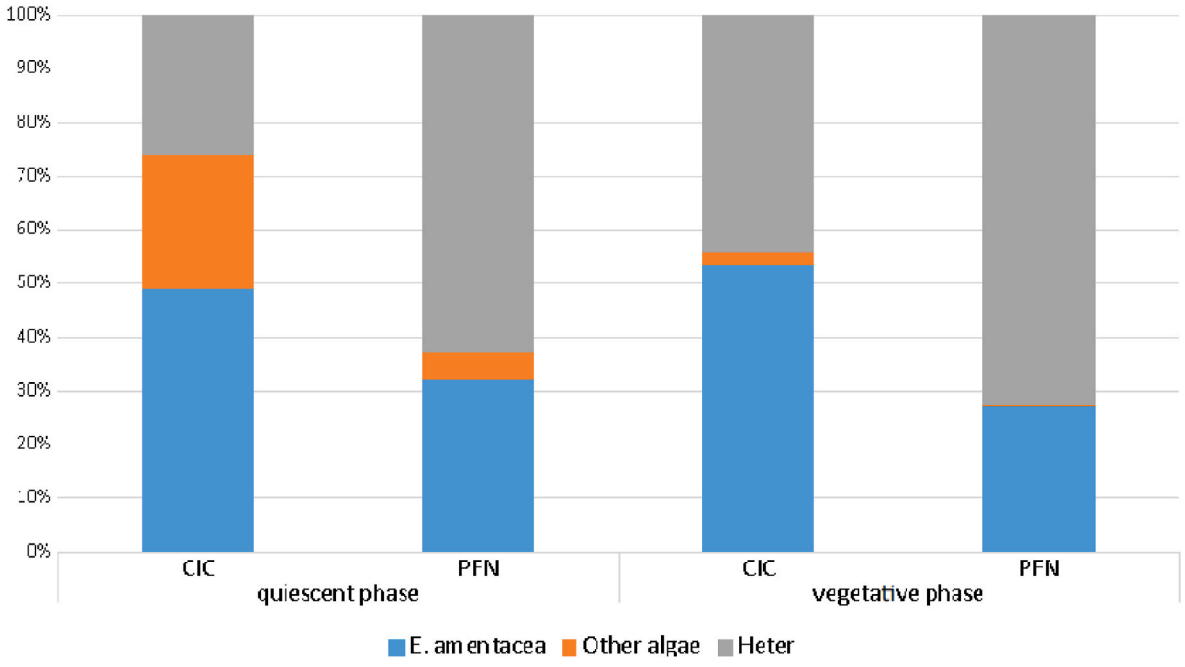

Fig. 8. percent contribution of autotrophs and heterotrophs to the total budget; autotrophs are *split into* Ericaria amentacea *and other macroalgae contribution.*

autotrophs in CIC even though no statistically significant difference was found. This difference may originate from different pathways in the self-organization of the systems, so that autotrophic and heterotrophic components set up differently at the two sites depending onthe different environmental settings, and the ecosystems establish a different trophic network to achieve the same total output in terms of natural capital. The mainland of PFN is sparsely anthropized, and the establishment of a land reserve in 1935 has effectively prevented the development of major land-based sources of pollution, minimizing their potential effects on nearby coastal habitats. On the contrary, CIC is a relatively small MPA with a low degree of enforcement, making it more susceptible to direct and indirect human impacts from nearshoreactivities (e.g., trampling, organic inputs). These conditions may have been reflected in the different distribution of autotrophs and heterotrophs between the two sites, favoring the spread of opportunistic turf-forming macroalgae and reducing the invertebrate component at CIC (Cannarozzi et al., 2023a,b).

Significant variability in natural capital values, however, was found at the scale of stations within sites, confirming the small-scale heterogeneity previously reported for *E. amentacea* stands and associated assemblages (Fraschetti et al., 2005; Piazzi et al., 2018; Cannarozzi et al.,

Table 6
results of ANOVA testing for spatial and temporal variations in the total natural capital of Ericaria amentacea associated assemblage. Significant tests are given in bold.

Total Natural Capital (sej/m^2)					
	df	SS	MS	*F*	*P-value*
Time = Ti	1	14.73	14.73	14.809	**0.0183**
Site = Si	1	0.79	0.79	0.684	0.4547
Station(Si) = St(Si)	4	4.64	1.16		
Ti × Si	1	0.94	0.94	0.948	0.3854
Ti × St(Si)	4	7.65	0.99	6.246	**0.0004**
Res	48	32.73	0.16		
Data transformation = log(x+1)					
Shapiro-Wilk $W = 0.981$, *P-value* = 0.4580					
Cochran's $C = 0.224$, *P-value* = 0.2652					

Table 7
results of ANOVA testing for spatial and temporal variations in the autotrophic and heterotrophic natural capital of Ericaria amentacea associated assemblage. Significant tests are given in bold.

Autotrophic Natural Capital (sej/m^2)					
	df	SS	MS	*F*	*P-value*
Time = Ti	1	8.97	8.97	13.098	**0.0224**
Site = Si	1	2.28	2.28	2.249	0.2081
Station(Si) = St(Si)	4	2.03	0.54		
Ti × Si	1	1.03	1.03	1.498	0.2881
Ti × St(Si)	4	2.74	0.68	7.017	**0.0002**
Res	48	4.69	0.10		
Data transformation = log(x+1)					
Shapiro-Wilk $W = 0.981$, *P-value* = 0.4741					
Cochran's $C = 0.245$, *P-value* = 0.1570					

Heterotrophic Natural Capital (sej/m^2)					
	df	SS	MS	*F*	*P*
Time = Ti	1	25.80	25.80	19.624	**0.0114**
Site = Si	1	10.84	10.84	5.663	0.0760
Station(Si) = St(Si)	4	7.65	1.91		
Ti × Si	1	0.01	0.01	0.005	0.9470
Ti × St(Si)	4	5.26	1.31	2.716	**0.0406**
Res	48	23.23	0.48		
Data transformation = log(x+1)					
Shapiro-Wilk $W = 0.981$, *P -value* = 0.4557					
Cochran's $C = 0.242$, *P-value* = 0.1710					

2023a,b). Nonetheless, this variability appears to be smoothed out when climatic regimes are considered on a broader scale, where emergy values remain relatively uniform, suggesting that differences in environmental conditions among sites do not markedly affect natural capital values, at least at the spatial scale investigated. These results set the stage for exploring whether the natural capital values assessed here could be representative of *E. amentacea* stands throughout Mediterranean region, imparting to the research a broader relevance.

When temporal variability was considered, significant differences were consistently detected in total natural capital values. These findings were compared with those reported by Cannarozzi et al. (2023a and b) to evaluate whether natural capital assessments yield more robust insights into ecosystem status than simpler ecological metrics. In their studies, Cannarozzi et al. (2023a,b) examined spatial and temporal variations in the biomass of *E. amentacea* and associated assemblages at the same sites and sampling periods. They found that temporal patterns were not always statistically consistent (Table 8), likely because only biomass was considered.

Nonetheless they noted temporal differences in biomasses of *E. amentacea* and its assemblages at the graphical level, reflecting specific site conditions.

Natural capital, being a holistic measure of system performance, integrates nboth the quantity (biomass) and the quality and complexity of the trophic network. As such, it can resolve uncertainties and detect differences that biomass alone may fail to capture, as verified in this study.

The observed temporal variations of natural capital are not surprising, given the well-known seasonal phenology of *E. amentacea* (Benedetti-Cecchi and Cinelli, 1993; Gómez Garreta et al., 2002; Mangialajo et al., 2008a,b; Giaccone, 2009; Chemello et al., 2022). Longer branches in spring/early summer (vegetative phase) not only increase algal biomass, but also create a complex, three-dimensional habitat that influences microclimate (e.g., humidity and temperature) (Bulleri et al., 2002; Falace et al., 2005; Riccato et al., 2009; Agnetta et al., 2015) and provide food, shelter and nursery areas (Bulleri et al., 2002; Riccato et al., 2009; Agnetta et al., 2015; Falace et al., 2018; Chiarore et al., 2019; De La Fuente et al., 2019). These ecosystem functions make *E. amentacea* canopies a biodiversity hotspot (Riccato et al., 2009) and trigger a cascade effect that catalyses colonization by heterotrophs thereby increasing natural capital. However, differences in the natural capital values between quiescent and vegetative phases may also be influenced by factors other than *E. amentacea* phenology, such as variation in nutrient availability, grazing pressure and human disturbances (regulated but not absent within MPAs and influenced by seasonality of tourists flows) (Fraschetti et al., 2012; Iveša et al., 2016; Monserrat et al., 2023; Orfanidis et al., 2021).

Within the framework of natural capital theory, the algal perennial cauloid can be associated with the stock (natural capital, considering both the vegetal and fauna components), while the annual deciduous branches represent the generated functions (flows).

Based on our results, the standing natural capital (quiescent phase) averaged 1.52 ± 0.14 em€/m^2, while the combined value of standing capital and flows (vegetative phase) averaged 4.77 ± 0.74 em€/m^2. The value of the flows alone (fronds) was therefore estimated at 3.26 em€/m^2.

This study provides the first detailed quantification of natural capital in midlittoral rocky fringe ecosystems characterized by *E. amentacea* canopies. These environments are rarely analyzed in such detail in

Table 8
Statistical results from Cannarozzi et al. (2023a and b). NA = not applicable, no = no significant statistically difference found, yes = significant statistically difference found.

	Ericaria amentacea			other macroalgae			invertebrates		
	temporal variation	spatial variation	spatio-temporal	temporal variation	spatial variation	spatio-temporal	temporal variation	spatial variation	spatio-temporal
PFN	no	no	no	no	no	no	yes	no	yes
CIC	no	no	yes	no	no	yes	no	no	no
Both sites	NA	NA	NA	NA	NA	NA	no	no	yes

natural capital assessments, as they are typically grouped within the broader category of photophilic algal communities, that include also the shallow subtidal. The protocol applied in this study builds upon emergy analysis but was specifically developed and tailored by Vassallo et al. (2017) for the assessment of natural capital in benthic coastal marine environments. Since its introduction, this protocol has been employed in multiple studies and provides a well-defined framework for each stage of the calculation process, from data collection to algorithm selection and the application of emergy analysis in this specific context.

Compared to traditional emergy analysis, the protocol seems to offer less flexibility and may appear more rigid and formal. For example, it prescribes a fixed set of environmental inputs to be included in the assessment, without allowing for habitat-specific selection, even when inputs vary among ecosystems depending on depth, coastal exposure, distance from shore, or other factors. Nevertheless, it should be noted that the protocol calculates natural capital based on the accounting of primary production that supports the creation and maintenance of biomass within the habitat and the trophic networks linking its organisms. Because this primary production is often generated outsidethe spatial boundaries of the habitat under consideration, the adoption of a standardized approach is justified. This standardization also enhances the scientific robustness of the method and improves comparability with previous and future assessments. Furthermore, it facilitates the integration of the results into broader natural capital evaluation frameworks, contributing to the advancement of knowledge in the field.

The targeted approach for studying midlittoral assemblages here proposed adopts this scientific rigor while introducing an important refinement: the explicit distinction between stocks and flows. This distinction is particularly relevant for systems where flows are generated more rapidly than stocks and are returned to the environment as complex biological resources capable of supporting other ecosystems.

E. amentacea was selected as a target model species for its vulnerability coupled with its ability to create structurally complex three-dimensional habitats that enhance natural capital in the midlittoral, where harsh environmental conditions typically limit biodiversity and productivity. The values reported here not only support the recognition of its ecological value in national and international conservation policies but also provide a quantitative tool for monitoring ecosystem condition over time. From a management perspective, perspective, maintaining or increasing natural capital values is essential to ensure ecosystem sustainability. Such synthetic measures are becoming increasingly crucial within global policy frameworks (e.g. European Green Deal and EU Biodiversity Strategy) claiming for the need to ensure the economic growth without depleting natural assets. In this context, developing highly detailed and quantitative knowledge about ecosystems value is fundamental for informed decision-making and sustainable marine resource management.

CRediT authorship contribution statement

L. Cannarozzi: Writing – review & editing, Writing – original draft, Resources, Investigation, Formal analysis, Conceptualization. **I. Rigo:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Data curation, Conceptualization. **F. Ruggeri:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Data curation. **V. Asnaghi:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **M. Chiantore:** Writing – review & editing, Supervision, Investigation, Formal analysis, Conceptualization. **A. Falace:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **R. Bordoni:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **P. Vassallo:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **C. Paoli:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Conceptualization. **S. Bevilacqua:** Writing – review & editing, Supervision, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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