

Population dynamics of *Ericaria zosteroides* (Ochrophyta, Fucales) in the central Mediterranean

Giuliana Marletta¹  & Andrea Lombardo¹ 

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Abstract. *Ericaria zosteroides* is a canopy-forming macroalga belonging to the order Fucales, which dominates Mediterranean deep-water stands. In the present research, populations of *E. zosteroides* from three locations (Santa Maria La Scala, Scalo Pennisi and Acque Fredde) along the central-eastern coast of Sicily (Italy, central Mediterranean) were monitored for five years (from 2017 to 2021). *E. zosteroides* from all locations in this area share a common phenology: recruits start to appear between January-February; then during spring the frond grows and becomes fertile; in summer it begins to thin out until the autumn when almost all branches have been lost; and finally at the beginning of winter, new primary branches start to grow from the tophules. Nonetheless, we detected a difference in the most frequent size class among the studied populations, being 9 cm at Santa Maria La Scala, 6 cm at Scalo Pennisi and 4 cm at Acque Fredde. This difference could be due to the current regime, related to the tidal currents of the Strait of Messina and upwelling currents of the Ionian Sea, and the coastal morphology which determines local variations in this regime, with multiple eddies characterised by marked directional instability. The low growth rate and dynamics of these stands make them very susceptible to recovery from anthropogenic impacts. Considering that *E. zosteroides* is a threatened species according to the Barcelona Convention, it would be crucial to ameliorate the conservation status of the investigated populations, which currently do not present any level of protection, in order to promote their future viability.

Keywords. brown algae, deep-water stands, *Ericaria*, Ionian Sea, population dynamics.

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Introduction

Canopy-forming macroalgae of the orders Laminariales and Fucales (Ochrophyta) are considered late-successional species which increase the structural complexity of marine ecosystems. Indeed, they provide shelter and food for many associated species (Steneck *et al.*, 2002; Schiel & Foster, 2006), and contribute to the benthic carbon cycle (Duarte & Cebrian, 1996). Increasing evidence demonstrated that the loss and reduction of canopy-forming macroalgae leads to the depletion of the composition, structure, and biodiversity of benthic assemblages (Steneck *et al.*, 2002; Ling *et al.*, 2015), with serious implications for the entire ecosystem functioning (Lotze *et al.*, 2006; Worm *et al.*, 2006; Smale *et al.*, 2013).

In the eastern Atlantic and in the Mediterranean Sea, the species of the genera *Cystoseira* C. Agardh, *Ericaria* Stackhouse and *Gongolaria* Boehmer (Fucales, Sargassaceae) dominate rocky-bottom communities from the littoral fringe down to the lower sublittoral

zone (Feldmann, 1937; Ballesteros, 1990 a,b; Giaccone *et al.*, 1994). Some of these species only thrive in deep waters where they constitute highly structured and diverse communities (Feldmann, 1937; Giaccone & Bruni, 1973; Ballesteros *et al.*, 1998).

There is evidence that the community complexity (i.e., diversity and species richness) increases (Ballesteros, 1991, 1992), and community dynamics (i.e., productivity, turnover and growth rates) decrease with depth (Ballesteros, 1991; Garrabou *et al.*, 2002). In fact, since they live close to the limits of the physiological light compensation point for their growth (Sant & Ballesteros, 2021a), these deep-water species have low growth rates, long lifespans, and low recruitment rates (Ballesteros, 1991; Ballesteros *et al.*, 1998; Garrabou *et al.*, 2002). Thus, the slow dynamics of these species make them very vulnerable to the increase of perturbations. Therefore, their recovery rate depends on both the arrival rate of propagules to the disturbed site and on their settlement capacity (Capdevila *et al.*, 2015).

The Mediterranean endemic *Ericaria zosteroides* (C. Agardh) Molinari & Guiry, previously known as

¹ Department of Biological, Geological and Environmental Sciences, University of Catania. I-95124 Catania, Italy.
E-mail: giulianamarletta93@gmail.com

Cystoseira zosteroides (Turner) C. Agardh and then as *Carpodesmia zosteroides* (Turner) Greville, is one of the main dominant canopy-forming species in deep-water assemblages (Giaccone, 1973). It occurs on rocky bottoms exposed to strong unidirectional currents and with light levels ranging between 1% and 0.3% of surface irradiance, between 15 and 50 m of depth depending on the water clarity (Giaccone & Bruni, 1973). Notwithstanding their widespread distribution and their floristic, biogeographic and ecological uniqueness, data on these stands are still scarce (Ballesteros, 1990a; Serio, 1994; Ballesteros et al., 2009) and the structure and dynamics of present populations are poorly known (Hereu et al., 2008).

According to Ballesteros et al. (2009), *Ericaria zosteroides* populations exhibit low growth rates (0.5 cm year^{-1}) and high longevity (more than 50 years). Their dynamics could depend on large-scale, low frequency catastrophic episodic events, which conduct to high mortality rates of adults, clearing the canopy and allowing intense pulses of recruitment. This effect, known as priority effect (De Meester et al., 2002) seems to be responsible of the strong genetic structure of *E. zosteroides* populations. Indeed, the gene flow can be limited by the density and the size of individuals, which can reduce new recruitments. Moreover, the dispersal of *E. zosteroides* zygotes is very reduced (10 m) (Capdevila et al., 2018) and this limit the gene flow between populations. For this reason, *E. zosteroides* populations are genetically differentiated from each other, even at short distances (Reynes et al., 2021).

As most of *Cystoseira* s.l. species, also *E. zosteroides* is extremely vulnerable to anthropogenic disturbances, especially to changes in water turbidity, sedimentation, direct pulling up by fishing nets, eutrophication, overgrazing by sea urchins, global change and competition with alien invasive species (Boudouresque et al., 1990; Cormaci et al., 2001; Thibaut et al., 2005; Serio et al., 2006). Moreover, it has been documented the decline of some *E. zosteroides* populations in several Mediterranean areas where they were until recently present, with large-scale effects at the community level (Giaccone & Bruni, 1973; Thibaut et al., 2005; Serio et al., 2006). Therefore, low-frequency natural disturbances such as extreme storms can lead to the extinction of local populations of *E. zosteroides* that are already affected by anthropogenic impacts (Navarro et al., 2011).

In this study, populations of *E. zosteroides*, located along the eastern coast of Sicily (Italy), have been monitored for five years (from 2017 to 2021) to analyse the phenology of this species and ultimately evaluate the seasonal periodicity of growth and reproduction of *E. zosteroides* along this area. Considering the endangered status of this species, the knowledge of the phenology and recruitment periods of *E. zosteroides* could be essential in light of conservation and active restoration actions.

Materials and Methods

Study Species

Ericaria zosteroides is a pseudoperennial species (Feldmann, 1937), which usually loses the branches during autumn, when only the principal cauloid is retained (Rodríguez-Prieto et al., 2013). This species is characterized by a short, truncated cauloid, simple or low branching, fixed to the substrate by strong aptera. The apex of the axis is smooth and slightly protruding from the insertion of the branches (Cormaci et al., 2012). The tophules, reservoir vesicles from which primary branches originate (Capdevila et al., 2016), are oblong to cylindrical-shaped, perfectly smooth and relatively spaced. Primary branches are cylindrical or slightly flattened, while upper-order branches, scattered with cryptostomata, are flattened and ribbon-like with a weak midrib (Cormaci et al., 2012). The branches, which are the deciduous part of the thallus, are renewed annually.

It is a monoecious species with a diplontic and iteroparous life-history. Gametes (antheridia and oogonia) are formed in reproductive structures (receptacles) (Ballesteros, 1990a). Receptacles are compact, fusiform-lanceolate, with knurled surface and often with small spines. They are intercalated on the primary and/or secondary branches, at the base of secondary laterals and they can be rarely in a terminal position (Giaccone & Bruni, 1973; Cormaci et al., 2012). Guern (1962) studied the embryogenesis of several *Cystoseira* s.l. species and reported that *E. zosteroides* belongs to the first embryological group for the following features: spherical oogonia, pigmented and branched antheridia, first and second zygote division parallel to each other, and the third perpendicular to the previous ones, embryo development that takes place directly on the substratum, and formation of 4 primary rhizoids.

Study sites

The study was conducted along the central-eastern coast of Sicily (Italy, Central Mediterranean), in three stations (Figure 1): Santa Maria La Scala (37.6125 N, 15.175389 E), Scalo Pennisi (37.639778 N, 15.184722 E) and Acque Fredde (37.637583 N, 15.181167 E). The first station lies within the land protected area “Timpa Nature Reserve”, which encompasses a massive coastal slope called Timpa. At this station, the bottom consists of a rocky escarpment that extends from 20 to 30 m depth (Catra et al., 2006) and hosts a population of *Ericaria zosteroides* from 20 to 26 m of depth. The station of Scalo Pennisi has a similar bottom topography with a rocky slope which begins at 10–15 m of depth and ends at about 30 m (Sciuto et al., 2017). Here, a population of *E. zosteroides* was observed from 16 m to 28 m of depth. Finally in the third station, Acque Fredde, from the surface to about 25 m of depth, the bottom consists of rocky boulders and gradually it becomes sandy. Here, the population of *E. zosteroides* is present both on soft and hard substrates, from 16 to 30 m of depth (Table 1) These populations do not fall within marine protected areas and do not possess any level of safeguard.

Table 1. Distribution of *E. zosteroides* population in the three study sites.

Station	Coordinates	Substrate	<i>E. zosteroides</i> depth range
Santa Maria La Scala	37.6125 N; 15.175389 E	Rocky slope	20 – 26 m
Scalo Pennisi	37.639778 N; 15.184722 E	Rocky slope	16 – 28 m
Acque Fredde	37.637583 N; 15.181167 E	Rocky boulders and sand	16 – 30 m

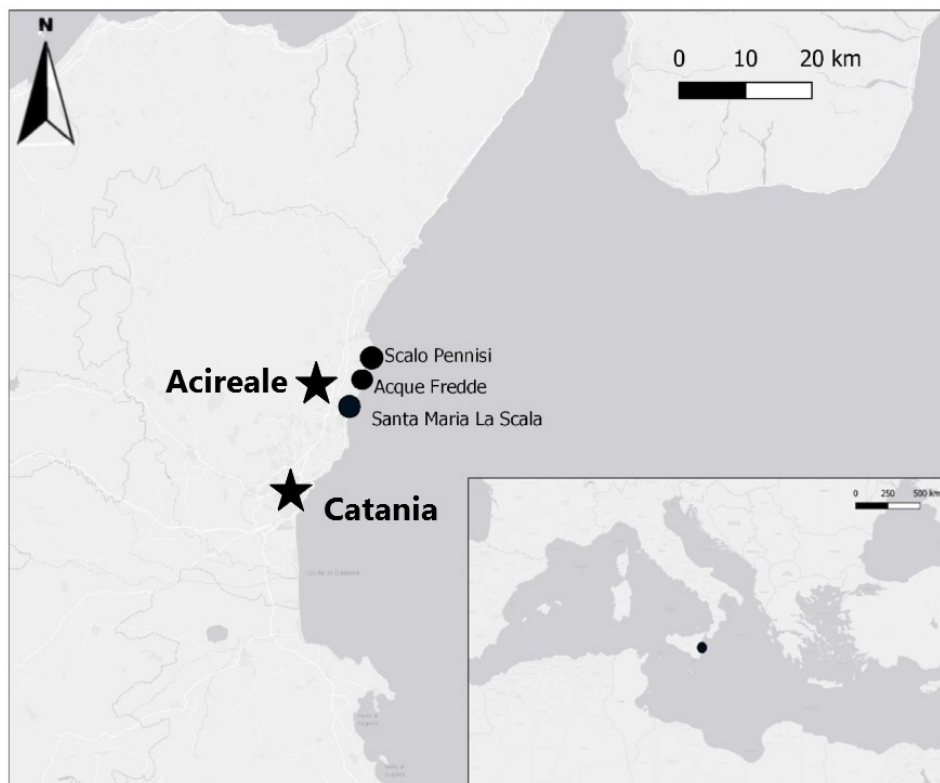


Figure 1. Location of the study sites (black circles) along the central-eastern coast of Sicily (Italy). The black stars indicate the main cities in the neighbourhood.

Experimental design

Ericaria zosteroides populations of the three sites were monitored for five years (from 2017 to 2021) taking monthly photos by means of an underwater camera (Olympus TG6) to follow the morphological and reproductive phenology of the species. At each site, to assess qualitatively the morphological and reproductive phenology of the species, an average of ten photos were taken and analysed for each month of every year, for a total of 1800 frames corresponding to 5 years and 3 sites.

During 2021, for each of the three populations, the length between the base of the holdfast and the most distant part of the longest axis (length of the main axis) was measured in situ monthly in five thalli randomly selected. Recruits were identified as individuals from 0.5 to 1 cm long. Moreover, from March to May, a thallus was monthly collected to measure the morphometric variables of the receptacles, conceptacles and gametes (length of the receptacle, diameter of the conceptacles, length of antheridia and oogonia).

For each month, the average length of the main axis was measured to estimate the size distribution

frequencies of *E. zosteroides* populations in the three sites ($n = 180$). Indeed, according to Ballesteros *et al.* (2009), this is the easiest morphometric measurement to carry out underwater and it is useful to determine the size structure of the populations.

Differences in the average length of the main axis among populations were compared using analysis of variance (one-way repeated measures ANOVA). Then, significant terms ($P < 0.05$) were examined through the post hoc test of Tukey's pairwise. The measurements were assigned by rounding into different size classes. The Chi-Square (χ^2) test of independence was used to check whether there was a significant association between size distributions and populations. Statistical analyses were performed using PAST version 4.03 and jamovi version 2.3.

Results

Phenology

The phenology of *Ericaria zosteroides* was observed through monitoring activities, performed over a

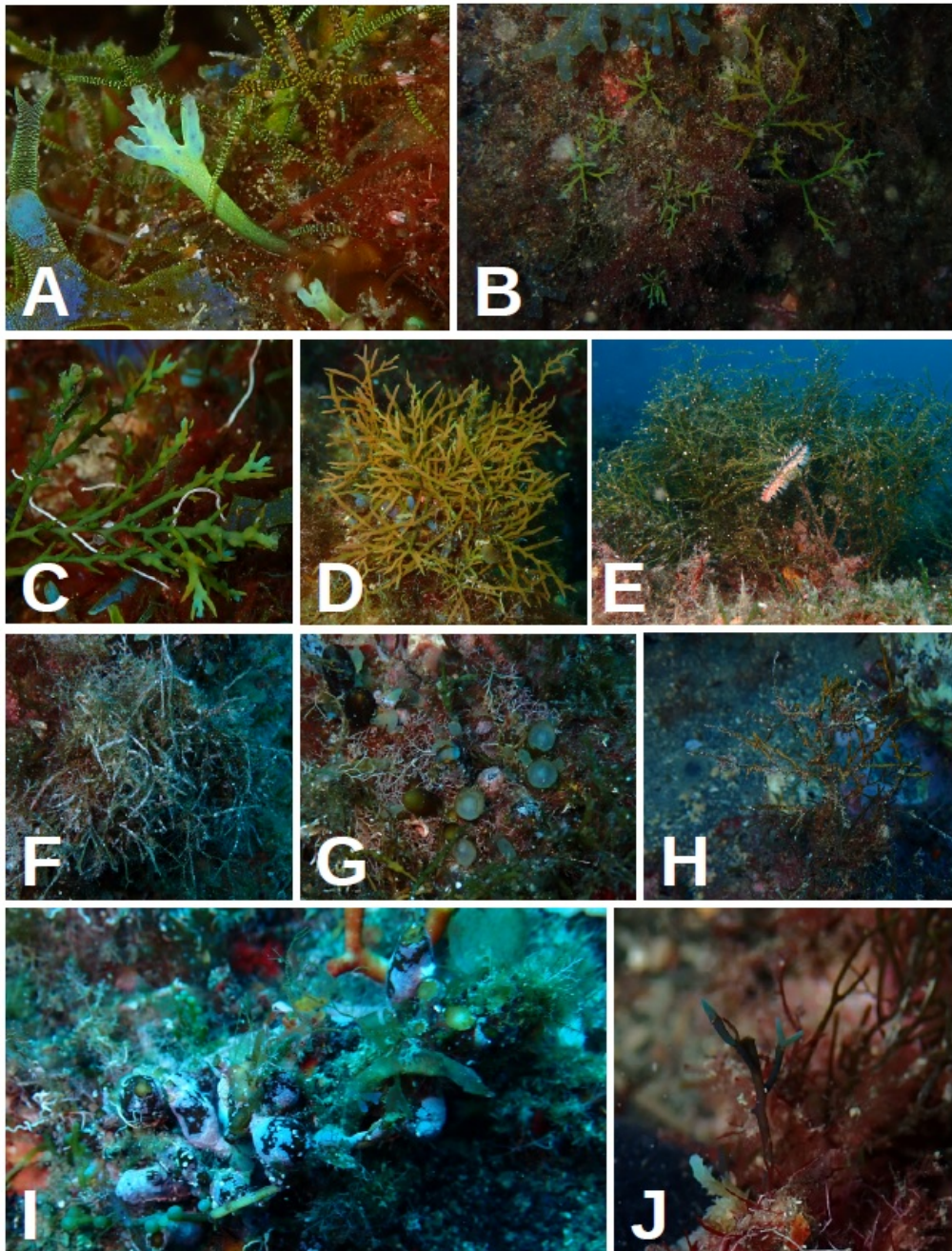


Figure 2. Habitus of *Ericaria zosteroides* throughout the year. A, New recruits in January-February; B, Growth of recruits in February-March; C, Development of receptacles in April; D, Brownish aspect of the thalli in May; E, Maximum height development in June; F, Frond completely covered by epiphytes in July; G, Beginning of the frond loss in August, the topophules were seen frequently eaten by herbivores; H, Blackish appearance of the thallus in September; I, Only the topophules are visible in October; J, Growth of primary branches from topophules in November-December.

period of five years in the three study sites, and it is summarized in Figure 2. From January-February, new recruits started to appear and grow (Figure 2A). At the end of February and the beginning of March, the recruits developed in height (Figure 2B). From April to June, the maximum vegetative and reproductive development of *E. zosteroides* occurred, indeed the receptacles became visible (Figure 2C), and the thalli were brownish in colour (Figure 2D). In June, the species had already reached its maximum height and it hosted several organisms, both algae and invertebrates (Figure 2E). From July the frond was completely covered by epiphytes (Figure 2F). In August, the species began to lose the frond and

the topophules became visible. During the observations, we noticed that they were often eaten by herbivores, probably fishes (Figure 2G, I). In September, the height of the frond continued to decrease, and it assumed a blackish colouring (Figure 2H). In October, the autumn storms removed completely the frond and only the topophules, which were completely covered by epiphytes, could be observed (Figure 2I). Between November and December, primary branches started to grow from topophules (Figure 2J).

From March to May 2021, a fertile thallus was monthly collected (Figure 3A) to characterize the morphometric variables of the conceptacles and

gametes. The receptacles were in an intercalated or terminal position (Figure 3B). They were elongated, scattered with small spines and measure about 0.9–1.5 cm in length (Figure 3B). In longitudinal section, the receptacles contained the conceptacles, which ran along each side of the midrib (Figure 3C). In cross section, the diameter of conceptacles was about 477–

500 μm . Within the conceptacles, there were paraphyses, branched and pigmented antheridia (23.85–39.75 μm) and ovoid oogonia (119.25–135.15 μm). The oogonia were positioned at the bottom of the conceptacle in the opposite direction to the ostiole, while the antheridia and paraphyses covered the walls of the conceptacle (Figure 3D).

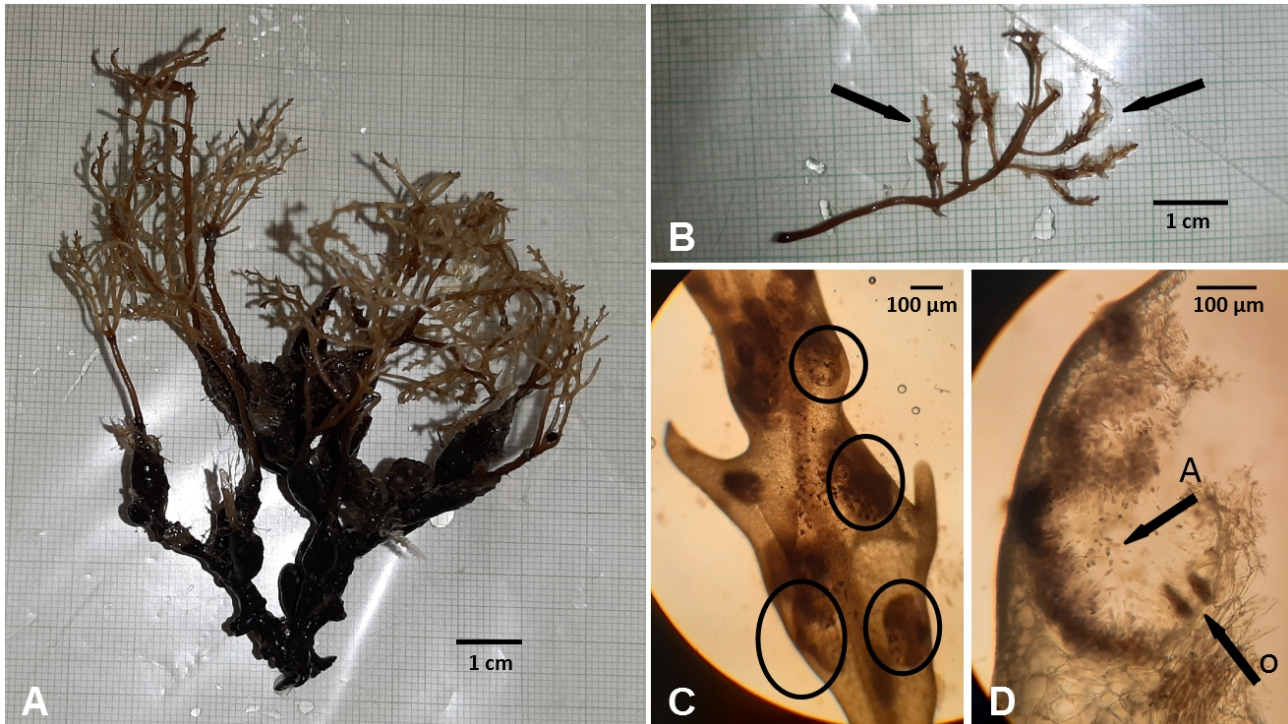


Figure 3. Reproductive traits of *Ericaria zosteroides*. A, Fertile thallus of *E. zosteroides* collected in March; B, Terminal receptacles (arrows); C, Longitudinal section showing the conceptacles (black circles) along each side of the midrib; D, Transverse section showing branched and pigmented antheridia (A) and ovoid oogonia (O).

Average length of the main axis

The average length of the main axis was measured in the three populations of *E. zosteroides* throughout 2021 (Figure 4A). Since a similar trend was noted between the three study sites, the overall phenology of *E. zosteroides* is shown in Figure 4B. During the year, it was observed that from January to March, the average length of the main axis in the individuals of *E. zosteroides* remained stable with a mean value of 5.64 ± 0.16 cm. Then, from April to June the maximum vegetative development of this species occurred, reaching a value of 9.98 ± 0.41 cm. From July and September, the average length of the main axis started to decline (6.09 ± 0.29 cm), followed by a significant decrease from October to December (4.36 ± 0.4 cm).

The one-way repeated measures ANOVA analysis showed a significant difference in the average length of the main axis among the populations of the three study sites ($P = 0.001$; $F = 9.54$). In particular, the test of Tukey's pairwise revealed a significant difference of the populations of Scalo Pennisi ($P = 0.0008554$) and Acque Fredde ($P = 0.022$) from the one of Santa Maria La Scala.

Size distribution frequencies

The Chi-Square test of independence revealed that size distribution frequencies were significantly correlated with the populations ($\chi^2 = 38.7$; $P = 0.007$). At Scalo Pennisi, the most frequent size classes were 6 cm and 3 cm, while at Santa Maria La Scala was 9 cm, and at Acque Fredde was 4 cm. In these two latter sites, larger individuals were observed compared to those found at Scalo Pennisi (Figure 5).

Discussion

Throughout the years of study, the morphological and reproductive phenology of *Ericaria zosteroides* was monitored in the three study sites and the following pattern was identified: the recruits start to appear between January-February, then during spring the frond grows and become fertile, in summer it begins to thin out until the autumn, when almost all branches have been lost, and finally at the beginning of winter new primary branches start to grow as from the topohules. Ballesteros (1990a) studied the structure and dynamism of a population of *E. zosteroides* located in the island of Tossa del Mar

(North-western Mediterranean) and he also observed that the vegetative development begins at the end of the winter, and it is maximum during spring. Moreover, our phenological observations correspond to those of Serio (1995), who found that the vegetative development of *E. zosteroides* at Ognina (eastern Sicilian coast, Central

Mediterranean) occurred from May to July, with a maximum in June. Indeed, this species can sustain growth of the branches even in periods when light levels are around the compensation point, thanks to the presence of tophules from which it can remove carbohydrates (Ballesteros, 1990a; Sant & Ballesteros, 2021a).

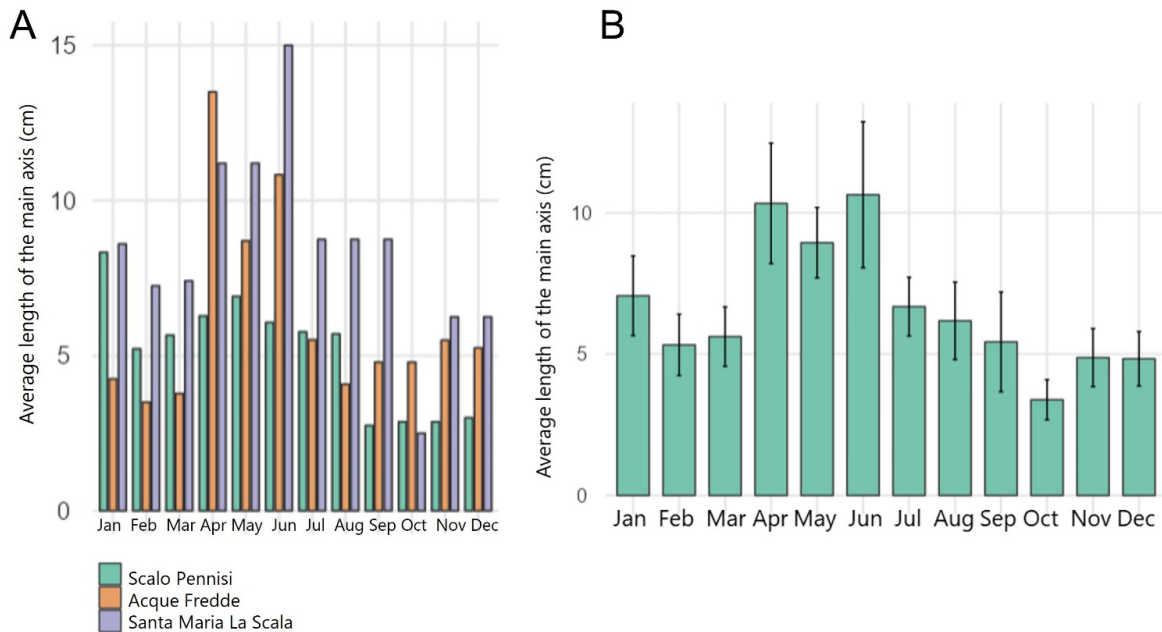


Figure 4. Phenology of *Ericaria zosteroides* in the study sites throughout the 2021 (n = 180). A, Average length of the main axis (cm) throughout the year in the three populations; B, Overall phenology of *E. zosteroides* during the year.

In the study sites, the populations of *E. zosteroides* develop principally on rocky bottoms in a range of depth of 16–30 m (Table 1), a bathymetric range similar to that found by Serio (1994;1995) (20–25 m; 25 m) and Navarro *et al.* (2011) (20, 24 m), but shallower than that reported by Hereu *et al.* (2008) (29–40 m, 32–35 m and 38–47 m) and by Ballesteros *et al.* (2009) (38–54 m and 38–43 m). This difference could depend on the lower transparency and high turbidity of water in the studied sites, which cause an ascent of deep-water species to optimise photosynthetic performance. Indeed, according to Sant & Ballesteros (2021b), *E. zosteroides* shows a higher capacity to photo-adaptation than other deep-water species, like *Gongolaria montagnei* (J. Agardh) Kuntze.

In the three sites we detected a difference in the size distribution frequencies among the investigated populations of *E. zosteroides*. At Santa Maria La Scala the most frequent size class was 9 cm, while at Scalo Pennisi was 6 cm and at Acque Fredde was 4 cm. Therefore, although there is a limited distance between the three sites, it was found heterogeneity in the distribution of size classes among the studied populations of *E. zosteroides*. This variability in the structure of *E. zosteroides* populations at small spatial scale have been attributed to environmental factors, which play an important role in shaping these stands (Navarro *et al.*, 2011). The study sites are located along the central-eastern coast of Sicily, a coastal strip that,

from a hydrogeological point of view, is influenced by the tidal currents of the Strait of Messina and upwelling currents of the Ionian Sea. However, the coastal morphology determines local variations in the general current regime, with multiple eddies characterised by marked directional instability (Catra *et al.*, 2006). This combination of factors might explain this variability in the studied *E. zosteroides* populations. Accordingly, Hereu *et al.* (2008) hypothesized that the differences in composition and structure of populations were related to current regimes. The dispersal distance of zygotes of *E. zosteroides* is about 10 m (Capdevila *et al.*, 2018), but occasional dispersal events due to currents can transport the zygotes above a few kilometers (Reynes *et al.*, 2021). In this way, populations of *E. zosteroides* can establish in a new area. As other fucoid species, it was observed that populations of *E. zosteroides* are genetically differentiated from each other, even at short distances (Reynes *et al.*, 2021). Therefore, through genetic studies, it would be possible to understand whether the populations here studied are spatially isolated and genetically differentiated, or they are connected due to occasional dispersal events, as currents.

The low connectivity observed among populations of *E. zosteroides* and their low dynamics makes them very vulnerable and less resilient to anthropogenic impacts (Navarro *et al.*, 2011) and this could be the reason why they are in regression in many Mediterranean areas (Thibaut *et al.*, 2005; Serio *et al.*, 2006). Indeed, these

deep-water species are highly sensitive to several factors, as increase in water turbidity, eutrophication, erosive effects of anchoring and fishing nets, overgrazing or introduction of invasive species (Ballesteros *et al.*,

2009). Along the eastern coast of Sicily, the population of *E. zosteroides* studied by Serio (1994, 1995) located at Ognina (Catania, Italy) has nowadays completely disappeared (authors' pers. obs.).

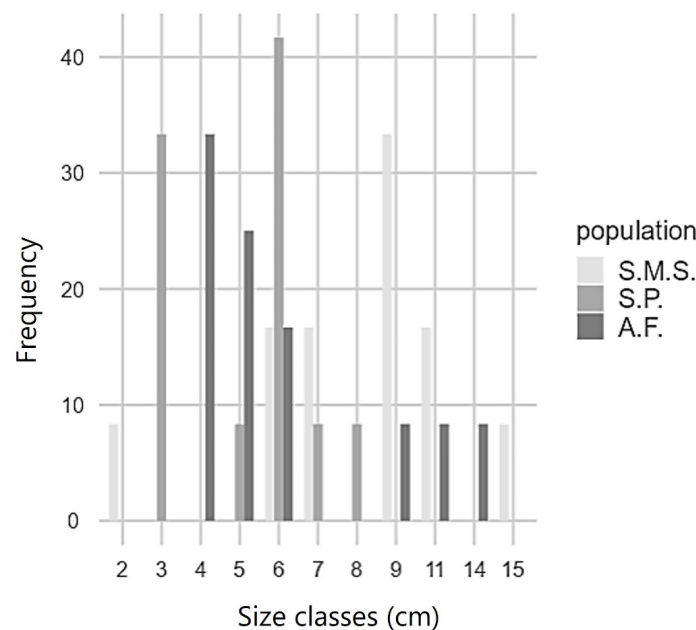


Figure 5. Size distributions of *Ericaria zosteroides* in 2021 at Santa Maria La Scala (S.M.S.), Scalo Pennisi (S.P.) and Acque Frede (A.F.) (n = 180).

Considering that *E. zosteroides* is included in the “List of Threatened or Endangered Species” of Barcelona Convention (Annex II) (Verlaque *et al.*, 2019), it would be crucial to improve the conservation status of the investigated populations, which currently do not present any level of protection, in order to establish effective safeguard measures and promote the future viability of these populations. In the context of UN Decade of Ecosystem Restoration, the knowledge of the phenology and recruitment periods of the endangered species, such as *E. zosteroides*, represents a priority for successful and long-term active restoration actions, which could ultimately enhance the natural recovery of *E. zosteroides* communities.

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Authorship contribution

GM: Conceptualization; Formal analysis; Research; Methodology; Writing

AL: Conceptualization; Research; Methodology; Management of the project; Writing

Conflict of interest

None.

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