

**Syntopic *Cystoseira* taxa support different molluscan assemblages in the Gulf of Naples
(southern Tyrrhenian Sea)**

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Abstract. Brown macroalgae belonging to the genus *Cystoseira* (Fucales: Sargassaceae) are canopy-forming organisms whose recent decline at basin and local scale has been widely documented, which urgently calls for research to fill knowledge gaps and support new and effective measures for protection. We hereby characterized the molluscan assemblages associated with three *Cystoseira* taxa (*C. amentacea*, *C. compressa*, and *C. crinita*) from Ischia Island (Italy, Tyrrhenian Sea), and tested whether different congeneric taxa may syntopically support a different biota. In particular, these assemblages were compared among three *Cystoseira* species, two times of sampling (June–July 2015 and June–July 2016), and six sites in terms of multivariate structure (identity and relative abundances of constituting taxa combined, and presence-absence composition), as well as for synthetic measures of diversity, including the total richness of taxa, the exponential Shannon index, and the reciprocal Simpson

index. A total of 24736 molluscan individuals were collected, overall belonging to 52 taxa. The majority of the identified species included micrograzers and filter feeders, in agreement with similar previous studies. The composition of associated molluscan assemblages, which was mainly represented by juvenile individuals, differed among the three *Cystoseira* species, suggesting that even congeneric taxa do not support an analogous benthic fauna. The present findings shed light on the molluscan biota associated with *Cystoseira* taxa in the Gulf of Naples and strengthen the importance of such habitat-forming macroalgae in structuring the local infralittoral invertebrate biodiversity and as a nursery for species-specific associated molluscs.

Additional keywords: Mediterranean Sea, infralittoral fringe, canopy-forming algae, nursery area, algae-specific assemblages.

Introduction

Marine seaweeds and seagrasses are important benthic primary producers worldwide (Mann 1973). In the Mediterranean Sea, especially in areas not subject to intense anthropogenic disturbance, species belonging to the order Fucales Bory de Saint-Vincent dominate on rocky substrates from the upper infralittoral to the upper circalittoral shore level, establishing structurally complex habitats, supporting diversified assemblages, and functioning as ecological engineers (Ballesteros 1992; Giaccone *et al.* 1994; Schiel and Foster 2006; Cormaci *et al.* 2012; Poursanidis *et al.* 2019). In particular, *Cystoseira* C. Agardh and *Sargassum* C. Agardh taxa are long-living macroalgae with a complex tridimensional structure, providing habitat, food, shelter, and nursery for a wide variety of species (Ballesteros 1992; Bulleri *et al.* 2002; Frascchetti *et al.* 2002; Mangialajo *et al.* 2008; Vergés *et al.* 2009; Sales *et al.* 2012;

[Cheminée et al. 2013](#)). They are also considered of special concern within the European Water Framework Directive (WFD, 2000/60/EC), where they are listed as coastal water quality indicators ([Orfanidis et al. 2001](#); [Ballesteros et al. 2007](#); [Orfanidis 2007](#)). Unfortunately, most of the *Cystoseira* assemblages in the Mediterranean Sea are declining, when not even disappearing completely, in response to cumulative impacts, including habitat destruction, eutrophication, water turbidity, out-competition by non-indigenous species, and human trampling ([Thibaut et al. 2005](#); [Iveša et al. 2016](#); [Blanfuné et al. 2016](#); [Gianni et al. 2017](#); [Falace et al. 2018](#)). Consequently, they may be substituted by less structured and opportunistic species, such as turf-forming filamentous seaweeds, mussels, or sea urchin-driven barrens. This shift may lead not only to an overall simplification of the architectural complexity of the dominant biological habitat, but also to the loss of their associated epibenthic diversity ([Benedetti-Cecchi et al. 2001](#); [Micheli et al. 2005](#); [Thibaut et al. 2005, 2015](#); [Mangialajo et al. 2008](#); [Perkol-Finkel and Airoidi 2010](#); [Sala et al. 2012](#); [Buia et al. 2013](#); [Grech et al. 2015](#); [Mancuso et al. 2018](#)).

Amongst the invertebrate fauna inhabiting *Cystoseira* associations, Mollusca were widely studied and often found to be among the most highly represented and dominant taxa, being also considered an important food source for higher trophic levels ([Milazzo et al. 2000](#); [Chemello and Milazzo 2002](#); [Pitacco et al. 2014](#); [Poursanidis et al. 2016](#); [Piazzini et al. 2018](#); [Lolas et al. 2018](#)). However, despite the long-lasting marine and malacological research in the Gulf of Naples (Tyrrhenian Sea), little is known on the molluscan fauna associated with such canopy-forming algae in the same area. Therefore, taking also into account the wide historical changes locally reported for *Cystoseira* taxa in the infralittoral zone, as well the loss of their natural habitats and the ongoing coastal transformation ([Grech et al. 2015](#)), empirical investigations of such assemblages are urgently needed. In this context, the main aims of this study were: i) to obtain a qualitative and quantitative characterization of the molluscan assemblages associated with *Cystoseira* belts around Ischia Island, i.e., the only portion of the

Gulf of Naples where these complex tridimensional structures still persist; ii) to test whether different congeneric taxa may support different molluscan assemblages syntopically, according to peculiar species-specific traits of the habitat-forming *Cystoseira* host taxon. Eventually, the obtained information would contribute to filling a knowledge gap regarding the ongoing biodiversity changes in the Mediterranean Sea and to confirming the importance of macroalgal biogenic habitats as preferential areas for the recruitment of molluscs.

Materials and methods

Study area

Ischia is a volcanic island located in the Gulf of Naples, southern Tyrrhenian Sea (Mediterranean Sea). It is the largest of the Phlegraean Islands, with about 34 km of coastline and an area of 46.3 km². In 2007, it was included in the Regno di Nettuno marine protected area (MPA), together with Procida and Vivara Islands. The northern side is characterized by low rocky coasts and few sandy beaches, and hosts the main harbor that daily connects the island with the mainland. In addition, it has the highest percentage of coastal artificial structures in the whole island. The western side is delimited by Punta Caruso and Punta Imperatore, and is characterized by high rocky coasts and two wide sandy beaches. The coastal morphology of the southern side is mainly characterized by cliffs, but also by the largest sandy beach of the island, namely Maronti. The eastern side is morphologically similar to the northern one, with low rocky coasts and some small sandy beaches.

Sampling design and collection of data

The study was carried out at six sampling sites distributed around Ischia Island: CA - Castello Aragonese, 40°43'47.8''N, 13°57'58.3''E; SP - San Pancrazio, 40°42'03.0''N, 13°57'15.7''E;

SA - Sant'Angelo, 40°41'39.8'' N, 13°53'29.6''E; SC - Scannella, 40°42'13.5''N, 13°51'39.7'' E; PI - Punta Imperatore, 40°42'39.6''N, 13°51'03.5''E; PC - Punta Caruso, 40°45'28.0''N, 13°51'45.2''E; see [Fig. 1](#)). These sites have comparable physical features, such as substrate slope (ranging from 0 to 30 degrees) and hydrodynamics (mid to high exposed rocky shores), and were selected according to the known presence of infralittoral fringes dominated by *Cystoseira* taxa, namely *Cystoseira amentacea* (C. Agardh) Bory de Saint-Vincent, *Cystoseira compressa* (Esper) Gerloff & Nizamuddin and *Cystoseira crinita* Duby ([Buia et al. 2013](#)). The six sampling sites spanned the entire coastline, with the exception of the northern side, where few scattered or even no *Cystoseira* individuals were recorded.

The sampling was carried out by snorkelling during June–July 2015 and June–July 2016, corresponding to the late spring/early summer period when *Cystoseira*'s thalli show the maximum development, before starting to lose the secondary branches ([Ballesteros 1992](#); [Hoffmann et al. 1992](#); [Falace et al. 2005](#); [Sales and Ballesteros 2012](#)). Based on the methodology already used by several authors (e.g. [Boudouresque and Belsher 1979](#); [Ballesteros 1992](#); [Bianchi et al. 2003](#)), three 20×20 cm quadrats (a few metres apart) were randomly selected at each site. After a visual counting of the total number of thalli of each *Cystoseira* species, all organisms in each quadrat were collected by scraping, sealed in plastic bags, and preserved in a cool box for subsequent analysis in the laboratory.

Laboratory processing of samples

Upon arrival to the laboratory, the density of *Cystoseira* in each replicate quadrat was estimated as the number of thalli per 400 cm². *Cystoseira*'s thalli were then carefully rinsed in seawater to separate the associated fauna. The length of each thallus was measured from the base of the holdfast to the distal tip of the frond ([Falace et al. 2005](#)) and the obtained data were used to calculate the mean size of the thalli of each species in each replicate. The biomass of

each *Cystoseira* species per quadrat was assessed as dry weight, after drying the thalli at 60°C for 60 hours.

The *Cystoseira*-associated fauna was sieved through a 0.5 mm mesh and subsequently preserved in 70% ethanol for further taxonomic determination. Molluscs were sorted out with a stereomicroscope and determined to the lowest possible taxonomic level, mostly using the identification keys of [Scaperrotta *et al.* \(2009–2016\)](#), [Gofas *et al.* \(2012\)](#), and [Trainito and Doneddu \(2014\)](#). They were subsequently counted, listed according to the updated taxonomy and nomenclature of the World Register of Marine Species database (WoRMS Editorial Board 2018), and assigned to different feeding guilds (FG) following [Solis-Weiss *et al.* \(2004\)](#), [Rueda *et al.* \(2009\)](#), and [Gofas *et al.* \(2012\)](#). The following categories were considered: C - carnivores feeding on other mobile organisms (predators); D - deposit feeders feeding on organic particles contained in the sediment; E - ectoparasites and specialised carnivores feeding on much larger organisms on which they live during their life cycle; FF - filter feeders capturing the particles in the water column with their gills and/or with mucous strings; MG - micrograzers and/or mesograzers feeding on microalgae, cyanobacteria or detritus attached to algal fronds; AG - grazers of macroalgae.

Statistical analyses

Differences in the percentage cover, biomass, number of thalli, and thallus length of each *Cystoseira* species between two times and among six sampling sites were tested with three-way analysis of variance (ANOVA), including the following crossed factors: ‘Time’ (random, two levels: June–July 2015 and June–July 2016), ‘*Cystoseira* species’ (fixed, two levels: *C. compressa*, *C. amentacea*, and *C. crinita*), and ‘Site’ (random, six levels: Castello Aragonese, San Pancrazio, Sant’Angelo, Scannella, Punta Imperatore, and Punta Caruso). The three quadrats sampled within each site at each time provided the replicates for this analysis. The

same type and model of analysis was used to test for differences in the total richness, the exponential Shannon index, and the reciprocal Simpson index.

Before each ANOVA, the homoscedasticity assumption was checked with Cochran's *C* test and data were transformed when necessary. When heterogeneity of variances could not be removed by transformation, the analysis was performed on untransformed data. Results were considered robust if not significant ($p > 0.05$), since the probability of Type II error is not affected by heterogeneous variances, or significant at $p < 0.01$, to compensate for increased probability of Type I error (Underwood 1997). Relevant post-hoc comparisons of levels of significant factors were done using the Student-Newman-Keuls (SNK) test.

A three-way permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) based on the same model of ANOVA and on Bray-Curtis dissimilarities was used to test for differences in the composition of molluscan assemblages associated with each *Cystoseira* species between times of sampling and among sites. To separate differences due to the identity and relative abundance of taxa that are combined by Bray-Curtis dissimilarities, this analysis was repeated using either the matrix of raw abundances, or that of presence vs. absence data as input. When relevant, Student's pair-wise *t*-tests were used for post-hoc multivariate comparisons.

The SIMPER procedure (Clarke 1993) based on presence-absence data was performed to calculate the absolute (δ_i) and percentage ($\delta_i\%$) contribution of each molluscan taxon to the total within-sample dissimilarity of the assemblage associated with each *Cystoseira* species, using 90% of cumulative dissimilarity as cut-off to exclude low contributions.

Finally, the cumulative ranked species abundance (or *k*-dominance) curves were computed to extract information on relative species abundance associated with the three *Cystoseira* species (Clarke 1990).

Results

Macroalgal features

The three *Cystoseira* species differed in percentage cover, biomass, and number of thalli depending on the sampled site (Table 1). *Cystoseira amentacea* and *C. compressa*, in particular, showed dense belts at all sampling sites, while *C. crinita* co-occurred with the other two species only at a single site, namely Scannella (Fig. 2A). At this site, however, all such abundance-related variables were comparable among the three macroalgal species (Fig. 2A, 2B, 2C-a). At the Castello Aragonese and Punta Caruso sites, instead, both the percentage cover and the individual abundance of *C. compressa* were larger compared to *C. amentacea*, while no differences in such variables between the same species occurred at the other sites (Fig. 2A, 2C-a). Analogously, *C. compressa* and *C. amentacea* showed comparable biomass at all sites (Fig. 2B). Moreover, a significant ‘Time × *Cystoseira* species’ interaction was detected for the abundance of thalli (Table 1), being higher for *C. compressa* than for *C. amentacea* in June–July 2015, but not in June–July 2016, and obviously lower for *C. crinita* compared to the other two *Cystoseira* species (Fig. 2C-b).

Finally, the differences in thallus length among *C. compressa*, *C. amentacea*, and *C. crinita* were also temporally and spatially variable (Table 1). Where the three species co-occurred, in June–July 2015 *C. crinita* was larger than both *C. compressa* and *C. amentacea*, while one year after *C. compressa* was significantly smaller than the other two species (Fig. 3). Where only two species co-occurred, *C. amentacea* was larger than *C. compressa* at all sites sampled in June–July 2015. In June–July 2016, the same pattern was shown only at two sites, i.e., San Pancrazio and Punta Caruso (Fig. 3).

Assemblage structure and species diversity of Cystoseira-associated molluscan fauna

A total of 24736 molluscan individuals were collected, belonging to 52 different taxa, three classes, and 29 families (Table 2). Most of the identified taxa were micrograzers (32 species) and filter feeders (11 species). In addition, five nudibranch taxa of specialized carnivores [*Hancockia uncinata* (Hesse, 1872), *Doto cervicenigra* Ortea & Bouchet, 1989, *Doto rosea* Trinchese, 1881, *Eubranchus* cf. *tricolor* Forbes, 1838, and *Trinchesia* sp.], two species of carnivores [*Pisania striata* (Gmelin, 1791) and *Raphitoma* sp.], one species of macroalgal grazer (*Aplysia* cf. *parvula* Mörch, 1863), and one species of deposit feeder [*Sinezona cingulata* (O. G. Costa, 1861)] were found. However, most of the collected individuals were juveniles. Gastropoda Cuvier, 1795 was the class represented by the highest number of families and species (22 and 41, respectively), followed by Bivalvia Linnaeus, 1758 (six and nine), and Polyplacophora Gray, 1821 (one and two). The most represented families were Rissoidae Gray, 1847 (10 species) and Trochidae Rafinesque, 1815 (five species) among gastropods, and Mytilidae Rafinesque, 1815 (four species) among bivalves. Bivalvia was the most abundant class, accounting for 24110 individuals, followed by Gastropoda with 622 individuals, and by Polyplacophora with four individuals (97.5%, 2.5%, and 0.02% of the total abundance, respectively). Within bivalves, however, *Mytilus galloprovincialis* Lamarck, 1819 alone accounted for 23654 individuals, contributing 95.6% to the total abundance, and it was also found in association with all the three *Cystoseira* taxa at all six sampling sites. Among the other molluscan species, *Eatonina pumila* (Monterosato, 1884), *Thylaeodus rugulosus* (Monterosato, 1878), *Musculus costulatus* (Risso, 1826), *Doto cervicenigra* Ortea & Bouchet, 1989 and *Mytilaster solidus* Monterosato, 1883 showed the highest dominance indexes (12.38%, 6.93%, 28.92%, 11.18% and 10.91%, respectively). *Doto cervicenigra*, however, was only found associated with *C. amentacea* and *C. compressa*, while the other species were shared among all three *Cystoseira* species. A total of 44 species (35 Gastropoda, seven

Bivalvia, and two Polyplacophora) were associated with *C. amentacea*, providing 59.5% of the total abundance. Among them, *M. costulatus* was the most frequent (88.9%) and abundant (37.8%), followed by *E. pumila* (72.2% of frequency, 13.7% of abundance). A total of 27 species (19 Gastropoda, seven Bivalvia, and one Polyplacophora) were associated with *C. compressa*, representing 39.5% of the total abundance. The most frequent (58.3%) and abundant (23.8%) of these was *M. solidus*, followed by *M. costulatus* (52.8% of frequency, 16.2% of abundance), *E. pumila* (47.2% of frequency, 9.9% of abundance), and *T. rugulosus* (39% of frequency, 18.5% of abundance). A total of 22 species (17 Gastropoda, four Bivalvia, and one Polyplacophora) were associated with *C. crinita*, contributing 1.0% to the total abundance. Out of these, *T. rugulosus* was the most frequent (88.3%), followed by *S. cingulata* and *Barleeia unifasciata* (Montagu, 1803) (66.7% of frequency each). The most abundant *C. crinita*-associated species, however, was *Columbella rustica* (Linnaeus, 1758) (21.8%).

The three *Cystoseira*-associated assemblages shared a total of 12 species, including eight Gastropoda, three Bivalvia, and one Polyplacophora (Table 2). The species exclusively associated with one or two algal species were as follow: six species exclusive of *C. compressa* (four Gastropoda and two Bivalvia), 17 species exclusive of *C. amentacea* (14 Gastropoda, two Bivalvia, one Polyplacophora), and one species, belonging to the *Steromphala adansonii* (Payraudeau, 1826) complex, exclusive of *C. crinita*. A total of seven molluscan species were shared between *C. compressa* and *C. amentacea* (six Gastropoda and one Bivalvia), seven species were shared between *C. amentacea* and *C. crinita*, while *Clanculus jussieui* (Payraudeau, 1826) and *Cardita calyculata* (Linnaeus, 1758) were shared between *C. compressa* and *C. crinita*.

A significant ‘Time × *Cystoseira* species × Site’ interaction was detected by PERMANOVA based on untransformed data (Table 3). This result, however, was mainly driven by obvious differences, though variable in their extent among sampling times and sites, due to the lack of *C. crinita* at all, but one, sites. Where the three *Cystoseira* species coexisted

(Scannella site), their associated molluscan assemblages were comparable in June–July 2015 (*C. compressa* vs. *C. amentacea*: $t = 0.82$, $p = 0.523$; *C. compressa* vs. *C. crinita*: $t = 0.70$, $p = 0.605$; *C. amentacea* vs. *C. crinita*: $t = 0.76$, $p = 0.575$), while they differed between *C. amentacea* and *C. crinita* in June–July 2016 (*C. compressa* vs. *C. amentacea*: $t = 1.96$, $p = 0.102$; *C. compressa* vs. *C. crinita*: $t = 1.26$, $p = 0.259$; *C. amentacea* vs. *C. crinita*: $t = 3.82$, $p = 0.004$). The only other significant difference was in June–July 2016 between *C. compressa*- and *C. crinita*-associated assemblages at Punta Imperatore ($t = 1.97$, $p = 0.040$).

The multivariate analysis repeated based on presence-absence data revealed a significant ‘*Cystoseira* species × Site’ interaction (Table 3). No specific differences apart from those related to the absence of *C. crinita* from five sites were found, while at Scannella the species composition of molluscan assemblages associated with the three *Cystoseira* species were all comparable (*C. compressa* vs. *C. amentacea*: $t = 1.01$, $p = 0.520$; *C. compressa* vs. *C. crinita*: $t = 1.01$, $p = 0.489$; *C. amentacea* vs. *C. crinita*: $t = 1.18$, $p = 0.347$).

Independently of the sampling time, the richness of associated molluscs differed spatially between *C. compressa* and *C. amentacea*, being higher for *C. amentacea* at Castello Aragonese and Sant’Angelo (Table 4; Fig. 4A). Where the three macroalgal species coexisted, they supported comparably rich associated assemblages of molluscs (Fig. 4A).

Both the Shannon (H') and the reciprocal Simpson ($1/D$) indexes varied interactively with the sampling time, the host *Cystoseira* species, and the site (Table 4). Specifically, at San Pancrazio in June–July 2015, *C. amentacea*-associated assemblages were characterized by a larger value of H' compared to *C. compressa*, while the opposite pattern was shown at Punta Caruso. In June–July 2016, at Scannella H' was higher for *C. crinita*-associated assemblages compared to the assemblages associated with the other two co-occurring *Cystoseira* species (Fig. 4B). The reciprocal Simpson index was consistently comparable between the two or the three coexisting macroalgae in June–July 2016, while one year after, at Scannella, it was higher for *C. crinita* compared to both *C. compressa* and *C. amentacea* (Fig. 4C).

The Mediterranean black mussel *Mytilus galloprovincialis* dominated the three *Cystoseira*-associated assemblages at all sites. As a consequence, it provided the highest contribution to the dissimilarity of samples belonging to each macroalga (Table 5). Adding to *M. galloprovincialis*, four other species, namely *M. solidus*, *M. costulatus*, *E. pumila*, and *S. cingulata*, were the main characteristic of assemblages associated with each *Cystoseira* species, although with varying contributions. The molluscan assemblages associated with both *C. amentacea* and *C. crinita* were also characterized by *T. rugosus*, while *Dendropoma cristatum* accounted for a considerable proportion of dissimilarity within *C. crinita* assemblages only (Table 5).

Consistently with the disproportionate large abundance of *M. galloprovincialis*, the *k*-dominance curves including this taxon showed high initial values of dominance and quickly reached the asymptote (Fig. 5A, 5C, 5E). When *M. galloprovincialis* was excluded, instead, the same curves displayed low initial values of dominance and slowly reached the asymptote (Fig. 5B, 5D, 5F).

Discussion

Molluscan assemblage associated with Cystoseira algae at Ischia Island

Molluscan assemblages associated with *Cystoseira* beds have been the subject of studies in several regions from the western to the eastern Mediterranean since the mid-1900s, due to the recognized importance of these canopy-forming algae in shaping and supporting local biodiversity (Bellan-Santini 1962, 1964, 1969; Zavodnik 1965; Kokataş 1978; Tiganus 1984; Poulicek 1985; Chemello 1986; Menioui 1992a, 1992b; Ergen and Çinar 1994; Russo 1997; Milazzo *et al.* 2000; Chemello and Milazzo 2002; Bedini *et al.* 2014; Mačić and Svirčev 2014; Pitacco *et al.* 2014; Lolas *et al.* 2018; Piazzì *et al.* 2018). In the Gulf of Naples, however, the historically most investigated habitat-forming species were *Posidonia oceanica* (Linnaeus)

Delile and *Cymodocea nodosa* (Ucria) Ascherson (Russo *et al.* 1983; Mazzella *et al.* 1989, 1992; Gambi *et al.* 1992, 1996; Scipione *et al.* 1996; Gambi 2002), with few recent exceptions represented by Corallinales taxa and *Sargassum vulgare* (Agardh) (Massa-Gallucci *et al.* 2006; Chiarore and Patti 2013). Therefore, our pioneer study contributes to filling a knowledge gap on the invertebrate fauna locally associated with habitat-forming taxa of the genus *Cystoseira*.

The examined molluscan assemblage included a relatively high number of taxa (52) belonging to three different classes and quite diverse trophic groups. These results are generally in agreement with previous studies (Zavodnik 1965; Bellan-Santini 1969; Kocatas 1978; Chemello 1986; Menioui 1992a; Chemello and Milazzo 2002; Lolas *et al.* 2018), as the number of molluscan species reported as living within *Cystoseira* beds usually varied from ~20 (Bellan-Santini 1962, 1964, 1969; Ergen and Çinar 1994; Russo 1997; Bedini *et al.* 2014) to ~70–100 (Poulicek 1985; Pitacco *et al.* 2014; Piazzini *et al.* 2018), with extreme values of five taxa reported by Mačić and Svirčev (2014) and 161 taxa reported by Milazzo *et al.* (2000). The former study, however, only investigated macro-epiphytes, whilst the latter one investigated photophilic assemblages as a whole, although largely dominated by *Cystoseira*. These may be the main reasons for their discrepancy compared to other Mediterranean studies.

Making comparisons with the literature is often challenging due to, among others, the natural variability among geographic areas, the different sampling methods adopted, and the level of taxonomic expertise of the authors. Nevertheless, some similarities between this and previous studies are noticeable. For instance, at the Class level, the trend here observed is consistent with the widely reported evidence of Gastropoda as the dominant *Cystoseira*-associated taxon in terms of species number, followed by Bivalvia and Polyplacophora. The same holds for the photophilic algae association as a whole. Although such a ranking also reflects the typical numerical pattern of molluscan biodiversity in the Mediterranean Sea (Templado and Villanueva in Coll *et al.* 2010), the limited presence of available substrates for burrowing bivalves suggests that their low diversity is not just a taxonomic artifact. At the

Family level, the two species-richest taxa (Rissoidae and Trochidae) were mostly represented by grazers feeding preferentially on diatoms and epiphyte microalgae of *Cystoseira* fronds, consistent with previous studies (e.g., [Bellan-Santini 1964](#); [Kocatas 1978](#); [Poulicek 1985](#); [Chemello 1986](#); [Chemello and Milazzo 2002](#)). Finally, many of the present *Cystoseira*-associated species were analogous to those described by previous research, such as the grazers *Acanthochitona fascicularis* (Linnaeus, 1767), *Tricolia pullus* (Linnaeus, 1758), and *Columbella rustica* (Linnaeus, 1758). Noteworthy, Mytilidae accounted for the third species-rich taxon, with *Mytilus galloprovincialis* being the most frequent and the dominant species of the molluscan assemblages studied here. More specifically, only juveniles (0.3–3 mm total height) were found within the algal canopies, whilst adult individuals were mostly observed attached to the rock among/below the holdfasts of macroalgae, where they may compete for space with the infralittoral algal associations ([Gros 1978](#); [Benedetti-Cecchi and Cinelli 1996](#); [Benedetti-Cecchi et al. 1996](#)). To the best of our knowledge, no mussel-dominated biota was ever reported within *Cystoseira* beds in the Mediterranean Sea. This would suggest the general lack of a strict association between such algae and molluscan assemblages, and that the *Cystoseira*-associated fauna may be also influenced by external factors operating on a regional scale.

Finally, the three habitat-forming algae analyzed mostly hosted juveniles of the majority of the associated molluscs, not only of mussels. This confirms the importance of *Cystoseira* species not only in structuring the local infralittoral invertebrate biodiversity in general, but also as a nursery area for molluscs ([Thibaut et al. 2005](#); [Pitacco et al. 2014](#)).

Species-specific assemblages in syntopic Cystoseira taxa

The examined *Cystoseira* beds differed in terms of architectural attributes. In particular, *C. compressa* and *C. amentacea*, the most widespread species, showed the highest density and

height, respectively. Indeed, *C. compressa* is usually smaller than *C. amentacea*. On the other hand, *C. crinita* only occurred closer to the sea surface at Scannella, where it also completely covered the walls of rock-pools (A. Chiarore, pers. obs.). Where present, however, it dominated in height over the other *Cystoseira* species. Differences among habitat-forming macroalgae, in terms of associated biota, were reported worldwide, since patterns of abundance and size structure of benthic fauna are influenced by several factors such as life cycles, chemical defenses, or algal architecture (Chemello and Milazzo 2002; Hauser *et al.* 2006; Veiga *et al.* 2014; Thiriet *et al.* 2016). In the present system too, apart from the dominance of *M. galloprovincialis* at all sites, the three *Cystoseira* species supported diversified molluscan assemblages. *Cystoseira amentacea* and *C. compressa* hosted a similar number of taxa, although *C. amentacea* always accounted for a relatively higher number of individuals. This may be due to the longer thalli of this species that would offer a wider area for colonization. The maximum total number of species at the ‘regional’ scale, however, as well as the maximum number of species per sampling unit, were found at Scannella for *C. crinita*. The same patterns were displayed by the diversity indexes. Moreover, the number of individuals associated with *C. crinita* at Scannella was comparable to that of the other two algal species at the same site. This, together with its high percentage of unshared species within the sampling site, indicates that the *C. crinita*-associated malacofauna was relatively more heterogeneous in terms of species composition.

With respect to the species-specific patterns of molluscan assemblages, the shape of the k-dominance curves built including *M. galloprovincialis* may suggest a poor structure of molluscan assemblages associated with the three *Cystoseira* species. After the removal of *M. galloprovincialis*, however, the same curves were initially characterized by low dominance and slowly reached the asymptote, suggesting that the *Cystoseira*-associated assemblages were actually well diversified, but that such a feature was masked by the disproportionately abundant mussels.

Among the 52 molluscan taxa censused, only 12 were shared among the three habitat-forming species, much less were shared between only two of them, and six, 16, and one species were exclusive of *C. compressa*, *C. amentacea*, and *C. crinita*, respectively. This clearly shows that even congeneric and syntopic taxa may not support benthic fauna in the same way. The presence of five rissoid taxa (accounting for 50% of Rissoidae) associated with *C. amentacea* was especially notable. Unfortunately, the available information on the malacofauna associated with this species, sometimes mentioned in the literature under its synonyms/varieties *C. stricta* or *C. spicata* (Bellan-Santini 1962, 1969; Tiganus 1984; Chemello 1986; Menioui 1992b; Ergen and Çinar 1994; Mačić and Svirčev 2014), is scant. Moreover, no authors have yet formally compared faunal assemblages between different *Cystoseira* taxa. The only partial exceptions were provided by Bellan-Santini (1969) and Chemello (1986), who just reported faunal lists associated with each investigated algal taxon. Such a knowledge gap crucially hinders any possibility to compare the present data with previous findings.

Conclusions

There is increasing evidence of a worldwide decline of canopy-forming algae (Eriksson *et al.* 2002; Thibaut *et al.* 2005; Coleman *et al.* 2008; Smale and Wernberg 2013; Bianchi *et al.* 2014), whose loss may trigger cascade effects on associated biodiversity and ecosystem services (Wilson *et al.* 2008; Schiel and Lilley 2011). Due to this, the conservation status of *Cystoseira* species has become a main management priority within the European Water Framework Directive in the Mediterranean basin. In spite of that, the overall knowledge of such canopies is still limited, and here we not only filled a gap by providing essential basic information on the patterns of diversity of *Cystoseira* species and their associated molluscan biota at Ischia Island (Italy, Mediterranean Sea), but also first suggest a species-specific role as habitat-formers being played by different sympatric *Cystoseira* taxa.

Although our study is intrinsically unable to elucidate the mechanisms involved, the broader implications of our findings are numerous. First, the knowledge of natural patterns of distribution and abundance of *Cystoseira* species would provide a reference for detecting changes due to anthropogenic disturbance (Chapman *et al.* 1995; Frascchetti *et al.* 2005), which is of particular importance in an area subject to a wide number of human activities of potential impact such as the Gulf of Naples (Bertocci *et al.*, 2019). Second, such knowledge is essential to optimize sampling and experimental designs suited to capture, in the most comprehensive way possible, the actual variability of the target organisms, thus avoiding possibly incorrect ecological interpretations (Underwood 1993; Benedetti-Cecchi *et al.* 2001). Finally, and strictly linked to the previous points, our findings have an important management value in the context of the growing awareness of spatial and temporal heterogeneity as a criterion for designing and assessing the effectiveness of MPAs. Specifically, it is acknowledged that the zoning and implementation of an effective MPA should guarantee a complete and accurate representation of the relevant scales of variation of the target populations and assemblages, as well as of their abiotic and biological drivers (Benedetti-Cecchi *et al.* 2003). In such a context, we here suggest an implementation of the local Regno di Nettuno MPA that should rely on the present data and rank at the maximum level of protection the whole infralittoral fringe hosting the above-mentioned *Cystoseira* species, thus taking into account their among-sites variation to include a representative sample of such target organisms. By contrast, the inclusion of just one or a few sites, possibly chosen *a priori* based on whatever criterion, would likely result in an oversimplified picture of the real situation and, eventually, a loss of considerable biodiversity.

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Table 1. Analysis of variance (ANOVA) testing for differences in percentage cover, biomass, number, and mean length of thalli of three *Cystoseira* species (*C. amentacea*, *C. compressa*, and *C. crinita*) (Cy) at two times (June–July 2015 and June–July 2016) (Ti) and six sampling sites (Castello Aragonese, San Pancrazio, Sant’Angelo, Scannella, Punta Imperatore, and Punta Caruso) (Si). * $p < 0.05$, ** $p < 0.01$, * $p < 0.001$.**

Source of variation	df	% cover		biomass		# thalli		mean length		Denominator
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	
Time	1	11.3	0.03	11.0	0.10	0.83	3.88	29.05	2.29	Ti × Si
<i>Cystoseira</i> species	2	55071.1	-	5842.5	-	32.07	-	834.88	-	no test
Site	5	3662.5	8.83*	557.2	4.93	0.87	4.07	51.86	4.09	Ti × Si
Ti × Cy	2	662.7	1.40	7.4	0.05	0.36	4.29*	17.46	1.10	Ti × Cy × Si
Ti × Si	5	414.7	1.37	112.9	1.04	0.21	3.13*	12.69	2.64*	Residual
Cy × Si	10	2590.5	5.46**	500.9	3.52*	0.97	11.39***	106.03	6.69**	Ti × Cy × Si
Ti × Cy × Si	10	474.4	1.56	142.3	1.31	0.09	1.24	15.85	3.30**	Residual
Residual	72	303.5		108.5		0.07		4.81		
Cochran’s test		<i>C</i> = 0.131		<i>C</i> = 0.212		<i>C</i> = 0.186		<i>C</i> = 0.166		
Transformation		None		None		Ln(x+1)		None		

Table 2. Molluscan assemblage found in *Cystoseira* belts in Ischia, with feeding guilds (FG), distribution groups (DG), and percentages of frequency of occurrence (%F) and dominance (%D). Abbreviations used. Sites: CA - Castello Aragonese; SP - San Pancrazio; SA - Sant'Angelo; SC - Scannella; PI - Punta Imperatore; PC - Punta Caruso. Feeding guilds: C - carnivores; D - deposit feeders; E - ectoparasites and specialised carnivores; FF - filter feeders; MG - micrograzers and/or mesograzers; AG - macroalgae grazers. Distribution groups: A - species shared among the three *Cystoseira* taxa; B - species exclusive for *C. compressa*; C - species exclusive for *C. amentacea*; D - species exclusive for *C. crinita*; E - species shared between *C. compressa* and *C. amentacea*; F - species shared between *C. compressa* and *C. crinita*; G - species shared between *C. amentacea* and *C. crinita*.

Family	Species	FG	DG	CA	SP	SA	SC	PI	PC	%F	%D
Acanthochitonidae	<i>Acanthochitona crinita</i> (Pennant, 1777)	MG	C		+					1.28	0.09
	<i>Acanthochitona fascicularis</i> (Linnaeus, 1767)	MG	A	+			+			3.85	0.28
Patellidae	<i>Patella caerulea</i> Linnaeus, 1758	MG	B	+						2.56	0.28
	<i>Patella ulyssiponensis</i> Gmelin, 1791	MG	C						+	1.28	0.09
Fissurellidae	<i>Diodora graeca</i> (Linnaeus, 1758)	MG	B						+	1.28	0.09
	<i>Fissurella nubecula</i> (Linnaeus, 1758)	MG	C				+			1.28	0.09
Scissurellidae	<i>Sinezona cingulata</i> (O.G. Costa, 1861)	D	A	+		+	+	+	+	29.50	3.23
	<i>Clanculus cruciatus</i> (Linnaeus, 1758)	MG	G			+	+			3.85	0.37
	<i>Clanculus jussieui</i> (Payraudeau, 1826)	MG	F				+		+	2.56	0.18
Trochidae	<i>Phorcus turbinatus</i> (Born, 1778)	MG	A		+	+	+	+	+	15.38	1.48
	<i>Steromphala adansonii</i> (Payraudeau, 1826) complex	MG	D				+			1.28	0.09
	<i>Steromphala varia</i> (Linnaeus, 1758)	MG	B				+			1.28	0.09
Phasianellidae	<i>Tricolia pullus</i> (Linnaeus, 1758)	MG	E	+	+					3.85	0.28
Cerithiidae	<i>Bittium latreillii</i> (Payraudeau, 1826)	MG	G		+		+			2.56	0.18
Triphoridae	<i>Marshallora adversa</i> (Montagu, 1803)	MG	B				+			1.28	0.09
Cingulopsidae	<i>Eatonina fulgida</i> (J. Adams, 1797)	MG	E	+	+	+	+			5.13	0.55
	<i>Eatonina pumila</i> (Monterosato, 1884)	MG	A	+	+	+	+	+	+	58.97	12.38
	<i>Alvania cf. cancellata</i> (da Costa, 1778)	MG	C	+						1.28	0.09
	<i>Alvania discors</i> (T. Allan, 1818)	MG	C			+				1.28	0.09
	<i>Alvania cf. lanciae</i> (Calcara, 1845)	MG	C					+		1.28	0.09
	<i>Crisilla beniamina</i> (Monterosato, 1884)	MG	C			+		+		2.56	0.28
Rissoidae	<i>Obtusella macilenta</i> (Monterosato, 1880)	MG	C			+				1.28	0.37
	<i>Rissoa guerinii</i> Récluz, 1843	MG	A	+	+	+	+			11.54	1.11
	<i>Rissoa lia</i> (Monterosato, 1884)	MG	G	+	+	+	+			8.97	2.31
	<i>Rissoa variabilis</i> (Megerle von Mühlfeld, 1824)	MG	A	+		+	+	+		12.28	0.92
	<i>Setia ambigua</i> (Brugnone, 1873)	MG	C		+	+				2.56	0.18
	<i>Setia fusca</i> (Philippi, 1841)	MG	C				+			1.28	0.09
Anabathridae	<i>Pisinna glabrata</i> (Megerle von Mühlfeld, 1824)	MG	G			+	+			3.85	1.11
Barleeiidae	<i>Barleeia unifasciata</i> (Montagu, 1803)	MG	A		+	+	+			10.26	1.20
	<i>Thylaeodus rugulosus</i> (Monterosato, 1878)	FF	A	+	+	+	+	+	+	34.62	6.93
Vermetidae	<i>Dendropoma cristatum</i> (Biondi, 1859)	FF	A	+		+	+	+	+	16.67	2.12
	<i>Columbella rustica</i> (Linnaeus, 1758)	MG	G		+			+		3.85	2.12
Raphitomidae	<i>Raphitoma</i> sp.	C	C					+		1.28	0.09
	<i>Rissoella diaphana</i> (Alder, 1848)	MG	C		+					1.28	0.09
Rissoellidae	<i>Rissoella inflata</i> (Monterosato, 1880)	MG	G		+		+			2.56	0.18
Pisaniidae	<i>Pisania striata</i> (Gmelin, 1791)	C	C					+		1.28	0.09
Omalogyridae	<i>Ammonicera fischeriana</i> (Monterosato, 1869)	MG	E		+	+		+	+	10.26	0.74
Aplysiidae	<i>Aplysia cf. parvula</i> Mörch, 1863	AG	C						+	1.28	0.09
Hancockiidae	<i>Hancockia uncinata</i> (Hesse, 1872)	E	E	+	+	+		+		6.41	2.31
	<i>Doto cervicenigra</i> Ortea & Bouchet, 1989	E	E	+	+	+	+	+	+	14.10	11.18
Dotidae	<i>Doto rosea</i> Trinchese, 1881	E	G				+	+		3.85	0.55
	<i>Eubranchus cf. tricolor</i> Forbes, 1838	E	C		+					1.28	0.09
Trinchesiidae	<i>Trinchesia</i> sp.	E	E	+	+	+	+	+	+	21.79	3.51
Mytilidae	<i>Modiolus barbatus</i> (Linnaeus, 1758)	FF	E		+			+	+	5.13	0.55
	<i>Musculus costulatus</i> (Risso, 1826)	FF	A	+	+	+	+	+	+	69.23	28.92
	<i>Mytilaster solidus</i> Monterosato, 1883	FF	A	+	+	+	+	+	+	55.13	10.91
	<i>Mytilus galloprovincialis</i> (Lamarck, 1819)	FF	A	+	+	+	+	+	+	100.00	----
Anomiidae	<i>Anomia ephippium</i> Linnaeus, 1758	FF	C		+					1.28	0.09
Carditidae	<i>Cardita calyculata</i> (Linnaeus, 1758)	FF	F	+	+		+			5.13	0.65
Lasaeidae	<i>Lasaea rubra</i> (Montagu, 1803)	FF	B			+	+			2.56	0.18
Cardiidae	<i>Parvicardium exiguum</i> (Gmelin, 1791)	FF	C		+					1.28	0.09
Hiatellidae	<i>Hiatella arctica</i> (Linnaeus, 1767)	FF	B		+	+	+			6.41	0.74

Table 3. Permutational multivariate analysis of variance (PERMANOVA) testing for differences in the composition of molluscan assemblages associated with three *Cystoseira* species (*C. amentacea*, *C. compressa* and *C. crinita*) (Cy) at two times (June–July 2015 and June–July 2016) (Ti) and six sampling sites (Castello Aragonese, San Pancrazio, Sant’Angelo, Scannella, Punta Imperatore, and Punta Caruso) (Si). Significant effects are indicated in bold.

Untransformed data					
Source of variation	df	MS	pseudo- <i>F</i>	p	# unique perm.
Time	1	1966.8	0.76	0.633	999
<i>Cystoseira</i> species	2	37548.0	6.02	0.001	999
Site	5	5886.7	2.27	0.004	997
Ti × Cy	2	3062.8	0.96	0.469	999
Ti × Si	5	2597.5	1.21	0.166	998
Cy × Si	10	3703.1	1.16	0.237	999
Ti × Cy × Si	10	3180.1	1.48	0.007	998
Residual	72	2154.8			
Presence – Absence data					
Source of variation	df	MS	pseudo- <i>F</i>	p	# unique perm.
Time	1	5191.1	1.86	0.038	999
<i>Cystoseira</i> species	2	34056.0	4.58	0.001	998
Site	5	4405.8	1.58	0.037	998
Ti × Cy	2	3898.5	1.45	0.073	998
Ti × Si	5	2784.7	1.25	0.072	997
Cy × Si	10	4127.6	1.53	0.008	998
Ti × Cy × Si	10	2693.5	1.21	0.058	994
Residual	72	2226.4			

Table 4. Analysis of variance (ANOVA) testing for differences in the species richness (S), the Shannon index (H') and the reciprocal Simpson index (1/D) of molluscan assemblages associated with three *Cystoseira* species (*C. amentacea*, *C. compressa*, and *C. crinita*) (Cy) at two times (June–July 2015 and June–July 2016) (Ti) and six sampling sites (Castello Aragonese, San Pancrazio, Sant'Angelo, Scannella, Punta Imperatore, and Punta Caruso) (Si). * p<0.05, ** p<0.01.

Source of variation	df	S		H'		1/D		Denominator
		MS	F	MS	F	MS	F	
Time	1	0.75	0.14	0.0001	0.00	0.02	0.16	Ti × Si
<i>Cystoseira</i> species	2	240.56	-	0.0917	-	8.90	-	no test
Site	5	12.28	2.27	0.0671	3.83	1.21	8.38*	Ti × Si
Ti × Cy	2	3.86	0.79	0.0213	1.49	0.22	1.44	Ti × Cy × Si
Ti × Si	5	5.42	1.54	0.0175	4.09**	0.14	2.51*	Residual
Cy × Si	10	18.25	3.76*	0.0345	2.40	0.99	6.49**	Ti × Cy × Si
Ti × Cy × Si	10	4.86	1.38	0.0143	3.35**	0.15	2.66**	Residual
Residual	72	3.52		0.0043		0.06		
Cochran's test		C = 0.113		C = 0.170		C = 0.808**		
Transformation		None		Square root(x+1)		None		

Table 5. Contribution (δ_i) of individual taxa from molluscan assemblages (presence vs. absence data) to the dissimilarity within each of three *Cystoseira* species. Only taxa cumulatively contributing $\geq 90\%$ to total dissimilarity are included. Values of $\delta_i/SD(\delta_i) \geq 1$ indicate that the contribution of a taxon to percentage dissimilarity was consistent among pairwise comparisons of samples.

<i>Cystoseira compressa</i>					
Taxon	Frequency (%)	δ_i	δ_i %	cumul. %	$\delta_i/SD(\delta_i)$
<i>Mytilus galloprovincialis</i>	100	22.93	45.86	45.86	3.36
<i>Mytilaster solidus</i>	58	6.23	12.46	58.32	0.66
<i>Musculus costulatus</i>	53	6.08	12.16	70.48	0.60
<i>Eatonina pumila</i>	47	5.07	10.13	80.61	0.56
<i>Thylaeodus rugulosus</i>	39	3.44	6.89	87.50	0.45
<i>Sinezona cingulata</i>	22	1.98	3.95	91.45	0.33
<i>Cystoseira amentacea</i>					
Taxon	Frequency (%)	δ_i	δ_i %	cumul. %	$\delta_i/SD(\delta_i)$
<i>Mytilus galloprovincialis</i>	100	17.94	33.54	33.54	3.37
<i>Musculus costulatus</i>	89	13.69	25.59	59.12	1.62
<i>Eatonina pumila</i>	72	9.21	17.21	76.33	0.94
<i>Mytilaster solidus</i>	56	6.63	12.40	88.74	0.79
<i>Sinezona cingulata</i>	31	1.54	2.88	91.61	0.34
<i>Cystoseira crinita</i>					
Taxon	Frequency (%)	δ_i	δ_i %	cumul. %	$\delta_i/SD(\delta_i)$
<i>Mytilus galloprovincialis</i>	17	16.98	44.58	44.58	3.36
<i>Musculus costulatus</i>	14	11.71	30.74	75.32	1.20
<i>Sinezona cingulata</i>	8	2.90	7.60	82.92	0.48
<i>Dendropoma cristatum</i>	6	1.21	3.18	86.10	0.26
<i>Thylaeodus rugulosus</i>	6	1.11	2.92	89.02	0.26
<i>Eatonina pumila</i>	6	1.03	2.69	91.71	0.26

LEGEND TO FIGURES

Fig. 1. Map illustrating (A) the location of the study area within the Mediterranean Sea, and (B) the six sampling sites around Ischia Island (CA= Castello Aragonese, SP= San Pancrazio, SA= Sant' Angelo, SC= Scannella, PI= Punta Imperatore, PC= Punta Caruso).

Fig. 2. Mean (+SE) percentage cover (A, n = 6), biomass (B, n = 6) and number of thalli (C-a, n = 6, and C-b, n = 18) of three *Cystoseira* species. Different letters above bars represent significantly different means (SNK test: only within-site comparisons are appropriate in panels A, B and C-a; only within-time comparisons are appropriate in panel C-b). Abbreviations as in Figure 1.

Fig. 3. Mean (+SE, n = 3) thallus length of three *Cystoseira* species at two times and six sampling sites. Different letters above bars represent significantly different means (SNK test: only within-site comparisons are appropriate). Abbreviations as in Figure 1.

Fig. 4. Mean (+SE) values of richness (A, n = 6), Shannon index (B, n = 3) and reciprocal Simpson index (C, n = 3) of molluscan assemblages associated with three *Cystoseira* species. Different letters above bars represent significantly different means (SNK test: only within-site comparisons are appropriate). Abbreviations as in Figure 1.

Fig. 5. *k*-dominance curves of molluscan assemblages (A, C and E: *Mytilus galloprovincialis* included, B, D and F: *M. galloprovincialis* excluded) associated with three *Cystoseira* species at six sampling sites. Cumulative dominance values reported as percentages. Abbreviations as in Figure 1. [Note that different plots are on different scales.](#)

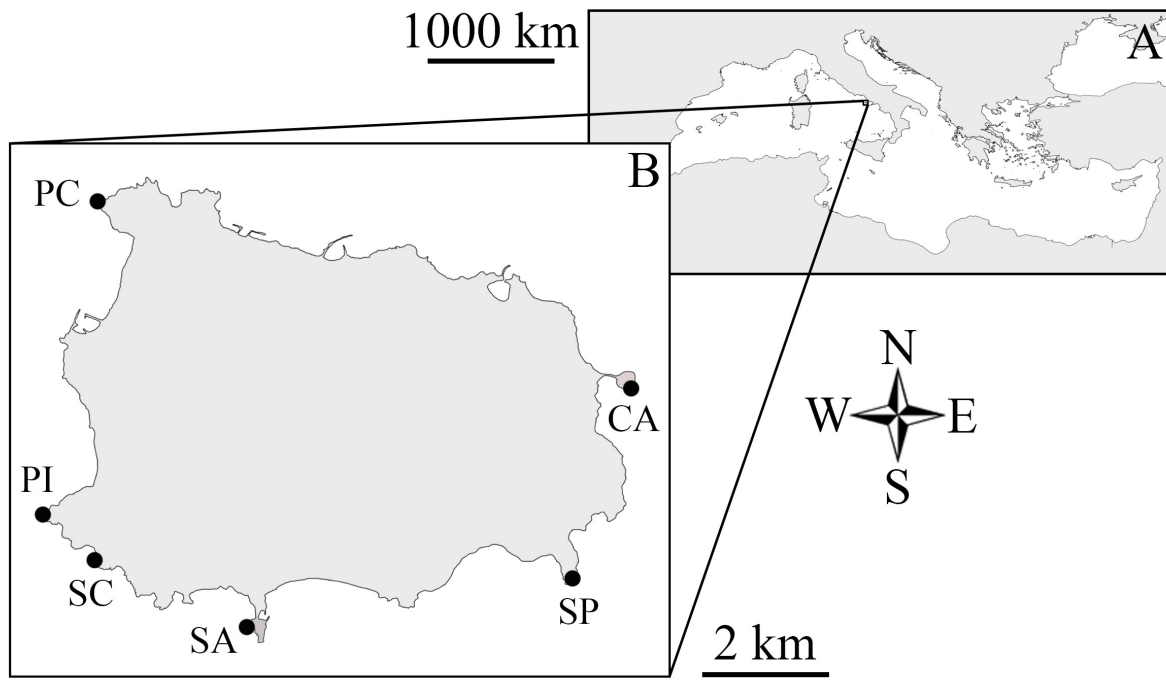


Fig. 1

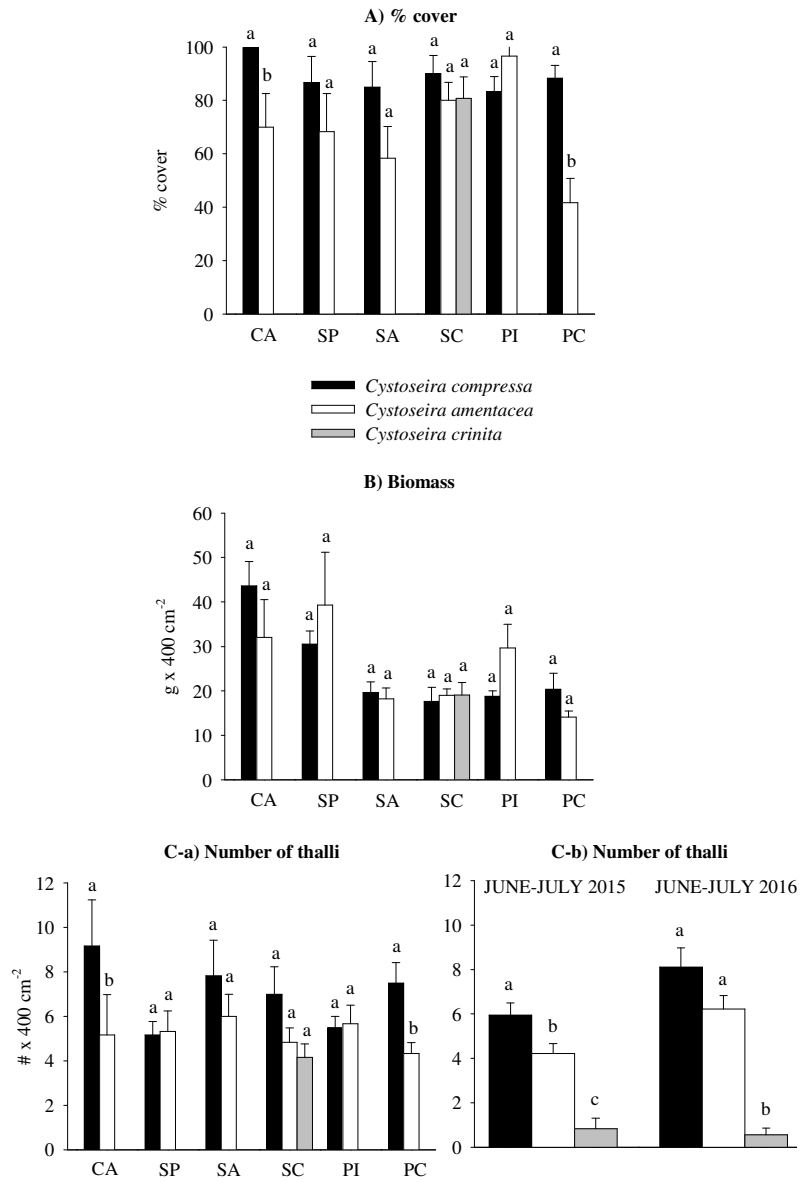


Fig. 2

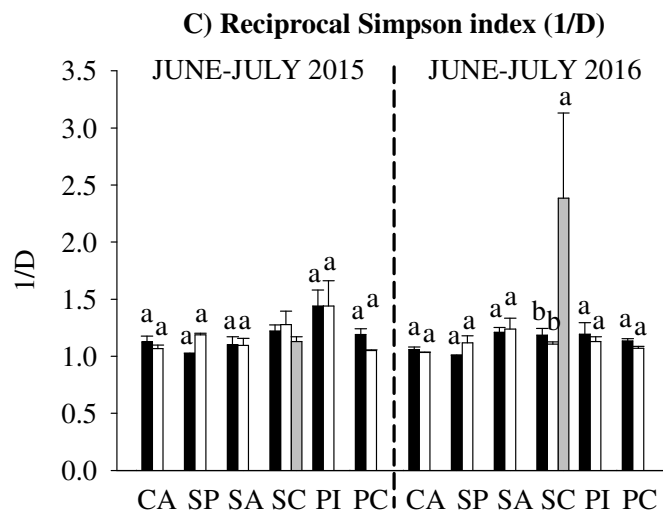
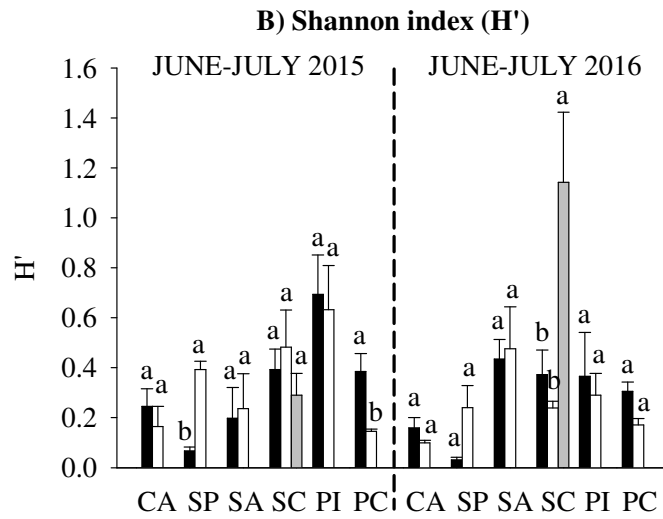
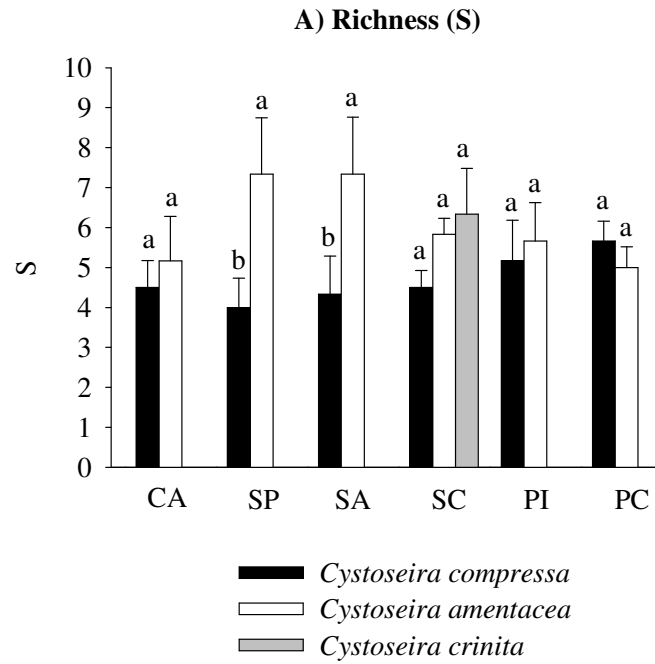


Fig. 4

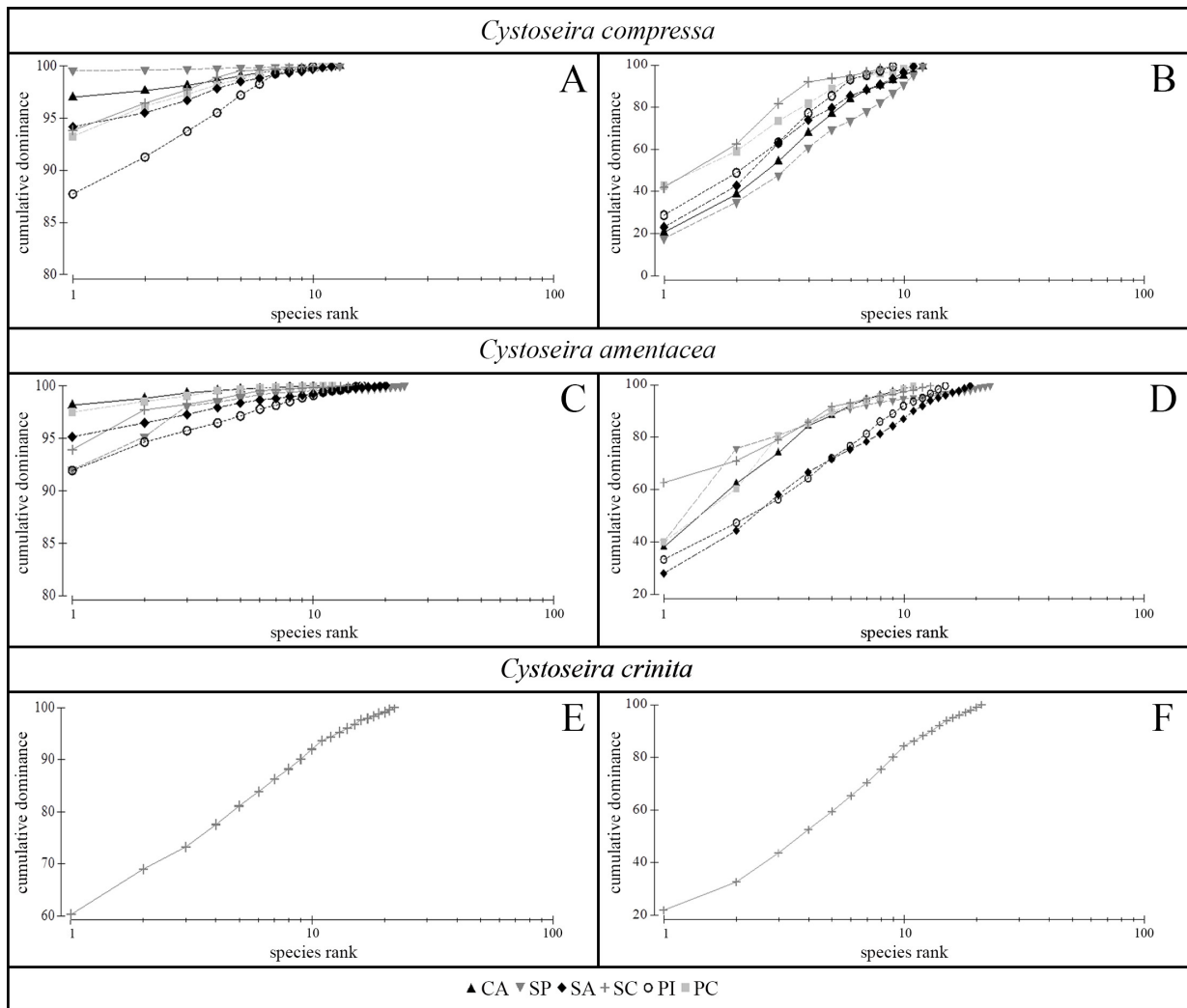


Figure 5