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Co-occurrence of a reef-building coral and canopy-forming macroalgae in the Mediterranean Sea

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Abstract

Canopy-forming macroalgae are among the main competitors of corals, affecting coral recruitment, growth of recruits and adults, fecundity, and in the worst-case scenario causing coral bleaching and necrosis. However, potentially reef-building coral *Cladocora caespitosa* (Linnaeus, 1767) and canopy-forming macroalgae of the order Fucales (*Cystoseira sensu lato*) are known to coexist at a few sites in the Mediterranean Sea. Here, we examine the small-scale relationships between *Cladocora* abundance and *Cystoseira s. l.* densities at three different sites where they coexist. We found that these relationships were both species- and site-specific, even though most were neutral, suggesting a predominant concurrence of corals and macroalgae at the small scale. These findings shed new light on the relationship between corals and fleshy macroalgae in a temperate environment and serve as a starting point for future studies addressing the interactions between *C. caespitosa* and *Cystoseira s. l.*

Keywords: *Cladocora caespitosa*; Fucales; *Cystoseira*; coral-algal interactions; Mediterranean Sea.

Introduction

Although reef-building corals and canopy-forming macroalgae usually dominate in different environments, competition between them is recurrent when they coexist (Tanner, 1995; Miller & Hay, 1998; McCook *et al*., 2001; Lirman, 2001). Corals and algae use both physical (e.g., sweeper tentacles, overtopping, abrasion) and chemical (allelopathy) defenses to compete for space and suitable light levels. Coral overgrowth by turf-algal mats or canopy-forming macroalgae can cause hypoxia in the neighboring coral tissue, severe damage such as bleaching and necrosis, and even disease (Hughes, 1994; Tanner, 1995; Nugues *et al*., 2004; Titlyanov *et al*., 2007; Barott *et al*., 2009, 2012; Kersting *et al*., 2015). Moreover, macroalgae can also inhibit coral recruitment, growth of coral recruits and adults, and coral fecundity (Box & Mumby, 2007; Hughes *et al*., 2007; Titlyanov *et al*., 2007; Birrell *et al*., 2008; Foster *et al*., 2008; Vermeij *et al*., 2009, 2010). The decrease in coral growth caused by algal overgrowth is also the result of a reduction in the photosynthetic activity of zooxanthellae (Lirman, 2001; Vermeij *et al*., 2010). In addition, allelochemical compounds produced by many macroalgae may reduce coral fitness (Titlyanov *et al*., 2007; Rasher & Hay, 2010; Rasher *et al*., 2011). Indirectly, macroalgal exudation/release of these secondary metabolites and dissolved organic compounds (DOC) can increase the abundance of potentially pathogenic bacteria and thereby directly transmit diseases from algae to corals or alter the microbial communities associated with corals (Nugues *et al*., 2004; Smith *et al*., 2006; Dinsdale *et al*., 2008; Barott *et al*., 2011). Although most evidence indicates negative effects of algae on corals, coral and algal interactions are not one-sided, since some studies have also reported inhibition of algal growth by corals or even overgrowth of algae by corals (McCook *et al*., 2001; Jompa & McCook, 2002; Titlyanov *et al*., 2007; Kersting *et al*., 2014; Kersting & Linares, 2019).

The Mediterranean is a warm temperate sea with shallow rocky environments dominated by macroalgae (Zabala & Ballesteros, 1989), although colonies of zooxanthellate, potentially reef-building coral *Cladocora caespitosa* (Linnaeus, 1767), create habitats in particular environments (Chintiroglou, 1996; Koukouras *et al*., 1998; Kružić & Benković, 2008; Kersting & Linares, 2012; Pitacco *et al*., 2014). *Cladocora caespitosa* can grow on sandy and rocky bottoms and can build bioherms formed by itself and coralline algae (Kružić & Benković, 2008; Kersting & Linares, 2012). It can thrive in muddy and nutrient-enriched waters (Peirano *et al*., 2005). *Cla-*

docora caespitosa also displays great plasticity in growth and morphologies, forming banks, beds, or even free-living coral nodules (coralliths) (Peirano *et al*., 1998; Kružić & Benković, 2008; Kersting & Linares, 2012; Kersting *et al*., 2017a, 2017b). Meanwhile, members of the order Fucales are the main canopy-forming algae in the Mediterranean Sea (Giaccone, 1973; Ballesteros, 1992; Cormaci *et al*., 2012; Gianni *et al*., 2013). Communities dominated by *Ericaria* spp., *Gongolaria* spp., and *Cystoseira* spp. (=*Cystoseira sensu lato* = *Cystoseira s. l.*) characterize Mediterranean infralittoral and upper circalittoral hard bottoms (Feldmann, 1937; Giaccone, 1973; Rodríguez-Prieto *et al*., 2013; Sales & Ballesteros, 2009). Species of *Cystoseira s. l.* are distributed along bathymetric and hydrodynamic gradients according to light and hydrodynamic exposure (Giaccone & Bruni, 1973; Verlaque, 1987; Sant & Ballesteros, 2021a) as well as their competitive capabilities and resistance to herbivores (Vergés *et al*., 2009).

Cladocora caespitosa and Mediterranean canopy-forming algae compete for light and space and therefore, spatial segregation could be expected, with a decrease in coral cover in places where individuals of *Cystoseira s. l.* are abundant. In fact, the recent expansion of the zooxanthellate coral *Oculina patagonica* de Angelis d'Ossat, 1908 in the western Mediterranean seems to be driven either by macroalgae overgrazing by sea urchins —which facilitates coral recruitment- (Coma *et al*., 2011) or by the provision of new, open space (Serrano *et al*., 2012, 2013). However, neutral and even positive relationships between *C. caespitosa* abundance and *Cystoseira s. l.* densities have recently been reported (Ballesteros & Pons-Fita, 2020; Pons-Fita *et al*., 2020), calling into question the notion of competitive exclusion between corals and macroalgae in the Mediterranean Sea.

In this study, we explored the relationships between *C. caespitosa* abundance and *Cystoseira s. l.* densities in three localities where they coexist. Our aim was to analyze empirical distribution data in order to assess the hypothesis that the presence of *C. caespitosa* does not prevent the abundance of different species of *Cystoseira s. l.*

Materials and Methods

Study sites

Sampling was performed in July 2019 at three sites in the western Mediterranean Sea: Es Banc (38.726238º N, 1.390446º E), located in the northwestern part of Formentera (Balearic Islands), Espardelló (38.785903º N, 1.484408º E), an islet located on the northeast side of Formentera, next to Espardell island, and Illa Grossa (39.895518º N, 0.686766º E) in the Columbretes archipelago, which is located 56 km off the Spanish coast (Fig. 1). At each study site, two areas measuring 40 x 40 m^2

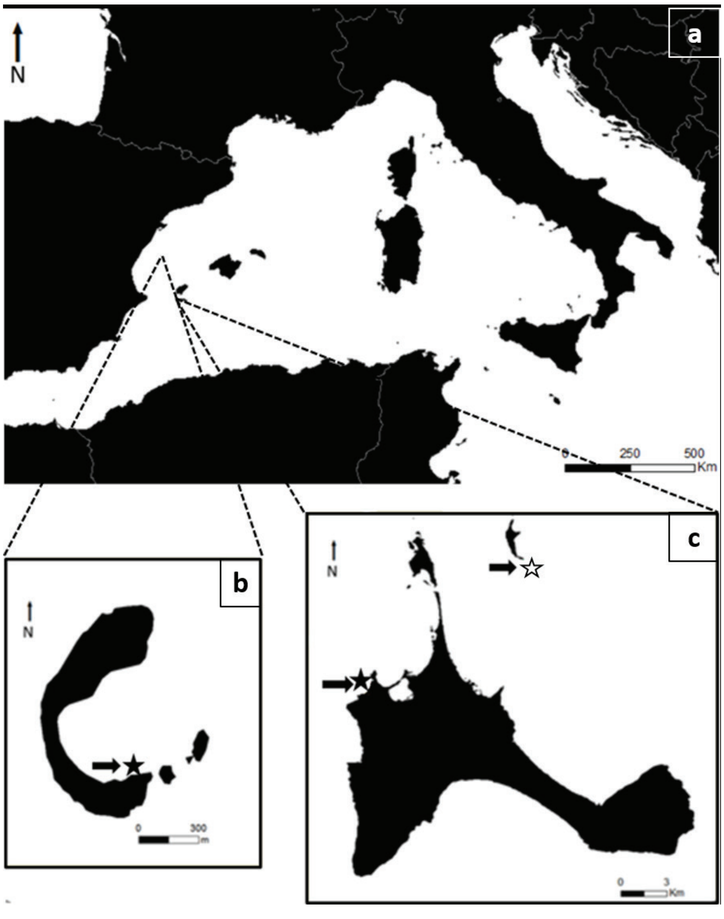

Fig. 1: Location of the sampling sites. (a) Western Mediterranean. (b) Sampling site (black star) in Illa Grossa Bay, Columbretes islands. (c) Sampling sites in Formentera: Espardelló (white star) and Es Banc (black star).

and located less than 200 m apart were selected at the same depth: one where both *C. caespitosa* and *Cystoseira s. l.* were present and one where only *Cystoseira s. l.* was present. Areas with and without *C. caespitosa* did not show any major environmental differences (i.e., same waterbody, same exposure, same geomorphology) other than the presence or absence of *C. caespitosa*. This sampling strategy prevented us from distinguishing between effects due to the presence of *C. caespitosa* and the natural variability of the system, for which more interspersed areas for each condition would have been necessary, but there were no other areas with *C. caespitosa* in the surroundings to replicate for the two conditions. In areas with *C. caespitosa* at Es Banc, colonies were present on a flat seafloor with a cover of 34% on average, at depths of between 8 and 12 m (Pons-Fita *et al*., 2020). At Espardelló, situated at between 7 and 13 m depth, *C. caespitosa* colonies were more fragmented due to moderate to high turbulence. Indeed, we observed a high occurrence of free-living coral nodules or coralliths (Kersting *et al*., 2017b) and the cover of *C. caespitosa* colonies was 20% on average (Kersting *et al*., 2017a). Columbretes presented the highest seafloor heterogeneity, with *C. caespitosa* spreading on rock crests and blocks at between 15 and 18 m depth and colonies attaining an average of 7% cover throughout the whole Illa Grossa bay (Kersting & Linares, 2012).

Espardelló and Columbretes are no-take marine protected areas (MPAs) and Es Banc is included in a MPA where artisanal fishing is allowed. All three sites host *C. caespitosa* colonies together with relatively high densities of *Cystoseira s. l.* (Kersting & Linares, 2012; Kersting *et al*., 2017a; Pons-Fita *et al*., 2020).

Sampling methods

To study the small-scale relationships between *Cystoseira s. l.* and *C. caespitosa*, densities and abundances were measured. *Cystoseira s. l.* individuals were identified to species level and counted using 625 cm^2 quadrat frames divided into 25 (5 cm x 5 cm) subquadrats. Quadrats were placed randomly inside an area measuring 40 x 40 m^2. *C. caespitosa* abundance was quantified using the same quadrats and measured as the number of subquadrats where *C. caespitosa* was present (Sala & Ballesteros, 1997; Sant *et al*., 2017; Teixidó *et al*., 2018). The number of quadrats per sampling site ranged between 188 and 237 (Columbretes: 188; Es Banc: 203; Espardelló: 237) in areas with *C. caespitosa*, and between 79 and 100 in areas without *C. caespitosa* (Columbretes: 79; Es Banc: 82; Espardelló: 100).

Data analysis

Linear regression analyses were used to determine the relationship between seaweed and coral abundances (0.05 significance level), and Student's *t*-tests were used to compare mean *Cystoseira s. l.* densities in sites with and without *C. caespitosa* colonies. Statistical analyses were performed using Systat 11.0 (SPSS Inc. 2004).

Results

All the sites presented a different composition of *Cystoseira s. l.* species, with only *Cystoseira compressa* (Esper) Gerloff & Nizamuddin and *Ericaria brachycarpa* (J. Agardh) Molinari-Novoa & Guiry being found at all three (Table 1). Columbretes hosted the highest diversity of *Cystoseira s. l.*, with six species, and Espardelló the lowest, with four species.

Areas with *Cladocora caespitosa*

In the areas with *C. caespitosa*, the most common seaweed in Es Banc was *Gongolaria montagnei* (J. Agardh) Kuntze, which accounted for 90% of all the specimens of *Cystoseira s. l.* (Fig. 2a). The remaining 10% consisted of *Ericaria brachycarpa* (6.3%), *Gongolaria* cf. *elegans* (Sauvageau) Molinari-Novoa & Guiry (3.2%), and *C. compressa* (0.3%). In Espardelló, the most frequent species was again *G. montagnei*, which accounted for 72% of all specimens, followed by *C. compressa* (18%) and *E. brachycarpa* (<10%) (Fig. 2b). In Columbretes, *C. compressa* was the most frequent species (46%), followed by

Table 1. Species composition of *Cystoseira s. l.* at the three sampling sites.

Species	Es Banc	Espardelló	Columbretes
Gongolaria montagnei	+	+	
Gongolaria cf. *elegans*	+		
Gongolaria sauvageauana			+
Gongolaria montagnei v. *compressa*			+
Ericaria brachycarpa	+	+	+
Ericaria zosteroides			+
Cystoseira compressa	+	+	+
Cystoseira foeniculacea	+	+	
Cystoseira foeniculacea f. *latiramosa*			+

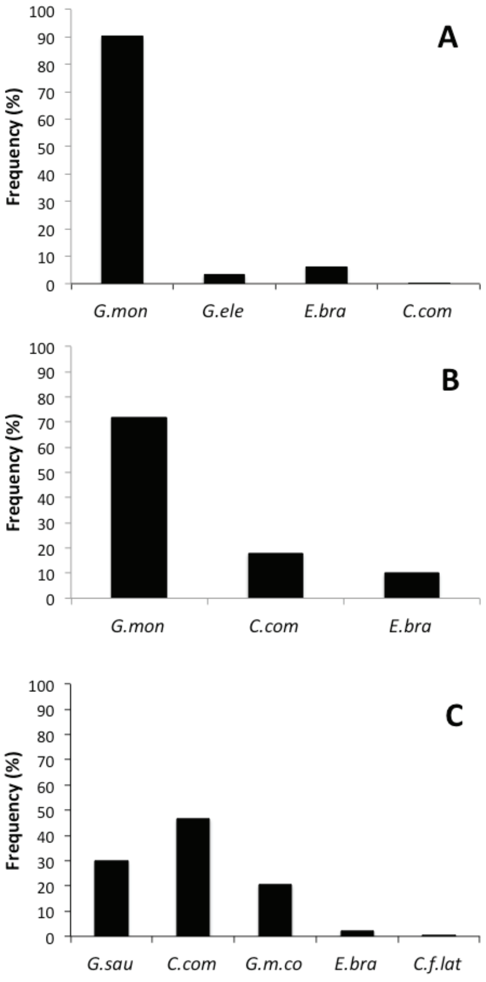

Fig. 2: Density-frequency distributions of *Cystoseira s. l.* species in places coexisting with *Cladocora caespitosa*. A) Es Banc (n=2885), B) Espardelló (n=2078) and C) Columbretes (n=931). Species abbreviations: *G.mon=Gongolaria montagnei*, *G.ele=Gongolaria* cf. *elegans*, *E.bra=Ericaria brachycarpa*, *C.com=Cystoseira compressa*, *G.sau=Gongolaria sauvageauana*, *G.m.co= Gongolaria montagnei* var. *compressa*, *C.f.lat=Cystoseira foeniculacea* f. *latiramosa.*

Gongolaria sauvageauana (Hamel) Molinari-Novoa & Guiry (30%), while *G. montagnei* var. *compressa* (Ercegovic) N. Sant & E. Ballesteros accounted for 21% of the specimens. *Ericaria brachycarpa*, *Ericaria zosteroides* (C. Agardh) Molinari-Novoa & Guiry, and *Cystoseira foeniculacea* (Linnaeus) Greville f. *latiramosa* (Ercegovic) A. Gómez-Garreta, M.C. Barceló, M.A. Ribera & J. Rull-Lluch only represented 3% of the total population (Fig. 2c).

Relationships between the densities of the main *Cystoseira s. l.* and *C. caespitosa* abundances are shown in Fig. 3. In Es Banc, *G. montagnei* densities were higher when *C. caespitosa* abundance was also higher (p=0.0005, n=202), whereas *E. brachycarpa* densities were lower when *C. caespitosa* showed higher abundances (p=0.02, n=65). No trend was observed for *G.* cf. *elegans*. In Espardelló, *G. montagnei* and *E. brachycarpa* densities did not show any trend (p=0.14 and p=0.09, respectively). In contrast, *C. compressa* densities were statistically higher when *C caespitosa* abundance was also higher (p=0.02, n=97). In Columbretes, *C. compressa* and *G. montagnei* var. *compressa* did not show any significant trend (p=0.62 and p=0.83). However, *G. sauvageauana* densities were statistically lower at increasing abundances of *C. caespitosa* (p=0.0001, n=159). Only a few individuals of *E. brachycarpa*, *E. zosteroides*, and *C. foeniculacea* f. *latiramosa* were sampled in Columbretes (n=21, n=6 and n=8, respectively), and therefore these were not included in the analyses.

Areas without *Cladocora caespitosa*

Gongolaria montagnei was also very abundant in Es Banc, although its density was slightly lower (51.6%), while densities of *G.* cf. *elegans* and *E. brachycarpa* reached 20.3 and 27.6%, respectively (Fig. 4a). *Cystoseira foeniculacea* (0.4%) and *C. compressa* (0.1%) showed very low frequencies. In Espardelló, the most frequent species was again *G. montagnei*, which accounted for 81% of all the specimens, followed by *E. brachycarpa* (18%) and *C. compressa* (<1%) (Fig. 4b). In Columbretes, *G. sauvageauana* and *C. compressa* were the most frequent species (52.1% and 24.1%, respectively), while *G. montagnei* var. *compressa* accounted for 16% of the specimens. *Ericaria brachycarpa*, *E. zosteroides*, and *C. foeniculacea* f. *latiramosa* only represented 7.7% of the total population (Fig. 4c).

Comparisons

Comparisons of *Cystoseira s. l.* densities in areas with and without *C. caespitosa* colonies mainly agreed with the patterns observed in the linear regressions (Table 2). The total number of *Cystoseira* s. l. individuals was similar in places with or without *C. caespitosa* in Es Banc, higher in places without *C. caespitosa* in Columbretes, and higher in areas with *C. caespitosa* in Espardelló. *Gongolaria montagnei* attained significantly higher densities in areas with *C. caespitosa*, *G. sauvageauana* showed higher abundances in areas without *C. caespitosa*, and *E. brachycarpa* showed lower abundances or no differences in areas with *C. caespitosa*. *Gongolaria* cf. *elegans* in Es Banc and *C. compressa* in Columbretes did not show any pattern. *C. compressa* was not analyzed in Espardelló because of its low densities. *Ericaria brachycarpa*, *E. zosteroides*, and *C. foeniculacea* f. *latiramosa* were not analyzed either in Columbretes because of these species' low densities.

Discussion

We found that densities of most *Cystoseira s. l.* species showed site-dependent relationships with *C. caespitosa* abundance. However, when considered at species level, most species showed neutral relationships with *C. caespitosa* abundance, in disagreement with the overall

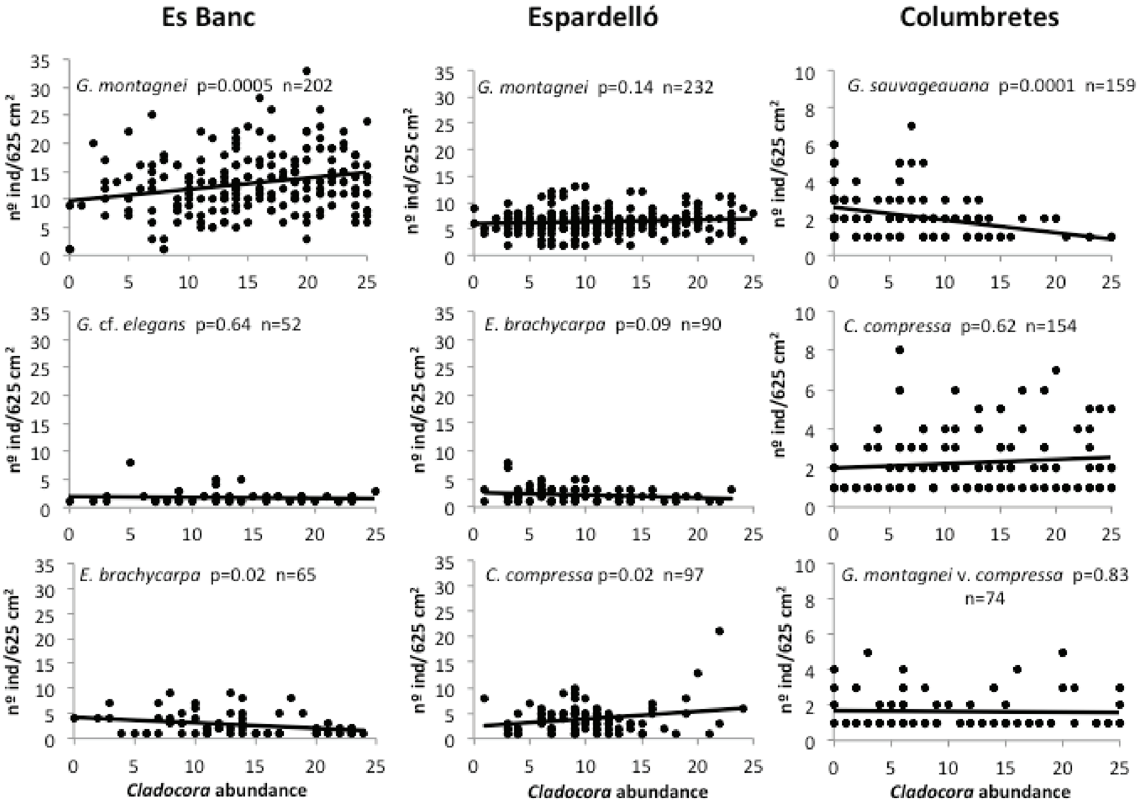

Fig. 3: Relationships between the densities of the different species of *Cystoseira s. l.* and *Cladocora caespitosa* abundance at the three sampling sites.

Table 2. Summary of the calculated probability or p-values from t-tests comparing densities of *Cystoseira s. l.* in places with and without *Cladocora caespitosa* presence. In *italics*: the algal species density is higher in places with *Cladocora*. In bold: the algal species density is higher in places without *Cladocora*.

Species	Es Banc	Espardelló	Columbretes
Cystoseira s. l.	0.824	*0.0001*	**0.017**
Gongolaria montagnei	*0.0001*	*0.0001*	
Gongolaria cf. *elegans*	0.10		
Ericaria brachycarpa	**0.0002**	0.56	
Cystoseira compressa			0.8
Gongolaria sauvageauana			**0.0004**
Gongolaria montagnei v. *compressa*			1

negative effects of fleshy macroalgae on scleractinian corals (see review by McCook *et al*., 2001; Rasher & Hay 2010). Moreover, Kersting *et al*. (2014) found that *C. caespitosa* possesses allelochemical mechanisms to avoid overgrowth by macroalgae. However, these alelochemicals do not seem to affect the co-occurrence of *C. caespitosa* and most *Cystoseira s. l.* species.

The interaction between the different species of *Cystoseira s. l.* was not tested in this study. Besides competition for space and the interaction with *C. caespitosa*, several other environmental factors play a significant role in their distribution, such as different levels of palatability to consumers and light availability (Vergés *et al*., 2009; Sant & Ballesteros, 2021a). The fact that sampling sites were located at approximately the same depth should reduce the importance of light availability, but the coexistence of species with high photosynthetic efficiencies, such as *G. montagnei* var. *compressa* and *E. zosteroides*, with others presenting low photosynthetic efficiencies, such as *E. brachycarpa*, suggests the high adaptability of these species to light environments, as reported by Sant & Ballesteros (2021b, 2021c). Species-specific relationships with *C. caespitosa* could be explained by the morphology of their thalli. For example, *G. montagnei* shows a monopodial growth pattern, with only one main axis arising from the holdfast, whereas *E. brachycarpa* shows a sympodial growth pattern, with extended holdfasts (Giaccone & Bruni, 1973), which may be unsuitable for growing over *C. caespitosa*. Further experimental work on recruitment processes in areas with and without *C. caespitosa* is required in order to shed some light on the patterns found in this study.

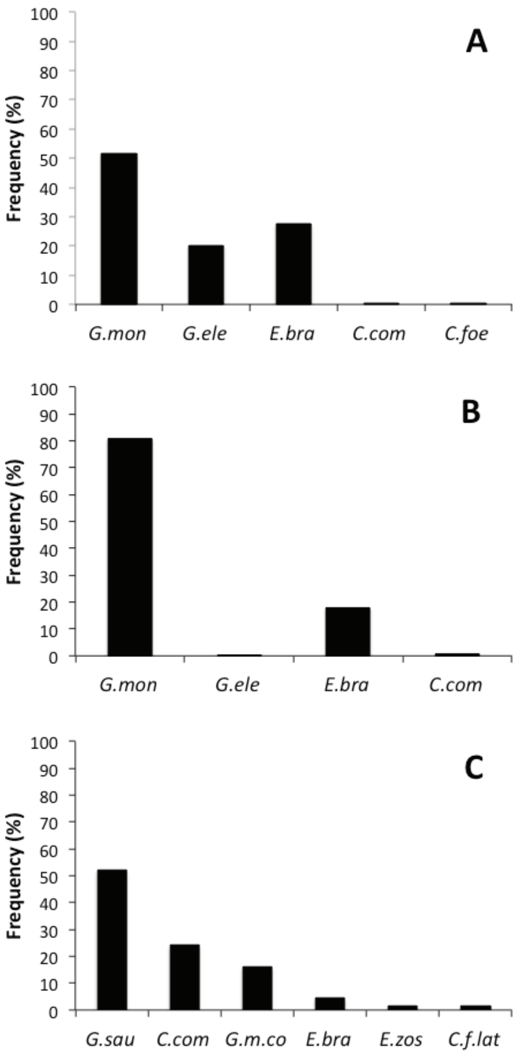

Fig. 4: Density-frequency distributions of *Cystoseira s. l.* species in places not coexisting with *Cladocora caespitosa*. A) Es Banc (n=1171), B) Espardelló (n=499) and C) Columbretes (n=349). Species abbreviations: *G.mon=Gongolaria montagnei*, *G.ele=Gongolaria* cf. *elegans*, *E.bra=Ericaria brachycarpa*, *C.com=Cystoseira compressa*, *C.foe=Cystoseira foeniculacea*, *G.sau=Gongolaria sauvageauana*, *G.m.co= Gongolaria montagnei* var. *compressa*, *E.zos=Ericaria zosteroides*, *C.f.lat=Cystoseira foeniculacea* f. *latiramosa.*

Damaged corals show a great ability to regrow from relatively few remnants of tissue following bleaching or colonization of dead coral by macroalgae (e.g., Loya, 1976; Riegl & Piller, 2001; Diaz-Pulido *et al*., 2009). *Cladocora caespitosa* polyps show fast recoveries after being exposed to damage on tissue and skeleton in controlled conditions (Casado *et al*., 2015) and are able to recolonize dead colony areas covered by epibionts (Kersting & Linares, 2019); these traits may be very advantageous when competing with *Cystoseira s. l.* and other colonizing algae.

Algal seasonality has also been reported as a mechanism that enables coexistence between corals and macroalgae (Diaz-Pulido *et al*., 2009; Brown *et al*., 2018), but the long-lived nature of most of the algae reported here (Ballesteros *et al*., 1998, 2009; Rodríguez-Prieto *et al*., 2013; Ballesteros & Pons-Fita, 2020) weakens its possible importance. However, species of *Cystoseira s. l.*, although perennial, show a high seasonality in branch development (Sauvageau, 1912; Barceló-Martí & Seoane-Camba, 1984; Pizzuto, 1999; Ballesteros, 1988, 1990a, 1990b; Sales & Ballesteros, 2012), which may be beneficial for the final competitive outcome. Interestingly, similar brown macroalgae of the genus *Sargassum*, again belonging to the order Fucales, may also have minor or no competitive effects on understory corals, and even the shading effect of algal canopies is apparently beneficial by mitigating radiation exposure and high temperatures (Jompa & McCook, 1998; McCook, 1999).

The relationships reported here were species-specific (i.e., positive for some species but negative or neutral for others), in agreement with the findings of other studies on coral reefs (Jompa & McCook, 2003; Nugues & Bak, 2006; Titlyanov *et al*., 2007; Barott *et al*., 2011; Bonaldo & Hay, 2014). They also seemed to be site-specific (i.e., the same species of *Cystoseira s. l.* might show a positive relationship in one site but a neutral one in another), in accordance with recent data obtained by Brown *et al.* (2018), who surveyed eight distinct zones in the southern Great Barrier Reef over a 23-month period and found that coral-algal interactions were context-specific.

Historically, *Cystoseira s. l.* originated in the Tethys Sea during the Mesozoic, but the radial process of speciation in the Mediterranean started after the Messinian Salinity Crisis (5.3 MY ago), when many Atlantic species entered the Mediterranean Sea (Oliveras Plá & Gómez-Garreta, 1989). *Cladocora caespitosa* originated after the Messinian Salinity Crisis (Aguirre & Jiménez, 1998). Thus, both *Cystoseira s. l.* and *C. caespitosa* have been into close contact for a very long time and have most probably been competing with each other and with other shallow benthic organisms, such as other algae and sessile invertebrates, for limiting resources (i.e., light and space) over millions of years. Since the coral and the macroalgae involved in the relationships studied here have both been thriving in the same habitats and probably have overlapping ecological roles and requirements to survive, grow, and reproduce, uncharted mechanisms and adaptations may have evolved in order to allow coexistence.

We have demonstrated that coral *C. caespitosa* and canopy-forming perennial macroalgae (*Cystoseira s. l.*) can coexist in Mediterranean shallow assemblages. We also contend that the close and lasting relationships between *Cystoseira s. l.* species and the coral *C. caespitosa* are species- and site-specific even though these relationships are mainly neutral. The mechanisms that promote this subtle coexistence are yet to be understood, but our results challenge the theory of competitive exclusion between *C. caespitosa* and fleshy macroalgae in the Mediterranean. These results can serve as a starting point for future studies addressing the interactions between *C. caespitosa* and *Cystoseira s. l.* The information reported here may also be used as a baseline for future monitoring of these habitats in light of future disturbances related to eutrophication, acidification, or climate change.

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