

Mediterranean Marine Science

Vol 22, No 3 (2021)

VOL 22, No 3 (2021)



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

ALÈSSIA PONS-FITA, DIEGO K. KERSTING, ENRIC BALLESTEROS

doi: [10.12681/mms.26967](https://doi.org/10.12681/mms.26967)

To cite this article:

PONS-FITA, A., KERSTING, D. K., & BALLESTEROS, E. (2021). Co-occurrence of a reef-building coral and canopy-forming macroalgae in the Mediterranean Sea. *Mediterranean Marine Science*, 22(3), 697–705. <https://doi.org/10.12681/mms.26967>

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

Alèssia PONS-FITA¹, Diego K. KERSTING² and Enric BALLESTEROS¹

¹Blanes Centre for Advanced Studies-CSIC, Blanes, Spain

²Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Barcelona, Spain

Corresponding author: kike@ceab.csic.es

Contributing Editor: Carla MORRI

Received: 5 May 2021; Accepted: 16 July 2021; Published online: 01 November 2021

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). *Cl-*

Cladocora caespitosa also displays great plasticity in growth and morphologies, forming banks, beds, or even free-living coral nodules (coralloliths) (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 (38.726238° N, 1.390446° E), located in the northwestern part of Formentera (Balearic Islands), Espardelló (38.785903° N, 1.484408° E), an islet located on the northeast side of Formentera, next to Espardell island, and Illa Grossa (39.895518° N, 0.686766° 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 m²

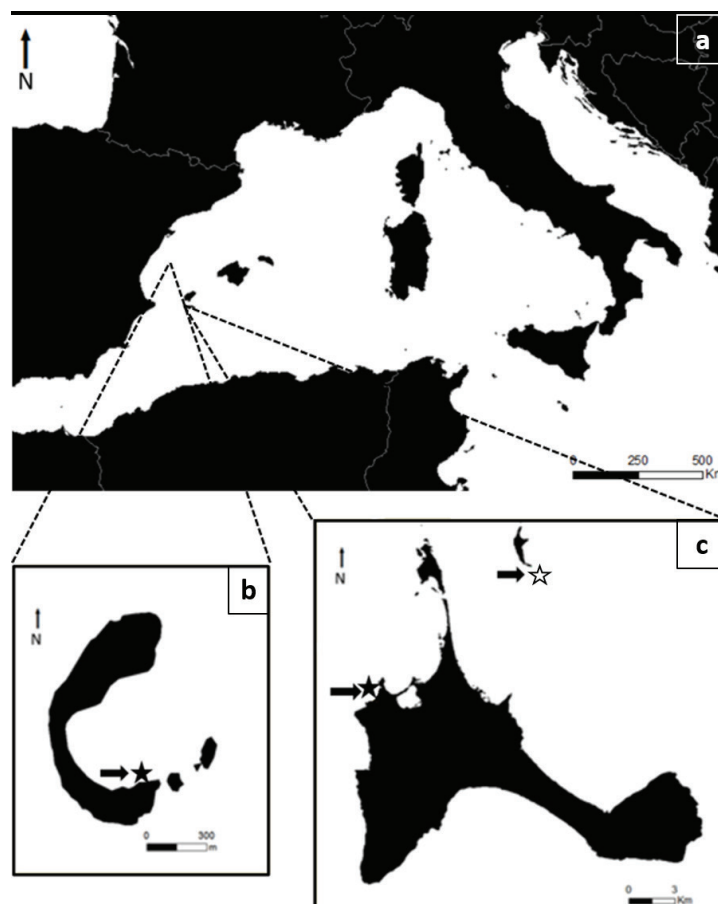


Fig. 1: Location of the sampling sites. (a) Western Mediterranean. (b) Sampling site (black star) in Illa Grossa Bay, Columbretes islands. (c) Sampling sites in Formentera: Espardelló (white star) and Es Banc (black star).

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 cm² quadrat frames divided into 25 (5 cm x 5 cm) subquadrats. Quadrats were placed randomly inside an area measuring 40 x 40 m². *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* (Ésper) 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
<i>Gongolaria montagnei</i>	+	+	
<i>Gongolaria cf. elegans</i>	+		
<i>Gongolaria sauvageauana</i>			+
<i>Gongolaria montagnei</i> v. <i>compressa</i>			+
<i>Ericaria brachycarpa</i>	+	+	+
<i>Ericaria zosteroides</i>			+
<i>Cystoseira compressa</i>	+	+	+
<i>Cystoseira foeniculacea</i>	+	+	
<i>Cystoseira foeniculacea</i> f. <i>latiramosa</i>			+

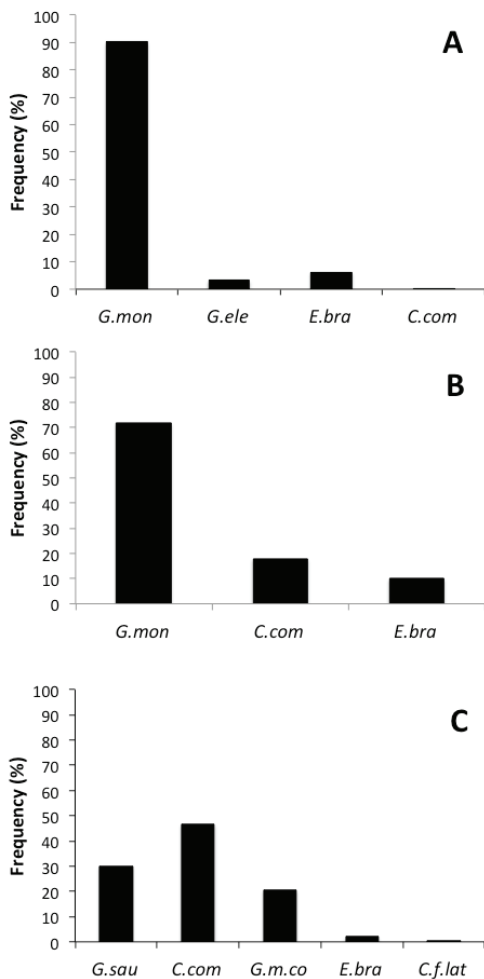


Fig. 2: Density-frequency distributions of *Cystoseira s. l.* species in places coexisting with *Cladocora caespitosa*. A) Es Banc (n=2885), B) Espardelló (n=2078) and C) Columbretes (n=931). Species abbreviations: *G.mon*=*Gongolaria montagnei*, *G.ele*=*Gongolaria cf. elegans*, *E.bra*=*Ericaria brachycarpa*,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

Gongolaria sauvagueauana (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. sauvagueauana* 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. sauvagueauana* 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. sauvagueauana* 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

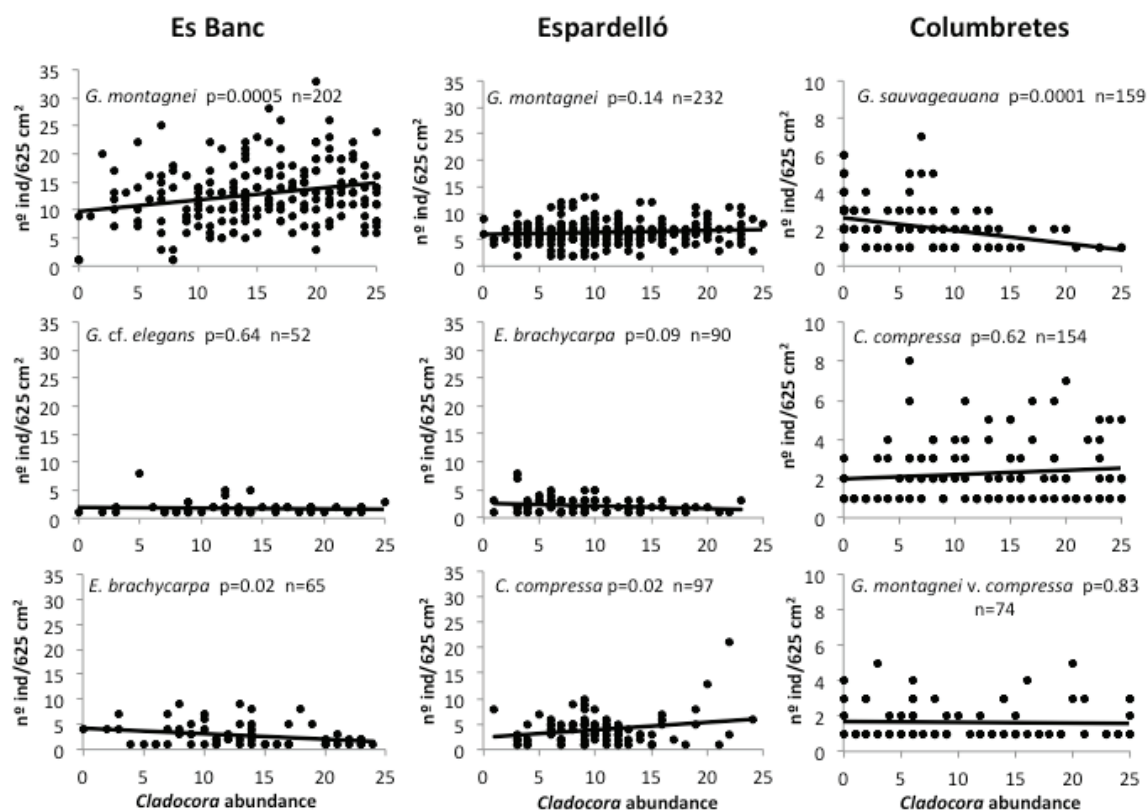


Fig. 3: Relationships between the densities of the different species of *Cystoseira s. l.* and *Cladocora caespitosa* abundance at the three sampling sites.

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
<i>Cystoseira s. l.</i>	0.824	<i>0.0001</i>	0.017
<i>Gongolaria montagnei</i>	<i>0.0001</i>	<i>0.0001</i>	
<i>Gongolaria cf. elegans</i>	0.10		
<i>Ericaria brachycarpa</i>	0.0002	0.56	
<i>Cystoseira compressa</i>			0.8
<i>Gongolaria sauvageauana</i>			0.0004
<i>Gongolaria montagnei v. compressa</i>			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 allelochemicals 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.

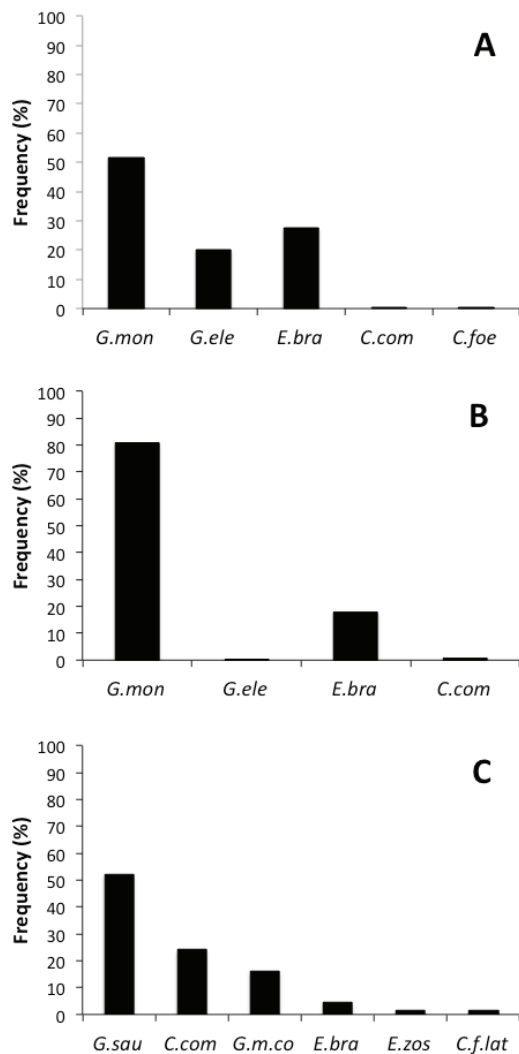


Fig. 4: Density-frequency distributions of *Cystoseira s. l.* species in places not coexisting with *Cladocora caespitosa*. A) Es Banc (n=1171), B) Espardelló (n=499) and C) Columbretes (n=349). Species abbreviations: *G.mon*=*Gongolaria montagnei*, *G.ele*=*Gongolaria cf. elegans*, *E.bra*=*Ericaria 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.

Acknowledgements

We are grateful to managers and staff of the Marine Reserve of “Freus d’Eivissa i Formentera” and the Marine Reserve of Columbretes Islands for diving permissions, research authorizations and support. Bàrbara Terrasa and the Natural Park of Ses Salines provided accommodation in Formentera. Javi Asensio was very helpful in solving parking and transportation issues in Formentera and Vell Marí Diving Center provided technical support. The rangers of Columbretes Islands assisted in diving operations. We also thank Dr. Susana Pinedo and Dr. Simone Mariani for statistical advice and Dr. Antoni Garcia-Rubies for general support. Funding has been provided by CSIC Intramural project PIE202030E180.

References

- Aguirre, J., Jiménez, A.P., 1998. Fossil analogues of present-day *Cladocora caespitosa* coral banks: Sedimentary setting, dwelling community, and taphonomy (Late Pliocene, W Mediterranean). *Coral Reefs*, 17 (3), 203-213.
- Ballesteros, E., 1988. Estructura y dinámica de la comunidad de *Cystoseira mediterranea* Sauvageau en el Mediterráneo Noroccidental. *Investigación Pesquera*, 52, 313-334.
- Ballesteros, E., 1990a. Structure and dynamics of the *Cystoseira caespitosa* Sauvageau (Fucales, Phaeophyceae) community in the North-Western Mediterranean. *Scientia Marina*, 54, 155-168.
- Ballesteros, E., 1990b. Structure and dynamics of the community of *Cystoseira zosteroides* (Turner) C. Agardh (Fucales, Phaeophyceae) in the Northwestern Mediterranean. *Scientia Marina*, 54 (3), 217-229.
- Ballesteros, E., 1992. Els vegetals i la zonació litoral: espècies, comunitats i factors que influeixen en la seva distribució. *Arxius Secció Ciències Institut d'Estudis Catalans*, 101, 1-616.
- Ballesteros, E., Pons-Fita, A., 2020. Corals and macroalgae can sometimes coexist. *Frontiers in Ecology and the Environment*, 18, 150.
- Ballesteros, E., Sala, E., Garrabou, J., Zabala, M., 1998. Community structure and frond size distribution of a deep water stand of *Cystoseira spinosa* Sauvageau in the Northwestern Mediterranean. *European Journal of Phycology*, 33 (2), 121-128.
- Ballesteros, E., Garrabou, J., Hereu, B., Zabala, M., Cebrian, E. *et al.*, 2009. Deep-water stands of *Cystoseira zosteroides* (Fucales, Phaeophyta) in the Northwestern Mediterranean: insights into assemblage structure and population dynamics. *Estuarine, Coastal and Shelf Science*, 82 (3), 477-484.
- Barceló-Martí, M.C., Seoane-Camba, J.A., 1984. Nota sobre la variación fenológica de *Cystoseira sauvageauana* Hamel en las costas de Alicante. *Anales de Biología*, 2, 45-54.
- Barott, K., Smith, J., Dinsdale, E., Hatay, M., Sandin, S. *et al.*, 2009. Hyperspectral and physiological analyses of coral-algal interactions. *PLoS ONE*, 4 (11), e8043.
- Barott, K.L., Rodríguez-Brito, B., Janouškovec, J., Marhaver, K.L., Smith, J.E. *et al.*, 2011. Microbial diversity associated with four functional groups of benthic reef algae and the reef-building coral *Montastrea annularis*. *Environmental Microbiology*, 13 (5) 1192-1204.
- Barott, K.L., Williams, G.J., Vermeij, M.J., Harris, J., Smith, J.E. *et al.*, 2012. Natural history of coral-algae competition across a gradient of human activity in the Line Islands. *Marine Ecology Progress Series*, 460, 1-12.
- Birrell, C.L., McCook, L.J., Willis, B.L., Diaz-Pulido, G.A., 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanography and Marine Biology: an Annual Review*, 46, 25-63.
- Bonaldo, R.M., Hay, M.E., 2014. Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PLoS ONE*, 9 (1), e85786.
- Box, S.J., Mumby, P.J., 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Marine Ecology Progress Series*, 342, 139-149.
- Brown, K.T., Bender-Champ, D., Kubicek, A., van der Zande, R., Achlatis, M. *et al.*, 2018. The dynamics of coral-algal interactions in space and time on the southern Great Barrier Reef. *Frontiers in Marine Science*, 5, 181.
- Casado, C., Kersting, D.K., Cebrian, E., Teixidó, N., Garrabou, J. *et al.*, 2015. Rapid recovery from injuries in the temperate long-lived coral *Cladocora caespitosa*. *Marine Biodiversity*, 45 (1) 135-137.
- Chintiroglou, C.C., 1996. Feeding guilds of polychaetes associated with *Cladocora caespitosa* (L.) (Anthozoa, Cnidaria) in the North Aegean Sea. *Israel Journal of Ecology and Evolution*, 42 (3), 261-274.
- Coma, R., Serrano, E., Linares, C., Ribes, M., Díaz, D. *et al.*, 2011. Sea urchins predation facilitates coral invasion in a marine reserve. *PLoS ONE*, 6 (7), e22017.
- Cormaci, M., Furnari, G., Catra, M., Alongi, G., Giaccone, G., 2012. Flora marina bentonica del Mediterraneo: Phaeophyceae. *Bollettino dell'Accademia Gioenia di Scienze Naturali di Catania*, 45 (375), 1-508.
- Diaz-Pulido, G., McCook, L.J., Dove, S., Berkelmans, R., Roff, G. *et al.*, 2009. Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. *PLoS ONE*, 4 (4), e5239.
- Dinsdale, E.A., Pantos, O., Smriga, S., Edwards, R.A., Angly, F. *et al.*, 2008. Microbial ecology of four coral atolls in the Northern Line Islands. *PLoS ONE*, 3 (2), e1584.
- Feldmann, J., 1937. Recherches sur la végétation marine de la Méditerranée: La côte des Albères. *Revue Algologique*, 10, 1-339.
- Foster, N.L., Box, S.J., Mumby, P.J., 2008. Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastrea annularis*. *Marine Ecology Progress Series*, 367, 143-152.
- Giaccone, G., 1973. Elementi di Botanica Marina, Parte I: Bionomia bentonica e vegetazione sommersa del Mediterraneo. *Pubblicazione dell'Istituto Botanico della Università di Trieste, Serie Didattica*, 43 pp.
- Giaccone, G., Bruni, A., 1973. Le Cistoseire e la vegetazione sommersa del Mediterraneo. *Atti Reale Istituto Veneto Scienze, Lettere ed Arti*, 131, 59-103.
- Gianni, F., Bartolini, F., Airoidi, L., Ballesteros, E., Francour, P. *et al.*, 2013. Conservation and restoration of marine forests

- in the Mediterranean Sea and the potential role of Marine Protected Areas. *Advances in Oceanography and Limnology*, 4 (2), 83-101.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 266, 1547-1551.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O. *et al.*, 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, 17 (4), 360-365.
- Jompa, J., McCook, L.J., 1998. Seaweeds save the reef?!: *Sargassum* canopy decreases coral bleaching on inshore reefs. *Reef Research*, 8 (5).
- Jompa, J., McCook, L.J., 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology*, 271 (1), 25-39.
- Jompa, J., McCook, L.J., 2003. Coral-algal competition: macroalgae with different properties have different effects on corals. *Marine Ecology Progress Series*, 258, 87-95.
- Kersting, D.K., Linares, C., 2012. *Cladocora caespitosa* bioconstructions in the Columbretes Islands Marine Reserve (Spain, NW Mediterranean): distribution, size structure and growth. *Marine Ecology*, 33 (4), 427-436.
- Kersting, D.K., Linares, C., 2019. Living evidence of a fossil survival strategy raises hope for warming-affected corals. *Science Advances*, 5, eaax2950.
- Kersting, D.K., Ballesteros, E., De Caralt, S., Linares, C., 2014. Invasive macrophytes in a marine reserve (Columbretes Islands, NW Mediterranean): spread dynamics and interactions with the endemic scleractinian coral *Cladocora caespitosa*. *Biological Invasions*, 16 (8), 1599-1610.
- Kersting, D.K., Cebrian, E., Casado, C., Teixidó, N., Garrahou, J. *et al.*, 2015. Experimental evidence of the synergistic effects of warming and invasive algae on a temperate reef-builder coral. *Scientific Reports*, 5 (1), 18635.
- Kersting, D.K., Cebrian, E., Verdura, J., Ballesteros, E., 2017a. A new *Cladocora caespitosa* population with unique ecological traits. *Mediterranean Marine Science*, 18 (1), 38-42.
- Kersting, D.K., Cebrian, E., Verdura, J., Ballesteros, E., 2017b. Rolling corals in the Mediterranean Sea. *Coral Reefs*, 36 (1), 245.
- Koukouras, A., Kühlmann, D., Voultziadou, E., Vafidis, D., Dounas, C. *et al.*, 1998. The macrofaunal assemblage associated with the scleractinian coral *Cladocora caespitosa* (L.) in the Aegean Sea. *Annales de l'Institut Océanographique*, 74, 97-114.
- Kružić, P., Benković, L., 2008. Bioconstructional features of the coral *Cladocora caespitosa* (Anthozoa, Scleractinia) in the Adriatic Sea (Croatia). *Marine Ecology*, 29 (1), 125-139.
- Lirman, D., 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs*, 19 (4), 392-399.
- Loya, Y., 1976. Skeletal regeneration in a Red Sea scleractinian coral population. *Nature*, 261 (5560), 490-491.
- McCook, L.J., 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs*, 18 (4), 357-367.
- McCook, L.J., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, 19 (4), 400-417.
- Miller, M.W., Hay, M.E., 1998. Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia*, 113 (2), 231-238.
- Nugues, M.M., Smith, G.W., van Hooidonk, R.J., Seabra, M.I., Bak, R.P., 2004. Algal contact as a trigger for coral disease. *Ecology Letters*, 7 (10), 919-923.
- Nugues, M.M., Bak, R.P., 2006. Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. *Marine Ecology Progress Series*, 315, 75-86.
- Oliveras-Plá, A., Gómez-Garreta, A., 1989. Corología del género *Cystoseira* C. Agardh (Phaeophyceae, Fucales). *Anales del Jardín Botánico de Madrid*, 46, 89-97.
- Peirano, A., Morri, C., Mastronuzzi, G., Bianchi, C.N., 1998. The coral *Cladocora caespitosa* (Anthozoa, Scleractinia) as a bioherm builder in the Mediterranean Sea. *Memoria Descrittiva Carta Geologica Italia*, 52, 59-74.
- Peirano, A., Abbate, M., Cerrati, G., Difesca, V., Peroni, C. *et al.*, 2005. Monthly variations in calyx growth, polyp tissue, and density banding of the Mediterranean scleractinian *Cladocora caespitosa* (L.). *Coral Reefs*, 24 (3), 404-409.
- Pitacco, V., Orlando-Bonaca, M., Mavric, B., Lipej, L., 2014. Macrofauna associated with a bank of *Cladocora caespitosa* (Anthozoa, Scleractinia) in the Gulf of Trieste (Northern Adriatic). *Annales Series Historia Naturalis*, 24, 1-14.
- Pizzuto, F., 1999. On the structure, typology and periodism of a *Cystoseira brachycarpa* J. Agardh emend. Giaccone community and of a *Cystoseira crinita* Duby community from the eastern coast of Sicily (Mediterranean Sea). *Plant Biosystems*, 133 (1), 15-35.
- Pons-Fita, A., Verdura, J., Santamaría, J., Kersting, D.K., Ballesteros, E., 2020. Coexistence of the reef-building coral *Cladocora caespitosa* and the canopy-forming alga *Treptacantha ballesterosii*: Description of a new Mediterranean habitat. *Scientia Marina*, 84 (3), 263-271.
- Rasher, D.B., Hay, M.E., 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. *Proceedings National Academy of Sciences*, 107 (21), 9683-9688.
- Rasher, D.B., Stout, E.P., Engel, S., Kubanek, J., Hay, M.E., 2011. Macroalgal terpenes function as allelopathic agents against reef corals. *Proceedings National Academy of Sciences*, 108 (43), 17726-17731.
- Riegl, B., Piller, W.E., 2001. "Cryptic" tissues inside *Acropora* frameworks (Indonesia): a mechanism to enhance tissue survival in hard times while also increasing framework density. *Coral Reefs*, 20 (1), 67-68.
- Rodríguez-Prieto, C., Ballesteros, E., Boisset, F., Afonso-Carrillo, J., 2013. *Guía de las macroalgas y fanerógamas marinas del Mediterráneo Occidental*. Ediciones Omega, Barcelona, 656 pp.
- Sala, E., Ballesteros, E., 1997. Partitioning of space and food resources by three fishes of the genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem. *Marine Ecology Progress Series*, 152, 273-283.
- Sales, M., Ballesteros, E., 2009. Shallow *Cystoseira* (Fucales: Ochrophyta) assemblages thriving in sheltered areas from Menorca (NW Mediterranean): Relationships with environmental factors and anthropogenic pressures. *Estuarine, Coastal and Shelf Science*, 84 (4), 476-482.

- Sales, M., Ballesteros, E., 2012. Seasonal dynamics and annual production of *Cystoseira crinita* (Fucales: Ochrophyta)-dominated assemblages from the northwestern Mediterranean. *Scientia Marina*, 76 (2), 391-401.
- Sant, N., Ballesteros, E., 2021a. Depth distribution of canopy-forming algae of the order Fucales along a bathymetric gradient is related to their photosynthetic features. *Marine Ecology*, 42, e12651.
- Sant, N., Ballesteros, E., 2021b. Photosynthetic performances of two deep-water canopy-forming fucoids across a depth gradient: interspecific variability and short-term adaptation to the light environment. *Marine Ecology*, 42, e12666.
- Sant, N., Ballesteros, E., 2021c. The canopy-forming alga *Ericaria brachycarpa* (J. Agardh) Molinari-Novoa & Guiry (Fucales, Phaeophyceae) shows seasonal and depth adaptation to the incoming light levels. *Cryptogamie, Algologie*, 42, 67-75.
- Sant, N., Chappuis, E., Rodríguez-Prieto, C., Real, M., Ballesteros, E., 2017. Cost-benefit of three different methods for studying Mediterranean rocky benthic assemblages. *Scientia Marina*, 81 (1), 129-138.
- Sauvageau, C., 1912. À propos des *Cystoseira* de Banyuls et de Guéthary. *Bulletin Station Biologique Arcachon*, 14, 133-556.
- Serrano, E., Coma, R., Ribes, M., 2012. A phase shift from macroalgal to coral dominance in the Mediterranean. *Coral Reefs*, 31, 1199.
- Serrano, E., Coma, R., Ribes, M., Weitzmann, B., García, M. *et al.*, 2013. Northward expansion of a coral species: evidence for fundamental modification of a temperate ecosystem. *PLoS ONE*, 8(1), e52739.
- Smith, J.E., Shaw, M., Edwards, R.A., Obura, D., Pantos, O. *et al.*, 2006. Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecology Letters*, 9 (7), 835-845.
- Tanner, J.E., 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology*, 190 (2), 151-168.
- Teixidó, N., Gambi, M.C., Parravacini, V., Kroeker, K., Micheli, F. *et al.*, 2018. Functional biodiversity loss along natural CO₂ gradients. *Nature Communications*, 9, 5149.
- Titlyanov, E.A., Yakovleva, I.M., Titlyanova, T.V., 2007. Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. *Journal of Experimental Marine Biology and Ecology*, 342 (2), 282-291.
- Vergés, A., Alcoverro, T., Ballesteros, E., 2009. Role of fish herbivory in structuring the vertical distribution of canopy algae *Cystoseira* spp. in the Mediterranean Sea. *Marine Ecology Progress Series*, 375, 1-11.
- Verlaque, M., 1987. *Contribution à l'étude du phytobenthos d'un écosystème photophile thermophile marin en Méditerranée Occidentale*. Ph.D. Thesis. Université d'Aix-Marseille, France, 389 pp.
- Vermeij, M.J.A., Smith, J.E., Smith, C.M., Thurber, R.V., Sandin, S. A., 2009. Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. *Oecologia*, 159, 325-336.
- Vermeij, M.J.A., Van Moorselaar, I., Engelhard, S., Hörnlein, C., Vonk, S.M. *et al.*, 2010. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. *PLoS ONE*, 5 (12), e14312.
- Zabala, M., Ballesteros, E., 1989. Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean. *Scientia Marina*, 53, 1-15.