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Coexistence of the reef-building coral *Cladocora caespitosa* and the canopy-forming alga *Treptacantha ballesterosii*: Description of a new Mediterranean habitat

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Summary: Shallow Mediterranean rocky environments are usually dominated by macroalgae, but the stony colonial zooxanthellate coral *Cladocora caespitosa* is able to build extensive banks in some particular areas. Although zooxanthellate corals and benthic macroalgae are expected to compete for light and space when overlapping in the same habitat, there is previous evidence that *C. caespitosa* and Mediterranean macroalgae do not suffer from competitive exclusion when living together. Here we characterize a new and unique Mediterranean habitat where the reef-building coral *C. caespitosa* and erect seaweeds of the order Fucales (*Cystoseira s.l.*) coexist. In this new habitat *C. caespitosa* reaches 34% cover and densities of *Cystoseira s.l.* (mainly *Treptacantha ballesterosii*) are much higher than values reported from other sites. Interestingly, abundances of *T. ballesterosii* and *C. caespitosa* show a positive relationship, suggesting that some kind of facilitation mechanism is taking place. These findings challenge the theory of competitive exclusion between corals and macroalgae and launch a wide array of possible open discussions on coral-macroalgae interactions.

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

Coexistencia del coral formador de arrecifes *Cladocora caespitosa* y la macroalga formadora de dosel *Treptacantha ballesterosii*: descripción de un nuevo hábitat mediterráneo

Resumen: Los ambientes rocosos someros del Mediterráneo están habitualmente dominados por macroalgas, no obstante, el coral colonial zooxantelado *Cladocora caespitosa* es capaz de formar bancos extensos en algunos lugares. Aunque es predecible que los corales con zooxantelas y las algas bentónicas compitan por la luz y el espacio cuando coinciden en el mismo hábitat, hay evidencias previas de que *C. caespitosa* y las algas mediterráneas no se excluyen competitivamente cuando viven juntas. En este trabajo se caracteriza un nuevo y único hábitat mediterráneo donde el coral formador de arrecifes *C. caespitosa* y algas erectas del orden Fucales (*Cystoseira s.l.*) coexisten. En este hábitat nuevo *C. caespitosa* alcanza coberturas del 34% y las densidades de *Cystoseira s.l.* (principalmente de *Treptacantha ballesterosii*) son mucho mayores que los valores encontrados en otros lugares. Remarcablemente, las abundancias de *T. ballesterosii* y *C. caespitosa* muestran una relación positiva, sugiriendo que existe algún tipo de mecanismo de facilitación. Este hallazgo pone en jaque la teoría de exclusión competitiva entre corales y macroalgas, a la vez que puede iniciar un amplio abanico de discusiones en las interacciones entre corales y macroalgas.

Palabras clave: *Cladocora caespitosa*; *Treptacantha*; *Cystoseira*; hábitat; interacciones corales-algas; mar Mediterráneo.

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INTRODUCTION

The most distinct trait of tropical marine ecosystems is the presence of coral reefs build by zooxanthellate scleractinian corals. Although coral reefs are scarce or absent outside tropical environments, there are a few Mediterranean scleractinian corals of the 37 existing ones that can potentially behave as reef-builders (Morri et al. 2000). Indeed, the unique zooxanthellate coral that has the capacity to build extensive beds and banks (*sensu* Peirano et al. 1998) is the Mediterranean pillow coral *Cladocora caespitosa* (Linné, 1767) (Zibrowius 1982, Morri et al. 1994, Peirano et al. 2001), which can be considered a habitat former in locations where colonies concentrate in high densities and reach large sizes (Kružić and Požar-Domac 2003, Kersting and Linares 2012).

Due to their reduced distribution, small size and generally low colony densities, Mediterranean coral bioconstructions have not been studied as extensively as tropical coral bioconstructions have. Nevertheless, an important effort has been made during the last few decades to study the distribution, characteristics and ecology of the main *C. caespitosa* bioconstructions in the Mediterranean Sea (e.g. Schiller 1993, Kersting et al. 2014a, Kersting and Linares 2019). *C. caespitosa* is characterized by slow growth, low recruitment rates and limited larval dispersal ability, which make this species very sensitive to disturbances (Kersting et al. 2014a). At present, shallow *C. caespitosa* bioconstructions have suffered a steep decline (Casado-Amezúa et al. 2015). The main anthropogenic causes, which often show synergistic effects, are pollution (Kružić and Požar-Domac 2007, El Kateb et al. 2016), warming (Rodolfo-Metalpa et al. 2005, Kersting et al. 2013, 2015) and invasive species (Kersting et al. 2014b, 2014c, 2015). All these relevant features urged IUCN to include this species in the Red List with the status “Endangered” (Casado-Amezúa et al. 2015) and the species also appears in the List of Endangered and Threatened Species of the Barcelona Convention (Annex II UNEP-MAP-RAC/SPA 2013).

Mediterranean shallow rocky bottoms are usually dominated by algal stands (Zabala and Ballesteros 1989). However, with the exceptions of the Alboran Sea and the Messina Strait, kelps are not present in Mediterranean shallow rocky bottoms and most existing canopy-forming algae belong to the order Fucales (Ochrophyta) (Rodríguez-Prieto et al. 2013). Until recently, only two genera of Fucales—*Cystoseira* and *Sargassum*—had been reported from the Mediterranean. Molecular tools identified up to three different clades inside the Mediterranean species previously included in the genus *Cystoseira* (Draisma et al. 2010, Bruno de Sousa et al. 2019), which resulted in the splitting of the former *Cystoseira* species into three genera, namely *Cystoseira*, *Treptacantha* and *Carpodesmia* (Orellana et al. 2019), a segregation that was also justified by morphological features (Orellana et al. 2019). Nevertheless, we will commonly refer here to the species included in these three genera as *Cystoseira sensu lato* (or *Cystoseira s.l.*), since they

share several ecological features. *Cystoseira s.l.* can make extensive canopy-forming algal beds from the upper infralittoral zone down to the upper circalittoral zone (0 to 50 m depth) (Giaccone and Bruni 1973, Sant 2003). These beds are very productive (Ballesteros 1988, 1990a, b) and highly structured in three-dimensions, making them a perfect site for nursery (Cheminée et al. 2013, 2017) and shelter and a source of food for a large number of species (Boudouresque 1971, 1972, Ballesteros et al. 1998). Accordingly, species of *Cystoseira s.l.* are the most representative macroalgae thriving in well-preserved Mediterranean environments.

Most species of Mediterranean Fucales are undergoing a severe decline (e.g. Bianchi et al. 2014, Thibaut et al. 2015, Mariani et al. 2019), although this is not always the case for all the species (Thibaut et al. 2014, Blanfuné et al. 2019) or all places (Sales and Ballesteros 2010, Thibaut et al. 2016, Blanfuné et al. 2016). Pollution is the main threat affecting the survival of *Cystoseira s.l.* populations (Munda 1974, Arévalo et al. 2007, Sales et al. 2011), although other pressures such as climate change, habitat destruction, overgrazing by sea urchins, outcompetition by mussels, increased turbidity, sediment loads, net fishing, human trampling and even scientific sampling have been blamed for declines of *Cystoseira s.l.* (Cormaci and Furnari 1999, Thibaut et al. 2005, Gianni et al. 2013). As a result, in many places algal communities have shifted from complex and productive forests of *Cystoseira s.l.* to simpler and less-productive habitats such as barren grounds, encrusting corallines and turf algae beds or low-complexity erect algae stands (Sala et al. 1998, Boudouresque 2004, Thibaut et al. 2005).

Due to the observed patterns of decline in several Mediterranean areas, the multiple pressures affecting populations of *Cystoseira s.l.* and their role as habitat formers, all the species (with the exception of *Cystoseira compressa*) have been included in the List of Endangered and Threatened Species of the Barcelona Convention (UNEP-MAP-RAC/SPA 2013), and some of them are listed in the Bern Convention (1979: Appendix I). Understanding the ecological interactions of their populations with other key community components is therefore extremely important to guide management towards the conservation of these species and the maintenance of their ecosystem functions.

Here we report on the discovery of a new Mediterranean habitat co-dominated by *C. caespitosa* and several species of *Cystoseira s.l.*, mainly *Treptacantha ballesterosii*. In particular, we aim at (1) describing *C. caespitosa* cover and colony size, (2) describing *Cystoseira s.l.* densities and sizes (when possible) and (3) inferring the relationship between macroalgal abundance (mainly *T. ballesterosii* density) and coral cover. The description of this new habitat will warn other scientists to look for this kind of formations in other Mediterranean localities and will serve as a baseline for the future monitoring of this newly discovered habitat and its highly threatened species and their relationships.

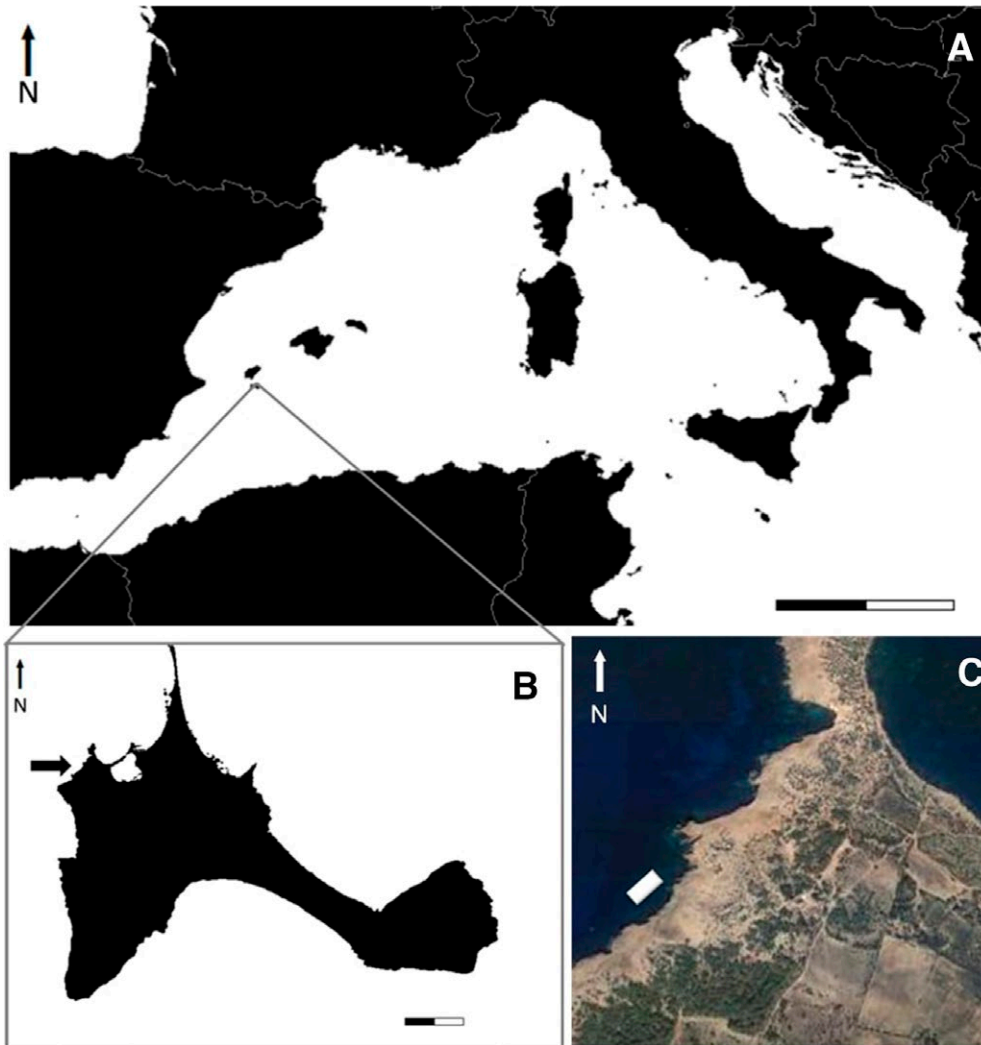


Fig. 1. – A, Western Mediterranean. Scale bar: 500 km. B, arrow indicates the sampling site, Es Banc, located on the northwestern side of Formentera island. Scale bar: 3 km. C, surveyed area of 1150 m² displayed as a white frame (source: Google Earth).

MATERIALS AND METHODS

Study site

Exploratory dives and sampling were performed in November 2017 and July 2019 in Es Banc (38.726564°N, 1.391309°E), located in the western part of Formentera (Balearic Islands, W Mediterranean Sea), close to Punta Gavina. The sampling site is included in the Freus d'Eivissa i Formentera marine protected area, where artisanal fishing is allowed. The area where both *C. caespitosa* and *Cystoseira s.l.* species coexist in large densities extends around 1150 m² (Fig. 1).

Sampling methods

Cladocora caespitosa cover in the sampling location was measured using a line-intercept method on a transect line (5 transects of 50 m length) (English et al. 1997, Kersting et al. 2017). The relationships between *C. caespitosa* abundance and *Cystoseira s.l.* densities were estimated using 625 cm² quadrat frames divided

into 25 (5×5 cm) subquadrats. The abundance of *C. caespitosa* was quantified as the number of subquadrats where *C. caespitosa* was present (Sala and Balasteros 1997, Sant et al. 2017, Teixidó et al. 2018). In the same quadrats, *Cystoseira s.l.* individuals were identified visually at the species level and counted. The size of each individual belonging to *Treptacantha balasterosii* and *Treptacantha cf. elegans* was measured as the length of the primary axis using a ruler (Balasteros et al. 1998, 2009). *Carpodesmia brachycarpa* and *Cystoseira compressa* do not have a primary axis since they are caespitose, i.e. have several primary axes arising from a single basal disc (Giaccone and Bruni 1973, Cormaci et al. 2012), and therefore size was not estimated.

Data analysis

Size of each coral colony was obtained as the length in cm of the transect line occupied by each colony (Kersting et al. 2017). Kolmogorov-Smirnov tests were performed to test normality of the size class frequency distributions of *C. caespitosa* and *Cystoseira s.l.* within



Fig. 2. – Views (November 2017, above; July 2019, below) of the habitat dominated by *Cladocora caespitosa* and *Treptacantha ballesterosii*. Note that most of the algal thalli are settled on coral colonies.

populations. For raw data series, descriptive statistics were calculated: minimum, maximum, mean values, standard deviation and skewness according to Sokal and Rohlf (1995). Linear regression analyses were used to determine how *Cystoseira s.l.* densities varied with *C. caespitosa* abundance, using 0.05 as the significance level. Statistical analyses were performed using Systat 11.0 (SPSS Inc. 2004).

RESULTS

Cladocora caespitosa colonies thrive at the study site between 8 and 12 m depth on a continuous rocky platform, sheltered from the prevailing winds (mainly east) (Fig. 2). The coral colonies concentrate in the area, forming a wide bed. *C. caespitosa* covers on average 33.7 ± 16.0 % (\pm SD, $n=5$) of the substrate and reaches values of up to 40% of cover. The size class frequency

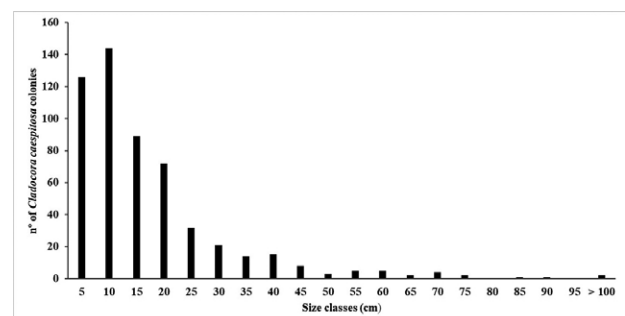


Fig. 3. – Size class structure of *Cladocora caespitosa* colonies starting at the class interval of 5 cm (colonies measuring 1-5 cm) ($n=546$).

distribution of this population is unimodal but does not follow a normal distribution (K-S, $d=0.77$, $p<0.0001$) (Fig. 3). The skewness of the distribution is significantly positive ($g_1=1.841$), which indicates the predominance

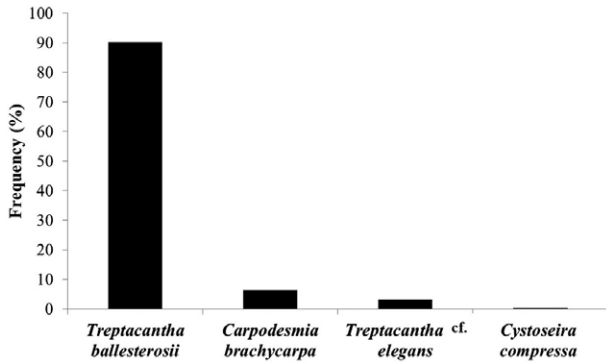


Fig. 4. – Density-frequency distributions of *Cystoseira s.l.* species (n=2885).

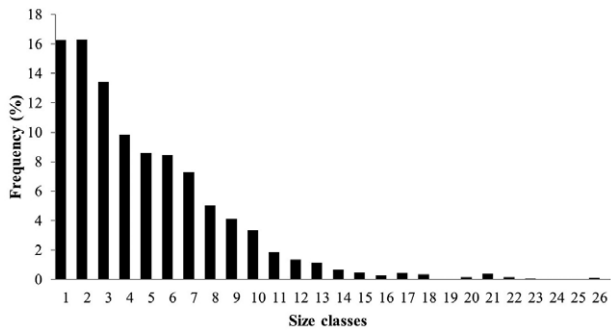


Fig. 5. – Size frequency distribution of *Treptacantha ballesterosii* starting at the class interval of 1 cm (main axes measuring 0.1-1 cm) (n=2603).

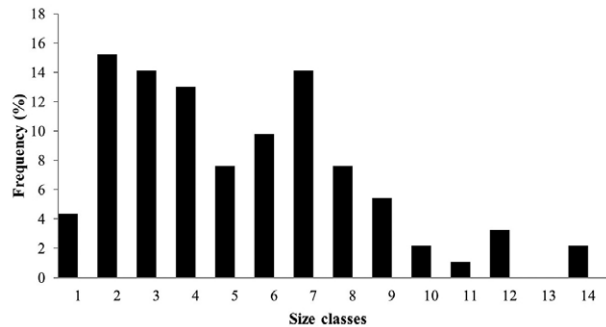


Fig. 6. – Size frequency distribution of *Treptacantha cf. elegans* starting at the class interval of 1 cm (main axes measuring 0.1-1 cm) (n=92).

of small classes in the population. The mean colony size is 15.7 ± 15.4 cm (\pm SD, n=546), ranging from 2 to over 100 cm, with a maximum size of 146 cm.

Treptacantha ballesterosii individuals are interspersed among and on the coral colonies and macroalgae (Fig. 2). *T. ballesterosii* stands for 90% of the individuals belonging to *Cystoseira s.l.*, while specimens identified as *T. cf. elegans*, *C. brachycarpa* and *C. compressa* show a much lower abundance (Fig. 4). The mean density of *T. ballesterosii* is 206 individuals m^{-2} . The main axes of *T. ballesterosii* support a considerable epiphytic load mainly composed of turf-forming algae like *Halitilon virgatum* (Fig. 2).

The size class frequency distribution of *T. ballesterosii* is unimodal but non-normal (K-S, $d=0.5$, $p < 0.0001$), with a prevalence of small individuals

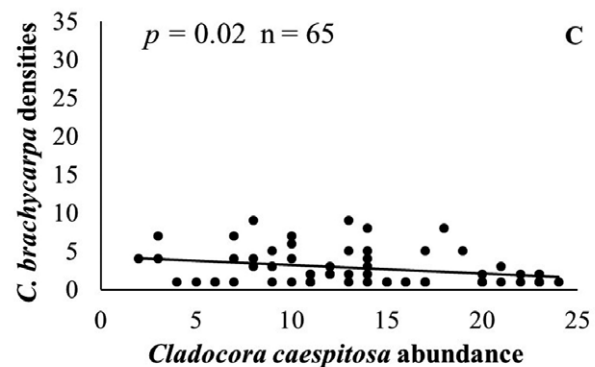
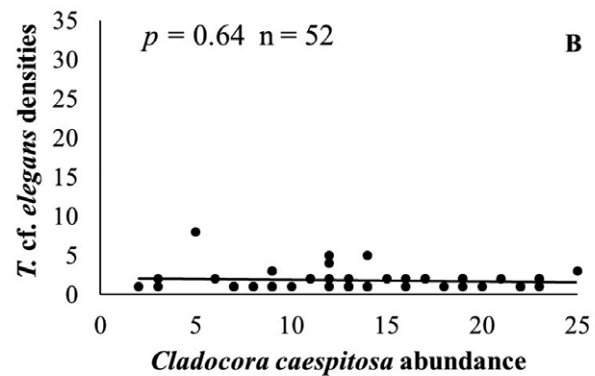
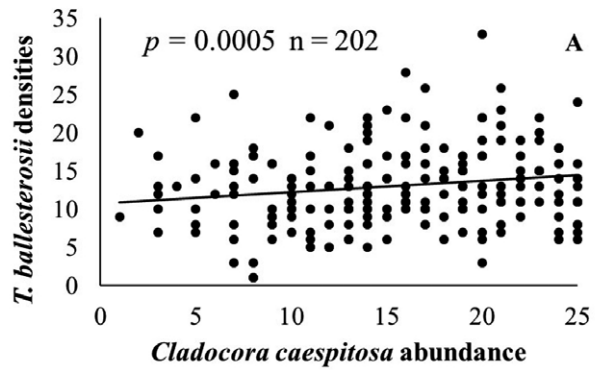


Fig. 7. – Relationship between the densities of the different species of *Cystoseira s.l.* and *Cladocora caespitosa* abundance: *Treptacantha ballesterosii* (A), *Treptacantha cf. elegans* (B) and *Carpodesmia brachycarpa* (C).

($g1=1.376$) (Fig. 5). The mean length of the main axis is 4.7 ± 3.8 cm (\pm SD, n=2603), with a maximum length of 26 cm obtained for three individuals, and 90% of the population ranging between 0.5 and 9 cm. The *T. cf. elegans* population shows two peaks at 2 and 7 cm and does not follow a normal distribution either (K-S, $d=0.84$, $p < 0.0001$) (Fig. 6). The mean length of the main axis is 5.3 ± 3.1 cm (\pm SD, n=92), with a maximum length of 14 cm.

Treptacantha ballesterosii, the most abundant macroalga, shows a slight but very significant positive relationship with *C. caespitosa* abundance ($p=0.0005$, $n=202$) (Fig. 7A). No significant relationship was found between *T. cf. elegans* densities and *C. caespitosa* abundance ($p=0.64$, $n=52$) (Fig. 7B). In contrast, densities of *C. brachycarpa* decline when *C. caespitosa* abundance increases ($p=0.02$, $n=65$) (Fig. 7C).

DISCUSSION

We have identified and characterized a new Mediterranean habitat constituted by a mixture of *C. caespitosa* colonies and *T. ballesterosii* stands. This kind of habitat is not reported in the EUNIS (Moss 2008) or RAC/SPA (UNEP-MAP-RAC/SPA 2006) habitat classification lists or in the Spanish List of Marine Habitats (Templado et al. 2012). Both the EUNIS and RAC/SPA lists only consider a “facies with *Cladocora caespitosa*” (III.6.1.14) and up to 12 associations with *Cystoseira s.l.* Furthermore, the Spanish List of Marine Habitats only lists two habitats harbouring *C. caespitosa* (i.e. 0301041408 “Infralittoral rock, moderately illuminated, without Fucales with *C. caespitosa*”, and 0301041607 “Infralittoral rock with low hydrodynamism, poorly lit dominated by invertebrates with *Cladocora caespitosa*”) and 19 habitats with *Cystoseira s.l.* We therefore suggest a new habitat type to be included in the Spanish List of Marine Habitats named “Infralittoral rock with low hydrodynamism, moderately lit, with *Cladocora caespitosa* and *Treptacantha ballesterosii*” and numbered 03010503.

The coexistence of *C. caespitosa* and *Cystoseira s.l.* has been previously reported at several Mediterranean sites: the Columbretes Islands (Kersting and Linares 2012) and the Balearic Islands (Kersting et al. 2017, Ballesteros and Pons-Fita 2020) in the western Mediterranean and Cyprus in the eastern Mediterranean Sea (Jiménez et al. 2016). However, none of these studies described the seaweed assemblages in terms of densities and stand size.

The population and individual sizes estimated in this study are very noteworthy for both the coral and the macroalgae. We have estimated a total area of *C. caespitosa* of 387.5 m², which is rather outstanding considering the 650 m² reported from Veliko Jezero lake (Mljet National Park, Adriatic Sea), which hosts the most compact reef of *C. caespitosa* known to date (Kružić and Požar-Domac 2003), and the 2900 m² covered by this coral in the Columbretes Islands (NW Mediterranean Sea), the most extensive *C. caespitosa*-covered area known in the Mediterranean Sea (Kersting and Linares 2012). The mean coral cover of 33.7% obtained in Es Banc, although lower than that found in Veliko Jezero lake, is slightly higher than the 31% found in the Bay of Piran (Schiller 1993) and much higher than the 20% from Espardelló islet (Kersting et al. 2017) and the 7% found in the Columbretes Islands (Kersting and Linares 2012).

Mean colony size is also higher than at other sites reported, such as the Bay of Piran, La Spezia and Espardelló islet (Schiller 1993, Peirano et al. 2001, Kersting et al. 2017). Es Banc holds some very large colonies (>100 cm), similar to Columbretes (Kersting and Linares 2012), but these are present in reduced numbers. However, Columbretes has twice the mean colony size of Es Banc (31.48 cm average diameter) (Kersting and Linares 2012), which may be related to depth and sea-floor morphology, since water motion and other disturbances related to exceptional storms are minimized with depth and hydrodynamic shelter

(Schiller 1993, Kersting and Linares 2012). In fact, Es Banc and Columbretes show different types of spatial coral colony development. In Columbretes, coral colonies are large, but their distribution is patchy and highly associated with sea-floor morphology, with large areas almost devoid, or with a very low density, of colonies (Kersting and Linares 2012). In contrast, coral colonies in Es Banc form a wide irregular carpet that covers the rocky bottom. This encrusting ecotype, which has been attributed mainly to mechanical stress from waves and currents (Riedl 1964), is also present in other localities in concurrence with macroalgae (e.g. Espardelló [Kersting et al. 2017], Vulcano [O. Ocaña, pers. comm.]). Other large colonies forming reef-like structures are reported from Veliko Jezero lake (Mljet, Croatia) (Kružić and Požar-Domac 2002, 2003), but the conditions of this site are extremely sheltered and not comparable to those of other localities located in open sea areas. Large *C. caespitosa* colonies are almost absent in Piran and La Spezia (Schiller 1993, Peirano et al. 1998, 2001). Small colonies (<10 cm) are very abundant, in agreement with other localities (Rodolfo-Metalpa et al. 2005, Kersting and Linares 2012, Kersting et al. 2017).

The population of *T. ballesterosii* from Es Banc is also outstanding. Mean density reaches 206 individuals m⁻², which is very high when compared with densities reported from Scandola Marine Reserve (Parc Naturel Régional de Corse, France), where *T. ballesterosii* var. *compressa* (as *Cystoseira spinosa* var. *compressa*) shows densities of 28 individuals m⁻² at 26–29 m depth, decreasing to 3 individuals m⁻² between 38 and 50 m depth (Ballesteros et al. 1998, 2009). Hereu et al. (2009) found *T. ballesterosii* v. *compressa* densities ranging from 0 to 7 individuals m⁻² between 35 and 47 m depth in Port-Cros National Park (France). However, thallus length of *T. ballesterosii* is much lower in Es Banc than in Scandola and Port-Cros deep waters, where mean lengths of 7 to 16 cm have been reported (Ballesteros et al. 1998, Hereu et al. 2009). The shape of the size class distribution of *T. ballesterosii* population in Es Banc is close to a negative exponential function, which has been associated with populations at equilibrium (Lorimer 1985, Edmonds et al. 1993, Berg and Hemrick 1994), where small size individuals are very abundant and the abundances progressively decline at increasing sizes. In contrast, Ballesteros et al. (1998) and Hereu et al. (2009) found log-normal distributions of size classes of *T. ballesterosii* v. *compressa* in Scandola and Port-Cros. Other deep-water *Cystoseira s.l.* populations (*Carpodesmia zosteroides*, *Treptacantha funkii*) also follow log-normal distributions (Hereu et al. 2009, Ballesteros et al. 2009, Navarro et al. 2011), which must be related either to unpredictable episodes of recruitment or to the dense canopy of large individuals that must inhibit the recruitment of new individuals.

In Es Banc, the shape distribution of size classes in *T. cf. elegans* population showing two peaks might indicate uneven recruitment events depending on the year, as has already been reported in other *Cystoseira*

s.l. populations (e.g. Ballesteros et al. 1998, 2009, Hereu et al. 2009) and other fucoids (e.g. Deysher and Norton 1982, Dayton et al. 1984, Fernández et al. 1990).

Another result of this study is the discovery of a positive relationship between *C. caespitosa* cover and the density of *T. ballesterosii*, which challenges the predicted competition for space between corals and macroalgae (McCook et al. 2001). This contrasts with reports of growth limitation of *C. caespitosa* by soft algae (Peirano et al. 1998) or the competition between *C. caespitosa* and macroalgae (*Codium*) found in other localities (Kružić and Benković 2008). In fact, the positive interaction between *C. caespitosa* and *T. ballesterosii* points to a possible facilitation mechanism. We suggest the hypothesis that the recruitment or survival of *T. ballesterosii* might be enhanced by the presence of *C. caespitosa*, but colonies do not seem to be affected by the presence of algal thalli. *Treptacantha* cf. *elegans* shows a neutral relationship while the relationship with *C. brachycarpa* is negative, probably due to the caespitose habit of this species, which cannot progress inside a coral colony. These results launch a wide array of possible open discussions on coral-macroalgae interactions.

In conclusion, here we report on a new habitat type for the Mediterranean Sea, which is co-dominated by an endemic colonial coral and an endemic canopy-forming alga. Both the coral and the macroalga show large cover and abundance, challenging the theory of competitive exclusion between these two functional groups (photosynthetic organisms versus photo-suspension feeders) in the marine benthos. Moreover, the fact that this habitat is dominated by species of high vulnerability and included in red lists and international conventions merits a special monitoring project and proper management actions in order to ensure its persistence over the years.

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