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Faculdade de Ciências e Tecnologia

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Declaração de autoria de trabalho: Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

Alèssia Pons Fita

Acknowledgements

First and foremost, I would like to thank my mentor, Dr. Kike Ballesteros for sharing his time and knowledge. As well as his willingness to guide and assist whilst giving invaluable advice throughout the fieldwork and writing process of the thesis. I am impressed with his positive way of thinking and living, his ongoing support and tireless positivity. This thesis would not have been possible without his exceptional spirit.

I would like to thank his staff members: Susana Pinedo and Dr. Simone Mariani for their help and cooperation dealing with the data analysis and statistics. Dr. Antoni Garcia-Rubies for his advices and support in the whole process of the thesis. I am also indebted to Dr. João Gil for the corrections of the Portuguese summary. Dr. Diego Kersting was very kind to provide information on *Cladocora caespitosa* and also was very helpful in the field mission in Columbretes islands.

I would also like to express my appreciation to Dr. Ester Serrão, for her feedback and efforts in checking and editing the thesis. I am also very grateful to Dr. João Varela for his suggestions and continued interest in the thesis ensuring it being a smooth process.

I also acknowledge the managers and rangers of the surveyed MPAs for the permissions and facilities provided.

In addition, I would like to give my sincere gratitude towards my family for the encouragement which has helped me in the completion of the thesis.

Abstract

Zooxanthellate corals and benthic macroalgae that overlap in the same habitat compete for limiting resources such as light and space and have physical and chemical clues to outcompete each other. There is a huge amount of literature based on coral-algal interactions that endorse the general assumption about the negative outcomes on corals once the algae proliferate due to increased nutrient loads or decreasing herbivory rates. Here we have discovered and characterized a new and unique Mediterranean habitat where the reef-building coral *Cladocora caespitosa* and erect seaweeds of the order Fucales (*Cystoseira s. l.*) coexist. In this new habitat *Cladocora caespitosa* reaches 34% cover and densities of *Cystoseira s. l.* (mainly *Treptacantha ballesterosii*) are much higher than reports from other sites provided by different authors. Interestingly, abundances of *Treptacantha ballesterosii* and *Cladocora caespitosa* show a positive relationship suggesting that some kind of facilitation mechanism is taking place. Comparing these *Cladocora-Cystoseira s. l.* relationships with other places where these taxa coexist, reveals that these relationships are species- and site-specific, although most of them are neutral or positive. Despite the mechanisms mediating coral-algae interactions are being poorly understood, description of positive to neutral long-lasting relationships between these principal Mediterranean habitat-formers challenges the expected competition for space between corals and macroalgae.

Keywords: *Cladocora caespitosa*, *Cystoseira*, interactions, competition, habitat, corals

Resumo

Os corais zooxantelados são os principais organismos engenheiros de habitat das águas superficiais dos mares tropicais e subtropicais, da mesma maneira que nos mares temperados essa função é desempenhada pelas macroalgas castanhas das ordens Laminariales, Fucales e Tilopteridales. No entanto, nos recifes de corais as interações entre algas e corais são frequentes, e os dois grupos competem entre si por recursos limitantes, como sejam a luz ou o espaço. Por essa razão, tanto as algas como os corais desenvolveram estruturas físicas e compostos químicos de defesa que usam contra os organismos competidores. Existe uma grande quantidade de bibliografia publicada analizando as interações corais-algas e que apoia o pressuposto geral sobre os efeitos negativos das algas sobre os corais, a partir do momento em que essas proliferam como consequência do aumento da carga de nutrientes no meio marinho ou da diminuição da taxa de herbivoria. Estes acontecimentos são normalmente mediados pelos humanos, mas também ocorrem naturalmente como consequência de situações pouco frequentes e catastróficas, como podem ser grandes tempestades, maremotos, aumento do escoamento superficial terrestre devido a episódios de chuvas fortes, ou surtos de doenças que eliminam herbívoros (p. ex. ouriços do mar). Em condições normais e estáveis, nas águas tropicais podemos encontrar recifes dominados tanto por corais como por algas, principalmente coralinas incrustantes, mas também algas filamentosas e macroalgas de talo ereto (*Sargassum*, *Turbinaria*).

O Mediterrâneo é um mar temperado e ameno, mas suficientemente frio no inverno para impedir que a maioria dos corais tropicais possam aí sobreviver. Existe no entanto um coral hermatípico endémico, *Cladocora caespitosa*, que tem a capacidade de ser a espécie dominante em localidades com características muito particulares e formar aí bioherms estruturalmente semelhantes a recifes de pequenas dimensões. No presente estudo descrevemos e caracterizamos um habitat mediterrânico novo e único, no qual coexistem o coral hermatípico *Cladocora caespitosa* e algas eretas da ordem Fucales (*Cystoseira s. l.*). Este novo habitat está localizado em Formentera (Ilhas Baleares), num local conhecido como “Es Banc” (38°43'19.2"N 1°23'09.2"E). Neste habitat o coral *Cladocora caespitosa* atinge uma cobertura de 33,7%, com uma superfície total de coberta de 387 indivíduos por m^2, enquanto que as densidades de *Cystoseira s. l.* (principalmente *Treptacantha ballesterosii*) podem atingir valores de 206 indivíduos por m^2, uma densidade muito superior aos valores obtidos por outros autores para outras localidades mediterrânicas.

Por outro lado, a longitude do eixo principal da *T. ballesterosii* é aqui de cerca de 5 cm, o que representa um valor muito inferior ao descrito para a espécie em estudos anteriores. Curiosamente, as abundâncias de *T. ballesterosii* e de *Cladocora caespitosa* mostram uma relação positiva, sugerindo algum tipo de mecanismo de facilitação pelo qual o recrutamento e/ou a sobrevivência de *T. ballesterosii* são reforçados pela presença de *Cladocora caespitosa*. De fato, muitos indivíduos de *T. ballesterosii* estão completamente rodeados por, ou localizados diretamente sobre, colónias vivas de *Cladocora caespitosa*. Outras espécies de *Cystoseira s. l.* não apresentam qualquer relação significativa com o coral (e.g. *Treptacantha elegans*) ou esta relação é negativa (e.g. *Carpodesmia brachycarpa*). Tanto a espécie *Cladocora caespitosa* como as espécies de *Cystoseira s. l.*, com exceção de *Cystoseira compressa*, denotam uma alta vulnerabilidade e estão em risco, pelo que foram incluídas em Listas Vermelhas de espécies ameaçadas e encontram-se protegidas por Convenções Internacionais. Por essa razão, este habitat dominado por *Cladocora caespitosa* e diferentes espécies de *Cystoseira s. l.* merece um projeto de monitorização especial e desenhado à sua medida, assim como ações de gestão adequadas para garantir a sua preservação e futura sobrevivência.

O estudo das relações entre *Cladocora caespitosa* e *Cystoseira s. l.* foi estendido a duas outras localidades mediterrânicas onde estes taxa coexistem, nomeadamente às Ilhas Columbretes (39º53.825’N, 0º41.214’E), e a s’Espardelló (38º47’14.2”N, 1º28’59.7”E). Desta maneira tentou-se comprovar se os padrões de interação entre *Cladocora caespitosa* e as diferentes *Cystoseira s. l.* encontrados em Es Banc se mantêm e se repetem noutras localidades, a nível regional. A cobertura média de coral obtida nas ilhas Columbretes é de cerca de 7%, enquanto que em s’Espardelló atinge um 20%. Nas Columbretes, *Treptacantha sauvageauana* e *Cystoseira compressa* são as espécies de algas mais frequentes (38% de abundância cada uma), enquanto que *Treptacantha ballesterosii* var. *compressa*, *Carpodesmia brachycarpa, Carpodesmia zosteroides* e *Cystoseira foeniculacea* var. *latiramosa* apresentam abundâncias muito menores. Já em s’Espardelló, a espécie mais comum é *Treptacantha ballesterosii*, que corresponde a um 72% de todos os exemplares de *Cystoseira s. l.* encontrados, seguida pela *Cystoseira compressa* com 18% e *Carpodesmia brachycarpa* com menos de 10%. Verificámos assim que as relações entre algas e coral são específicas para cada espécie e localidade, apesar de que a maior parte delas são neutras ou positivas. *Treptacantha ballesterosii* e *Cystoseira compressa* têm geralmente relações positivas ou neutras, *Carpodesmia* *brachycarpa* é sempre neutra, exceto num caso em que é negativa, *Treptacantha sauvageauana* é negativa e *Treptacantha elegans* é neutra. Assim, estes resultados não concordam com a visão generalizada acima referida sobre os efeitos negativos das macroalgas carnudas sobre os corais escleractinianos.

Não existem estudos específicos sobre a competição entre os corais e as macroalgas *Cystoseira s. l.*, mas sabe-se que essas algas produzem compostos alelopáticos (principalmente terpenóides) que atuam como mecanismos químicos de defesa contra os herbívoros, bactérias e fungos. No entanto, esses aleloquímicos não parecem afetar a interação entre *Cladocora caespitosa* e a maior parte das espécies de *Cystoseira s. l.*. Por sua vez, o coral *Cladocora caespitosa* possui mecanismos aleloquímicos para evitar o crescimento excessivo de macroalgas mas, uma vez mais, isso não parece afetar a interação entre *C. caespitosa* e a maioria das espécies de *Cystoseira s. l.*. A feofícea *Sargassum* spp., também pertencente à ordem Fucales, mostra igualmente ter poucos ou nenhum efeito negativo sobre os corais do sub-bosque, enquanto que o efeito do sombreamento provocado pela cobertura dessas algas é aparentemente positivo, ao mitigar os níveis de exposição solar excessiva e proteger os corais das altas temperaturas. Quanto ao coral *Cladocora caespitosa*, ele apresenta uma rápida recuperação após sofrer danos nos seus tecidos e esqueleto, o que pode ser muito vantajoso na sua competição com as *Cystoseira s. l.* e outras algas colonizadoras.

Historicamente, as *Cystoseira s. l.* originaram-se no Mar de Tétis, durante o Mesozóico, mas o seu processo de especiação radiativa no Mediterrâneo começou após a Crise de Salinidade Messiniana (5,3 MY atrás), quando muitas espécies atlânticas invadiram o Mar Mediterrâneo. Quanto a *Cladocora caespitosa*, também teve a sua origem após a Crise de Salinidade Messiniana. Assim, tanto as *Cystoseira s. l.* como o coral *Cladocora caespitosa* têm estado em estreito contato desde há muito tempo, e tiveram necessariamente que competir entre si, assim como com outros organismos bentónicos de pouca profundidade como outras algas e invertebrados sésseis, pelos recursos limitantes (e.g. luz e espaço). No presente trabalho defendemos que as relações próximas e duradouras estabelecidas entre as espécies de *Cystoseira s. l.* e o coral *Cladocora caespitosa* desenvolveram uma variedade de efeitos, positivos, negativos ou neutros, que são específicos segundo as espécies de algas envolvidas e o local no qual ocorrem. Estas ocorrem nos mesmos habitats, e devem ter aí papéis e requisitos ecológicos compatíveis para poderem sobreviver, crescer e reproduzir-se, o que provavelmente forçou o desenvolvimento de adaptações e mecanismos que permitissem a sua coexistência.

Em resumo, no presente trabalho demostramos que o coral hermatípico *Cladocora caespitosa* e as macroalgas perenes formadoras de bosques *Cystoseira s. l.*, são capazes de coexistir e formar associações nas águas superficiais do Mediterrâneo. A relação entre corais e macroalgas é específica para cada espécie e local, e embora a maior parte das espécies apresente efeitos neutros, em algumas delas (e.g. *Treptacantha ballesterosii*) parece existir um efeito facilitador do coral sobre as algas. Apesar de que os mecanismos que permitem esta coexistência estejam longe de ser compreendidos, a descrição destas relações de longo prazo, neutras e positivas, entre dois dos principais grupos de organismos construtores de habitats marinhos mediterrânicos em águas superficiais, desafia a esperada competição pelo espaço e pela luz entre corais e macroalgas.

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State of the Art

Coral reefs are generally associated with tropical, warm and shallow waters, although coral reef ecosystems are also present in cold, deep waters (> 100 m), in habitats void of sunlight (Hoegh-Guldberg et al. 2017). In the Mediterranean, shallow water coral reefs are almost inexistent. The Mediterranean Sea is characterized by strong seasonal variations in environmental factors and shallow reef corals cannot cope with such conditions (Zabala & Ballesteros 1989). Nevertheless, there are at least two coral species, *Cladocora caespitosa* (Linnaeus 1767) and *Oculina patagonica* (Angelis 1908) that have the capacity to develop reef-like structures, comparable to tropical reefs, in the Mediterranean.

The forming-reef corals are called hermatypic. Coral reefs are mainly built by thousands of coral polyps, which are responsible for secreting a calcium carbonate ($CaCO_3$) skeleton. Corals that grow and make up this skeleton-like structure, have been named hard corals. Furthermore, hard shallow water corals are often in symbiosis with microscopic algae (zooxanthellae), a type of dinoflagellates living in their tissue. While not all the corals are zooxanthellate, the association between corals and photosynthetic dinoflagellates greatly enhances coral growth, increasing calcification rates (Muscatine 1981, Barnes & Crossland 1982). Therefore, shallow and zooxanthellate or photosymbiotic corals have more potential of developing vast reefs since they have a reliable source of organic matter from zooxanthellae.

In the case of *Cladocora caespitosa* reefs, large and extensive reefs have been reported from the fossil record (Bernasconi et al. 1997; Aguirre & Jiménez 1998; Peirano et al. 1999), although at present only a few locations host large *Cladocora caespitosa* bioconstructions (Kružic & Požar-Domac 2003; Kersting & Linares 2012).

Habitat, ecology and morphology of *Cladocora caespitosa*

Cladocora caespitosa occurs on rocky bottoms, from the first meters below the sea surface down to 30 m depth (Kružic & Benković 2008). Accordingly, it can grow from photophilic communities (Kersting & Linares 2012) to circalittoral assemblages, where light is a limiting factor (e.g. Kersting et al. 2015). In addition, *Cladocora caespitosa* can set on sandy, rocky bottoms and bioherms formed by itself and coralline algae (Rhodophyta) (e.g. Aguirre & Jiménez 1998; Kružic & Benković 2008). In addition, it can also thrive in muddy and nutrient enriched waters (e.g. terrestrial run-off into the sea, resuspension of bottom sediments) (Peirano et al. 2005) with unstable hydrodynamic conditions (Zibrowius 1980). These environmental conditions are commonly found in winter in the Mediterranean, where *C. caespitosa* is used to a larger food supply. However, the best conditions for *C. caespitosa* growth is a combination of temperatures no higher than 23ºC (mid temperature in summer) and without food scarcity (Rodolfo-Metalpa et al. 2008). *C. caespitosa* also displays a 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. 2017) (Figure 1 a-b). The different shapes and growths of the scleractinian coral may be a result of many factors: global and regional hydrodynamic forces (e.g. ocean currents, storm waves, run-off) (Pomar 1991; Vennin et al. 2004), sediment inputs (Kružić & Benković 2008), temperature, feeding availability (Rodolfo-Metalpa et al. 2008) and competition for space (e.g. algae and other competitors) (e.g. River & Edmunds 2001; Titlyanov et al. 2007).

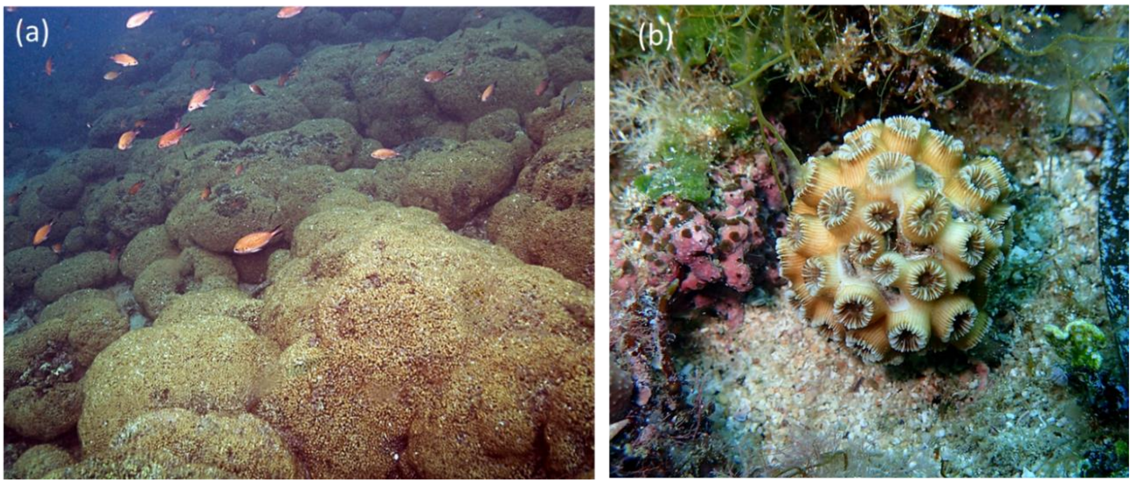

Figure 1: (a) View of the largest *Cladocora caespitosa* reef recorded from Veliko Jezero lake (Mljet National Park) in the Adriatic Sea (photo from Kružic & Požar-Domac 2003). (b) Colony of *Cladocora caespitosa* with a spherical morphology that enables it to move around by rolling (photo from Kersting et al. 2017).

Origin of *Cladocora caespitosa*

The oldest fossil records of *Cladocora caespitosa* were found in Almería Bay, in southern Spain and were dated to the Plio-Pleistocene (5 MY ago) by Aguirre & Jiménez (1998). *C. caespitosa* seems to be an endemic species originated after the Messinian Salinity Crisis, 5.3 MY ago. However, there are small and patchy *C. caespistosa* colonies distributed in the adjacent areas of the Atlantic, close to the Mediterranean, including in Portugal and Morocco (Zibrowius 1983; Schiller 1993), which opens the discussion of whether *Cladocora caespitosa* is a neoendemism or whether it originated in the Atlantic and entered the Mediterranean during the flood of Atlantic waters into the Mediterranean basin. Presently, *C. caespitosa* populations are widely dispersed around the whole Mediterranean Sea.

Cladocora caespitosa reefs distribution

Cladocora caespitosa is a hermatypic zooxanthellate coral and at present, roughly fifteen living banks or beds and scattered coralliths (non-reef forming colonies) have been described in the Mediterranean Sea (reviewed by Casado-Amezúa et al. 2015): La Spezia region in Italy (Morri et al. 1994, 2000; Peirano et al. 2001, 2005; Rodolfo-Metalpa et al. 2005), Bay of Piran in Slovenia (Schiller 1993), Rovinj (Zibrowius 1980), Pag, Iz and Prvić islands (Zibrowius 1980; Kružić & Benković 2008) and lake Veliko jezero (Mljet National park) in Croatia (Kružic & Požar-Domac 2003), Port-Cros island that is part of Îles d'Hyères in the French coast (Laborel & Laborel-Deguen 1978), Greece (Laborel 1961), Tunisia (Zibrowius 1980), Cyprus (Jiménez et al., 2016), Cap de Creus, Medes and Columbretes islands in the Western Mediterranean Sea (Kersting & Linares 2012; Kersting et al., 2013a, 2014c) and Balearic Islands, mostly, in the localities of Cala Galdana, Minorca (Fayos pers. comm. 2014) and Cap Blanc, Mallorca (Aguilar pers. comm. 2014). The latest records are in S'Espardelló islet (Kersting et al. 2017) and Racó des Banc, in Formentera (present work). The largest *C. caespitosa* formations are described from Mljet National Park (Kružic & Požar-Domac 2003). Other southern Mediterranean localities have been almost unexplored and probably, *C. caespitosa* is also present and perhaps abundant. *C. caespitosa* point-occurrence records were collected from the Global Biodiversity Information Facility (GBIF) in order to have a better idea of the actual distribution of the species in the Mediterranean basin (Figure 2). However, GBIF data notoriously contains inaccurate species identifications, imprecise data (e.g. in Cantabrian Sea, northern coast of Spain) and it requires much more data mining (e.g. Columbretes Islands populations and adjacent populations from Atlantic coasts do not appear).

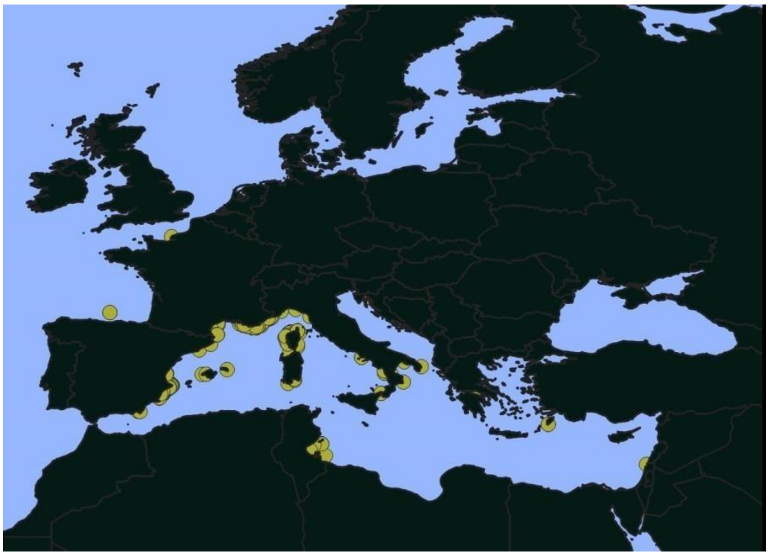

Figure 2: Occurrence records of *Cladocora caespitosa* in the Mediterranean Basin according to GBIF data (yellow points).

Phylogeography and reproduction strategy of *Cladocora caespitosa*

Regardless of being a fairly widespread species around the Mediterranean Sea, *C. caespitosa* populations are considered genetically isolated (Casado-Amezúa et al. 2014). According to Kružić et al. (2008) the fertilization of *C. caespitosa* occurs in the water column (external fertilization) but eggs are not spread away, in contrast with the sperm. Eggs are bound together as clumps a mucus coating on the polyp surfaces. This strategy of retaining eggs on the top of the colony, despite being broadcast spawners, might explain the high levels of self-recruitment already found by Kersting & Linares (2012) and Kersting et al. (2014b). Indeed, *C. caespitosa* populations situated relatively close such as the ones in Columbretes and L'Ametlla de Mar (northeastern Spain), show a significant level of genetic differentiation, indicating low connectivity among them (Casado-Amezúa et al. 2014). Therefore, the dispersal capacity of *C. caespitosa* populations seems exclusively linked to global and local water currents, rafting events and physical barriers such as eddies or upwelling systems (Pineda et al. 2007). However, the behavior and dispersal abilities of *C. caespitosa* planulae in relation to the environmental factors have not yet been studied in sufficient detail but are key and it is a paramount piece to better understand the gene flow of *C. caespitosa* populations.

Cladocora caespitosa colonies seem to reproduce annually (Kersting et al. 2013b) with low recruitment rates and high juvenile mortality (Kersting et al. 2014b). However, the published information related to the reproductive biology and the spawning time of *C. caespitosa* is contradictory, suggesting striking differences between sites. Schiller (1993) and Kružić et al. (2008) indicated that *C. caespitosa* is hermaphroditic, with spawning occurring at the beginning of summer (rising seawater temperatures) in the Adriatic Sea. Meanwhile, Kersting et al. (2013b) found it to be gonochoric, with spawning happening at the end of the summer (decreasing seawater temperatures) in Columbretes Islands (western Mediterranean Sea). However, coral sexual reproduction is in general consistent across locations within most species and genera (Harrison 2011), although there are some cases of changes in sexual condition among populations from different localities (e.g. *Astroides calycularis* is also a temperate coral with gonochoric populations according to Goffredo et al. 2010 and hermaphroditic according to Lacaze-Duthiers 1873). Asexual reproduction in *C. caespitosa* typically takes the form of budding or fragmentation [further information about the mechanisms in Zibrowius (1980) and Kružić (2005)]. The periodicity of clonal propagation or asexual reproduction mode is poorly investigated in this coral but it would be restricted to periods of favorable environmental conditions since reproduction requires a large proportion of its energy budget (e.g. Titlyanov et al. 2001).

Threats facing *Cladocora caespitosa* and protection status

The warming trends in Mediterranean sea surface temperatures severely threaten survival of *C. caespitosa*. A continuous decline of *C. caespitosa* populations has been observed after hot summers, producing bleaching, direct tissue necrosis and mortalities (Schiller 1993; Metalpa et al. 2000; Kružić et al. 2012; Kersting et al. 2013a). The bleaching state is caused by the loss of zooxanthellae that contribute to the corals' pigmentation. After a long period of abnormal high temperatures, zooxanthellae are expelled from the stressed corals, making the corals more vulnerable or prone to be attacked by corallivorous gastropods (Kružić et al. 2013) and pathogenic organisms (bacteria, viruses, fungi) (Weynberg et al. 2015). A high occurrence of algal cover is another threat that may weaken *C. caespitosa* development (e.g. Peirano et al. 1998; Rodolfo-Metalpa et al. 1999) and that will be discussed later on. Indeed, *C. caespitosa* mortalities also are directly attributed to humankind activities, which entail high levels of pollution, sewage discharge and aggressive fishing practices (e.g. trawling) that accelerate and maximize the risk of leading *C. caespitosa* to extinction (Kružić & Požar-Domac 2007; El Kateb et al. 2016).

Since it is an endemic species, an important ecosystem engineer and it is highly threatened, *Cladocora caespitosa* is considered to be an endangered species by the International Union for Conservation of Nature (IUCN) red List and the Annex II of the Barcelona Convention (Casado-Amenzúa et al. 2015; UNEP-MAP- RAC/SPA, 2013).

Macroalgal assemblages intermixed with *Cladocora caespitosa* colonies

As mentioned previously, the largest *C. caespitosa* bioconstructions known up-to-date are situated in Mljet National Park in the Adriatic Sea (Kružić & Požar-Domac 2002), where it creates a continuous and homogenous dome and reef-like structure (Peirano et al. 1998). Moreover, high densities of *C. caespitosa* colonies, comparable with the ones from Mljet National Park, were observed in Columbretes Islands. However, in Columbretes, the colonies are thriving among diverse macroalgal communities in sciaphilic and photophilic habitats (mainly *Halimeda tuna*, Fucales and calcareous algae) (Kersting & Linares 2012). Indeed, similar habitat traits were found in other sites such as S'Espardelló islet (Kersting et al. 2017) and Racó des Banc, in Formentera (Balearic Islands) (present work), where *C. caespitosa* colonies are also withstanding dense canopies of brown canopy-forming seaweed species of the order Fucales, (Phaeophyceae).

Habitat, ecology and morphology of *Cystoseira sensu lato*

Brown and perennial macroalgae belonging to the genera *Treptacantha*, *Carpodesmia* and *Cystoseira* (Fucales, Phaeophyceae) inhabit the eastern Atlantic, including the Mediterranean Sea, the Adriatic Sea and the Macaronesian archipelagos (Sangil et al. 2011; Rožić et al. 2012; Blanfuné et al. 2016a). These genera were all included in the genus *Cystoseira* until very recently, when Orellana et al. (2019) found both genetic and morphological criteria to segregate the genus into three. We will refer to the genus *Cystoseira sensu lato* from now on when referring to the genus as conceived before the study by Orellana et al. (2019).

In the Mediterranean Sea, species of *Treptacantha*, *Carpodesmia* and *Cystoseira* are canopy-forming algae that dominate several macroalgal assemblages (e.g. Sauvageau 1912; Feldmann 1937; Giaccone 1973) and they have been widely used to describe Mediterranean phytobenthic assemblages (e.g. Feldmann 1937; Giaccone 1973; Verlaque 1987; Ballesteros 1990a,b). They are habitat-forming species that create complex habitats that host a large amount of organisms (Ballesteros 1992; Ballesteros et al. 1998). They also occupy a wide range of depths, from the upper infralittoral to the upper circalittoral zones. The morphology of basal and apical regions, position and shape of reproductive structures (receptacles), the presence and shape of air vesicles (aerocysts) and tophules are used to distinguish between the species of these genera. They are attached to the sea bottom by a conical disc or haptera that supports a single or several primary axes (cauloids). Primary axes can be divided into several axes and branches of several orders arise from the axes. Branches have the fertile structures, called receptacles, in which hermaphroditic conceptacles are present [see further information about morphological traits in Gómez Garreta et al. (2000), Cormaci et al. (2012) and Kim (2015)] and the life cycle is diploid, only gametes are haploid (Rodríguez-Prieto et al. 2013).

Morphological differentiations among genera and species of *Cystoseira s. l.* are subtle (e.g. Roberts 1978; Draisma et al. 2010; Orellana et al. 2019). Despite their typical seasonal growth patterns, as in other Mediterranean seaweeds (Ballesteros 1989, 1991), with the maximum biomass usually present in late spring, there is a considerable variation between species and even within the same species on different regions (Ballesteros pers. comm.). At the end of the growth season, frond biomass tends to break off the holdfast in most populations and only the basal parts persist overwintering. Changes in phenotypes may rely on the variations in predominant environmental forces (e.g. wave action, average temperatures) among sites and often trigger taxonomic confusion.

Evolution of *Cystoseira sensu lato*

The Mediterranean Sea is considered a center of speciation for *Cystoseira s. l.* (e.g. Bolton 1994). Indeed, more than two thirds (36), out of 51 specific and infraspecific taxa (Guiry et al. 2014; Thibaut et al. 2014), are present in the Mediterranean Sea and 30 are endemic (Gallardo et al. 2016). The Mediterranean is a semi-enclosed sea, divided into several sub-basins (Coll et al. 2010) which, together with local circulation and other basin-scale environmental factors (Hopkins 1985; Bosc et al. 2004), have led to a great process of differentiation and speciation that continues nowadays (Ercegovic 1952; Amico et al., 1985; Giaccone & Motta 1987).

The high similarity among species might be related to the ongoing speciation initiated 5 MY ago by species of *Treptacantha*, *Carpodesmia* and *Cystoseira* that probably recolonized the Mediterranean from the Atlantic Ocean after the Messinian salinity crisis. Recent studies support the importance of life-history traits such as selfing and low dispersal and prior colonization effects rather than reproductive barriers as the main drivers of genetic differentiation among closely related clades (Bermejo et al. 2018). Moreover, climate changes during the Quaternary glaciations caused fluctuations of sea level and temperature that resulted in range expansions and contractions of the species that have been critical for the evolution of *Cystoseira s. l.* species and most other taxa (Neiva et al. 2016).

Cystoseira sensu lato distribution

Species of *Cystoseira s. l.* are distributed along bathymetric and hydrodynamic gradients in function of light and hydrodynamic exposure (Giaccone 1971) and the competitive abilities and resistance to herbivores (Vergés et al. 2009). Some species are widely geographically distributed such as *Cystoseira compressa*, *Treptacantha barbata* or *Carpodesmia crinita* (Cormaci et al. 2012) while other species show geographically restricted distributions such as *Carpodesmia caespitosa* (Rodríguez-Prieto et al. 2013) and *Treptacantha rayssiae* (Mulas et al. in press). In other cases, like in the *Carpodesmia tamariscifolia* complex (including *C. tamariscifolia*, *C. amentacea* and *C. mediterranea*) the supposed previously distinct species with different geographical distributions resulted to be a single, morphologically plastic species according to genetic analyses (Bermejo et al. 2018). Thus, considering the high plasticity of most species of *Carpodesmia*, *Treptacantha* and *Cystoseira* and the current confusion in the delimitation of species (e.g. Sellam et al. 2017) it seems reasonable to be very cautious on the distribution of most taxa until the ambiguities in taxonomic classification are solved.

Threats facing *Cystoseira sensu lato* and protection status

Over the last decades, most of the *Cystoseira s. l.* species have experienced a significant decrease in abundance in many places in the Mediterranean Sea mainly due to anthropogenic pressures (mainly related to pollution, coastal development and net fishing) (e.g. Munda 1974, 1982, 1993, Soltan et al. 2001, Arévalo et al. 2007, Thibaut et al. 2005, 2015; Blanfuné et al. 2016b). Because of their vulnerable status and their importance as habitat formers in the Mediterranean, all species of *Cystoseira s. l.* except *Cystoseira compressa* have been listed as vulnerable under the Annex II of Barcelona Convention (2010). In addition, some species of *Cystoseira s. l.* are being used as indicators of high and good water quality water bodies regarding the implementation of the UE Water-Framework Directive (2000/60/EC) (Ballesteros et al. 2007, Pinedo et al. 2007; Nikolic et al. 2013; Bermejo et al. 2013; Blanfuné et al. 2016b, 2017) because they are very sensitive to pollution.

Competition between hermatypic corals and macroalgae

Tropical coral reef ecosystems require conditions with low variability, with ocean temperatures over 18ºC, low nutrient concentrations, strong and regular wave action, constant alkaline pH for calcium precipitation and hard substrate. Meanwhile, ecosystems dominated by large macroalgae (e.g. Fucales, Laminariales) are set on more eutrophic places with higher seasonal variability on environmental conditions (Zabala & Ballesteros 1989). However, coral reefs can become threatened by macroalgal overgrowth when their stability is changed by factors such as increasing nutrient concentrations or a decrease in herbivory levels (e.g. Hughes 1994; Lapointe 1997).

There are several methodologies to assess the status or dynamics of macroalgal and coral populations such as using visual line transects, visual quadrats, photographic belt transects, video transects, and other approaches. According to the aims of the research, some methods are more appropriate than others (Sant et al. 2017). Here we used a combination of transect lines and quadrats to estimate cover of *Cladocora caespitosa* and densities of *Cystoseira s. l.*. Transect lines are more suitable to get data from broad areas while quadrats divided into sub-quadrats are more adequate for detailed analysis of the community structure and interactions (e.g. Foster et al. 1991; Meese & Tomich 1992; Whorff & Griffing 1992). Thus, the cover of *Cladocora caespitosa* is more effectively measured by transect lines, whereas quadrat frames are likely most accurate in the assessment of macroalgae-coral relationships at the spatial scale in which interactions take place.

Chapter I

Introduction

The most distinct trait of tropical marine ecosystems are coral reefs. Although coral reefs are absent from temperate seas, there are a few Mediterranean scleractinian corals (8), out of the 37 existing, which can potentially behave as reef-builders (Morri et al. 2000). Indeed, the unique coral that has the capacity to build extensive banks, more than one meter thick and several tens of meters wide, is the Mediterranean pillow coral, *Cladocora caespitosa* (Zibrowius 1980, 1982; Morri et al. 1994; Peirano et al. 1998, 2001; Kružic & Požar-Domac 2003). Reef building corals can create a new habitat for many species by changing the morphological and physico-chemical characteristics of the geological substrate. Thus, *Cladocora caespitosa* is, in fact, the only Mediterranean scleractinian coral that is similar to tropical reef-building corals and can be considered as a habitat former (Chefaoui et al. 2017).

Due to their reduced distribution, small size and colony densities, Mediterranean coral bioconstructions have not been studied as extensively as tropical coral reefs have. *Cladocora caespitosa* is characterized by slow growth, low recruitment rates and limited larval dispersal ability, which makes this species very sensitive to disturbances (Peirano et al. 1999; Kružic & Požar-Domac 2002; Kersting & Linares 2012; Kersting et al. 2014b). At present, shallow *Cladocora caespitosa* bioconstructions have suffered a steep decline (Casado de Amezúa et al. 2015). The main anthropogenic causes, which often show synergistic effects, are pollution, fishing, invasive species, urban development, direct physical disturbances and climate change (Rodolfo-Metalpa et al. 2005; Kersting & Linares 2009; Kersting et al. 2014a-c, 2015; Casado de Amezúa et al. 2015; El Kateb et al. 2016). All these relevant features urged IUCN to include this species in the Red List with the status “Endangered” (Casado de 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).

In the Mediterranean shallow rocky bottoms, are usually dominated by algal stands (Zabala & Ballesteros 1989) and not corals as it is not a tropical sea. 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 former genus *Cystoseira* (Draisma et al. 2010; Bruno de Sousa et al. 2019), which resulted in the splitting of the previous *Cystoseira* species into three genera, namely *Cystoseira*, *Treptacantha* and *Carpodesmia* (Orellana et al. 2019). This segregation is 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 features of great ecological significance. *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 & Bruni 1973; Sant 2003). These beds are very productive and highly structured in three dimensions, leading to a perfect site for nursery, shelter, and source of food for a large number of species (Boudouresque 1971, 1972; Ballesteros 1988, 1990a, b; Ballesteros et al. 1998, 2009; Hereu et al. 2009). Accordingly, *Cystoseira s. l.* are the most representative macroalgae thriving in well-preserved Mediterranean environments. However, most species of Mediterranean Fucales are undergoing a severe decline (e.g. Cormaci & Furnari 1999; Thibaut et al. 2005; Serio et al. 2006; Bianchi et al. 2014; Thibaut et al. 2015, 2016; Blanfuné et al. 2016b; Mariani et al. 2019) although this is not always the case for all the species and everywhere (Sales & Ballesteros 2010; Thibaut et al. 2014; Blanfuné et al. 2019). Pollution is the main threat affecting the survival of *Cystoseira s. l.* populations (Munda 1974, 1982, 1993; Arévalo et al. 2007; Mangialajo et al. 2008; 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 to account for declines of *Cystoseira s. l.* (Cormaci & 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, 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 (Annex II; UNEP-MAP-RAC/SPA, 2013) and some of them are listed in the Annex I of the Bern Convention. Understanding the ecological interactions of their populations with other key community components is therefore extremely important to guide management towards conservation of these species and their ecosystem functions.

Here we report on the discovery of a new Mediterranean habitat co-dominated by *Cladocora caespitosa* and several species of *Cystoseira s. l.*, mainly *Treptacantha ballesterosii*. In particular, we aim at (1) describing *Cladocora caespitosa* cover and colony size, (2) describing *Cystoseira s. l.* densities and sizes (when possible) and (3) inferring the relationship between macroalgal abundance (mainly *Treptacantha ballesterosii* density) and coral cover. The description of this new habitat will warn other scientist 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 relationship.

Material & Methods

Study site

Exploratory dives and sampling were performed in November 2017 and July 2019 in Es Banc (38°43'19.2’’N 1°23'09.2’’E) located in the western part of Formentera (Balearic Islands), close to Punta Gavina. The sampling site is included in the MPA “Freus d’Eivissa i Formentera” although it is not a no-take area (artisanal fishing is allowed). The area where both *Cladocora caespitosa* and *Cystoseira s. l.* species coexist in large densities extends around 1150 m^2 (Figure 3).

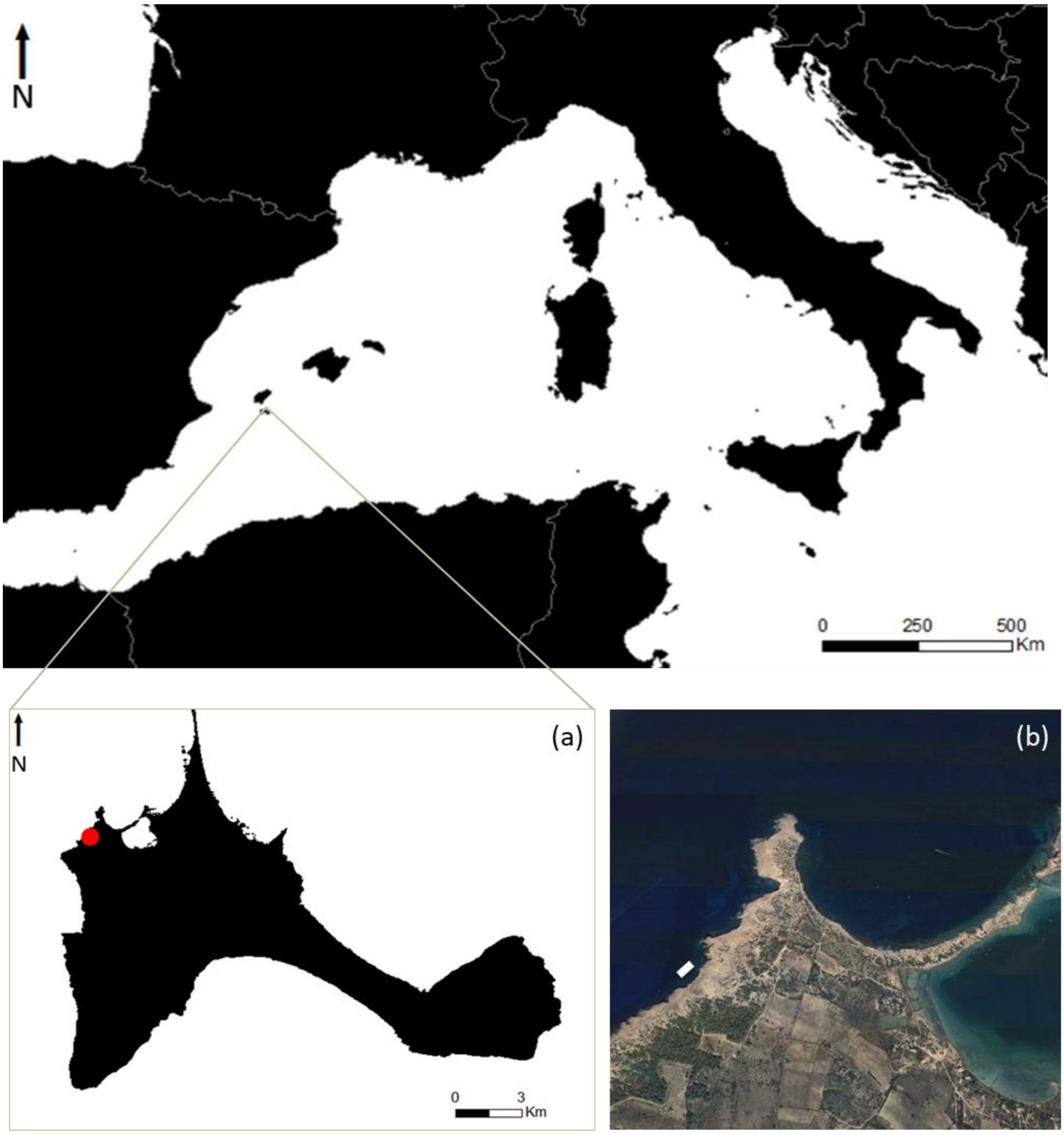

Figure 3: Sampling site (red dot) (a) and detailed position of the survey area (white frame) (Source: Google Earth).

Sampling methods

Cladocora caespitosa cover was measured using a line-intercept method on a transect line (5 transects of 50 m length) (English et al. 1997; Kersting & Linares 2012; Kersting et al. 2017) as shown in Figure 4.

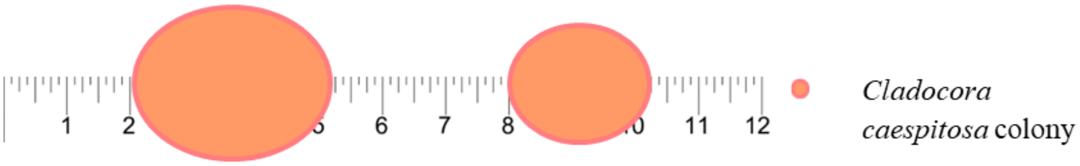

Figure 4: Simplified illustration of the line-intercept method used to quantify *Cladocora caespitosa* coverage and colony sizes along a transect. In this example, there are two colonies of 3.3 and 2.3 cm and total cover is (3.3 + 2.3)/12, i.e. 46.66 %.

Cystoseira s. l. densities were estimated using 625 cm^2 quadrat frames divided into 25 (5 cm x 5 cm) subquadrats (Figure 5). *Cystoseira s. l.* individuals were identified visually at the species level, and counted. The size of each individual belonging to *T. ballesterosii* and *T. elegans* was measured as the length of the primary axis using a ruler (Ballesteros 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 & Bruni 1973; Cormaci et al. 2012), and size was therefore not estimated.

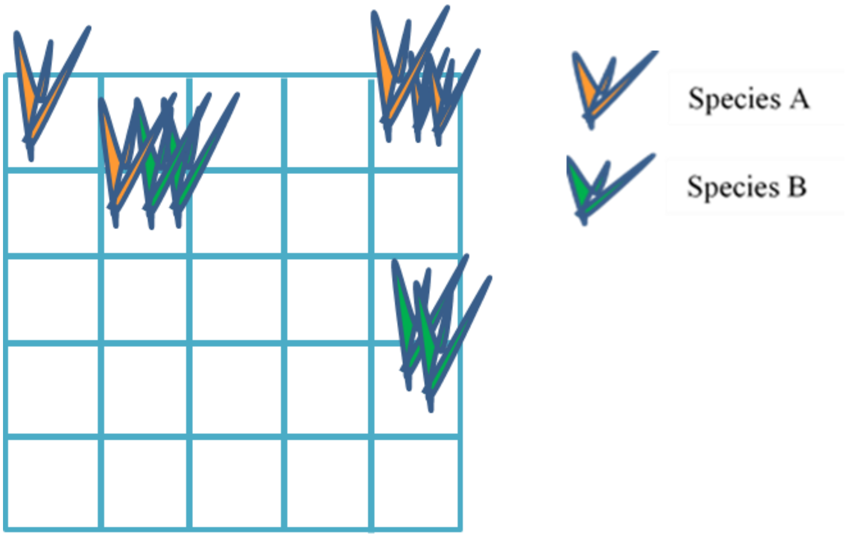

Figure 5: Graphic example of density counts in *Cystoseira s. l.* using the reticulated quadrats of 625 cm^2. Species A has five individuals and species B has four individuals.

The abundance of *Cladocora caespitosa* was quantified at the same quadrats using two different approaches: (a) number of subquadrats where *Cladocora caespitosa* was present; and (b) visual estimation of *Cladocora caespitosa* cover (see Figure 6).

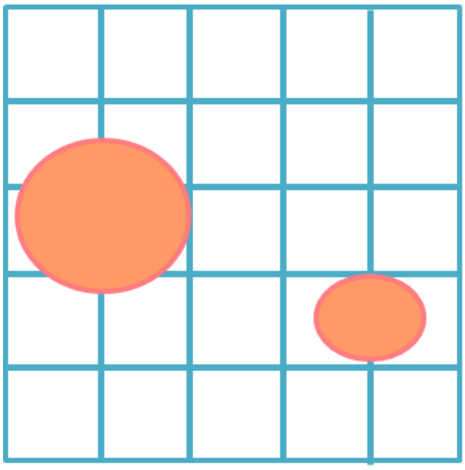

Figure 6: Example of the two quantification approaches used in this study to measure *Cladocora caespitosa* abundance. Using the first approach -number of subquadrats with presence of *Cladocora caespitos*a- the abundance is 8 (32% of the subquadrats) while using the second approach –visual cover estimate of *Cladocora caespitosa*- the abundance would be around 16%.

Data analysis

Kolmogorov-Smirnov tests were performed to test normality of the size class frequency distributions of *Cladocora caespitosa* and *Cystoseira s. l.* within populations. For raw data series, descriptive statistics were calculated: minimum, maximum, mean values, standard deviation, skewness and kurtosis according to Sokal & Rohlf (1995). Linear regression analysis were used to determine how *Cystoseira s. l.* densities varied with *Cladocora caespitosa* abundance, using 0.05 as significance level. Statistical analyses were performed using Systat 11.0 (SPSS Inc. 2004).

Results

The habitat of *Cladocora caespitosa* and *Cystoseira sensu lato* species

Cladocora caespitosa colonies thrive between 8 and 12 m depth in a continuous rocky platform, sheltered from the prevailing winds (mainly East) (Figure 7).

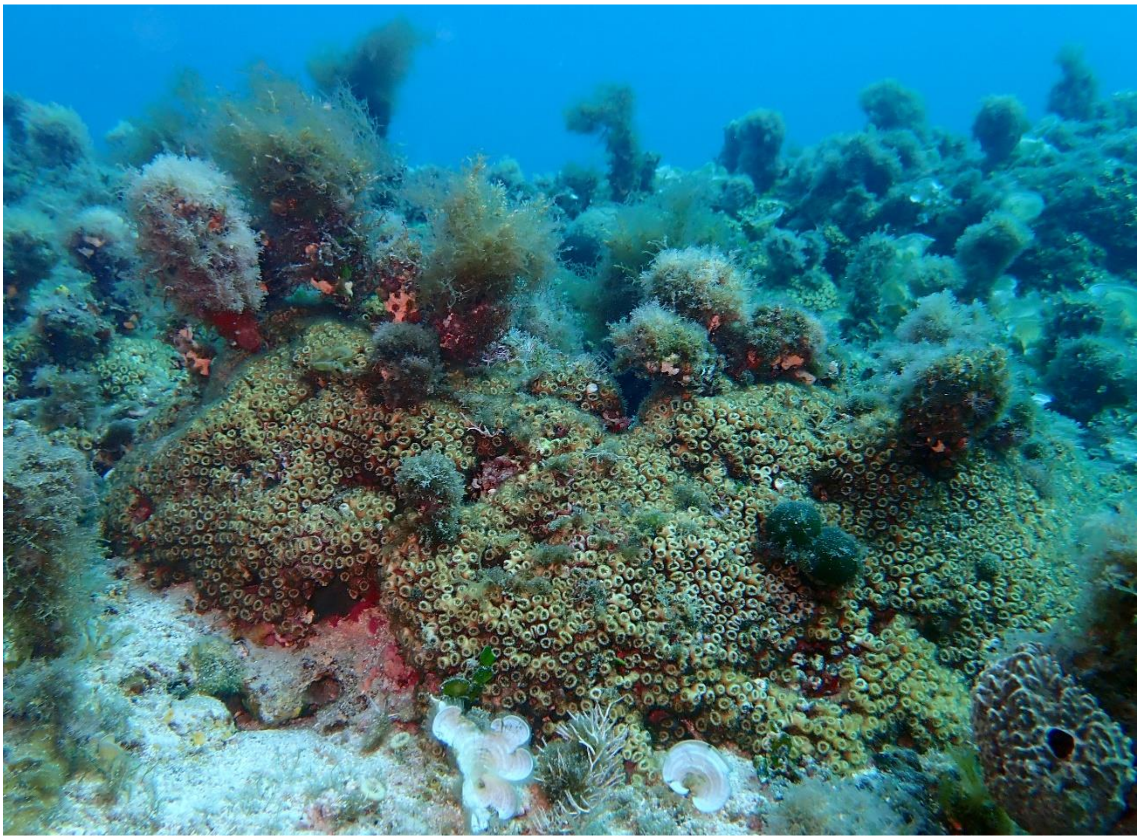

Figure 7: View of the habitat dominated by *Cladocora caespitosa* and *Cystoseira s. l.* species. Erect *Treptacantha ballesterosii* are settled around and on the surface of the *Cladocora caespitosa* colonies.

The coral colonies are living more or less tightly, forming a wide bed. *Cladocora caespitosa* covers 33.7±16.0 % (± SD, n=5) of the substrate and reaches the highest value of 40% in one transect. The size class frequency distribution of this population is unimodal but does not follow a normal distribution (K-S, d=0.77 $p<0.0001$) (Figure 8). The skewness of the distribution is significantly positive (g1= 1.841; Sokal & Rohlf 1995), which indicates the predominance of small classes in the population. The mean colony diameter is 15.7±15.4 cm (±SD), ranging from 2 to over 10 cm, with the maximum diameter of 146 cm. *Cystoseira s. l.* individuals are interspersed amongst and above the coral colonies, making a special seascape dominated by both *Cladocora* and *Cystoseira s. l.* (Figure 8; Video included in electronic annexes). The main seaweed species has been identified as *Treptacantha ballesterosii* -which stands for 90% of the individuals- while specimens identified as *Treptacantha elegans, Carpodesmia brachycarpa* and *Cystoseira compressa* show a much lower abundance (Figure 9). Mean density of *Treptacantha ballesterosii* is 206 individuals m^{-2}. The main axes of *Treptacantha* spp. are also supporting a considerable epiphytic flora mainly composed by turf-forming algae like *Haliptilon virgatum.*

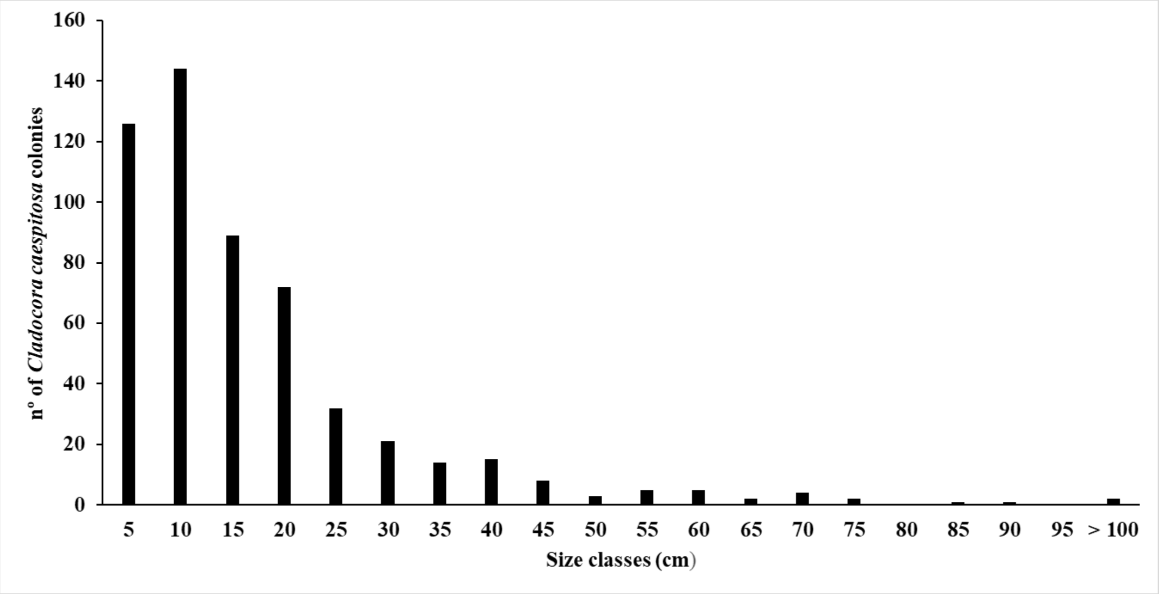

Figure 8: Size class frequency distribution of *Cladocora caespitosa* colonies, grouped in 5 cm intervals (n=546).

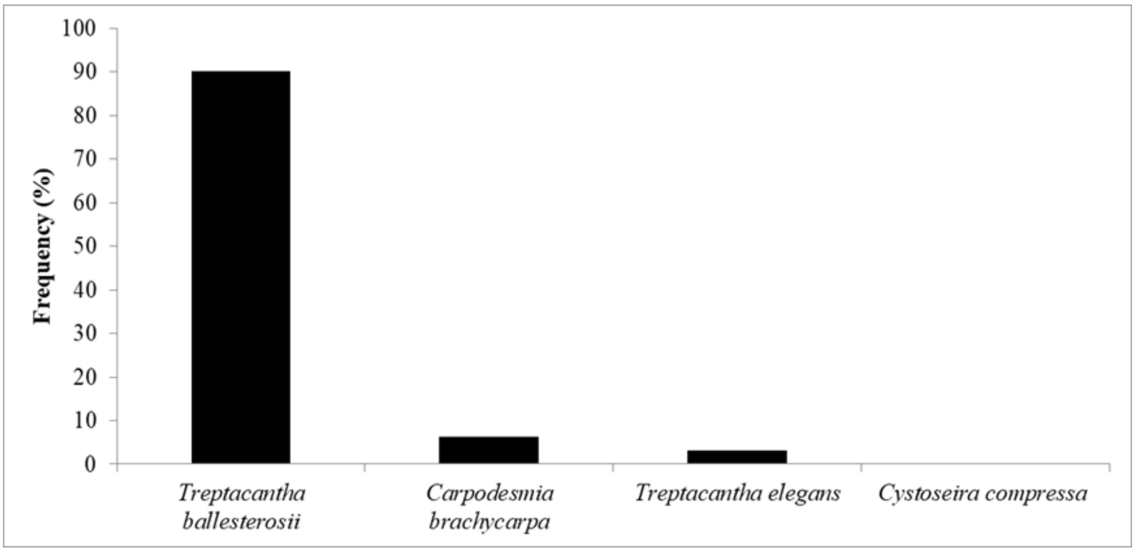

Figure 9: Density-frequency distributions of *Cystoseira s. l.* species in the mixed habitat with *Cladocora caespitosa* colonies (n=2885).

The size class frequency distribution of *Treptacantha ballesterosii* is unimodal but non-normal (K-S, d=0.5 p<0.0001), with a prevalence of small individuals (g1=1.376; Sokal & Rohlf 1995) (Figure 10). The mean length of the main axis is 4.7±3.8 cm (± 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. *Treptacantha elegans* population shows two peaks at 2 and 7 cm and does not follow either a normal distribution (K-S, d=0.84, p<0.0001) (Figure 11). The mean length of the main axis is 5.3±3.1 cm (± SD, n=92) with a maximum length of 14 cm.

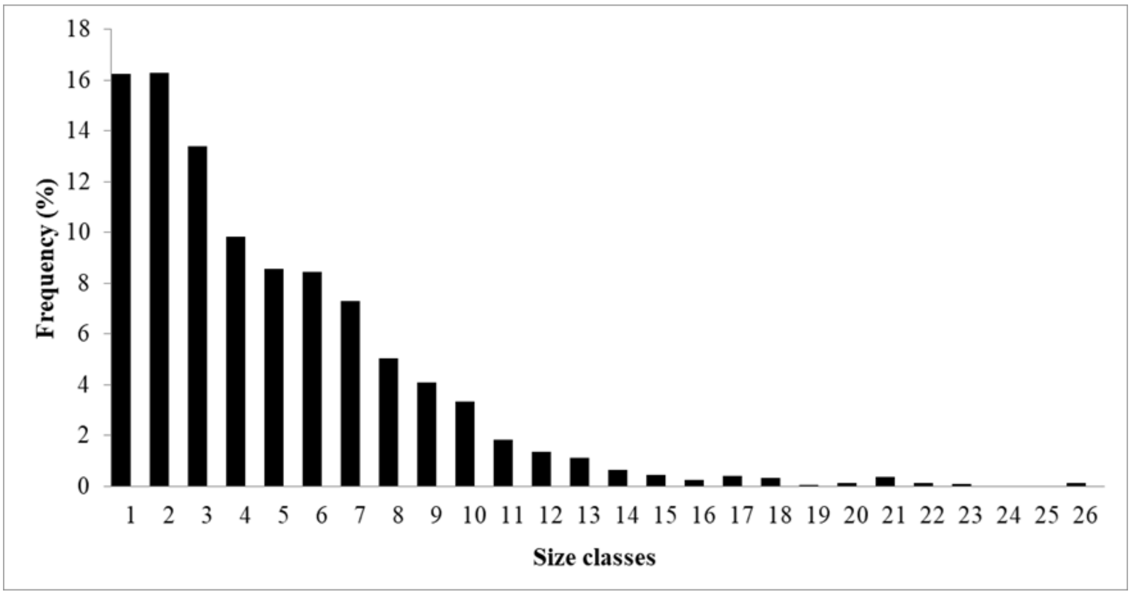

Figure 10: Size class frequency distribution of *Treptacantha ballesterosii* grouped in 1 cm intervals (n=2603).

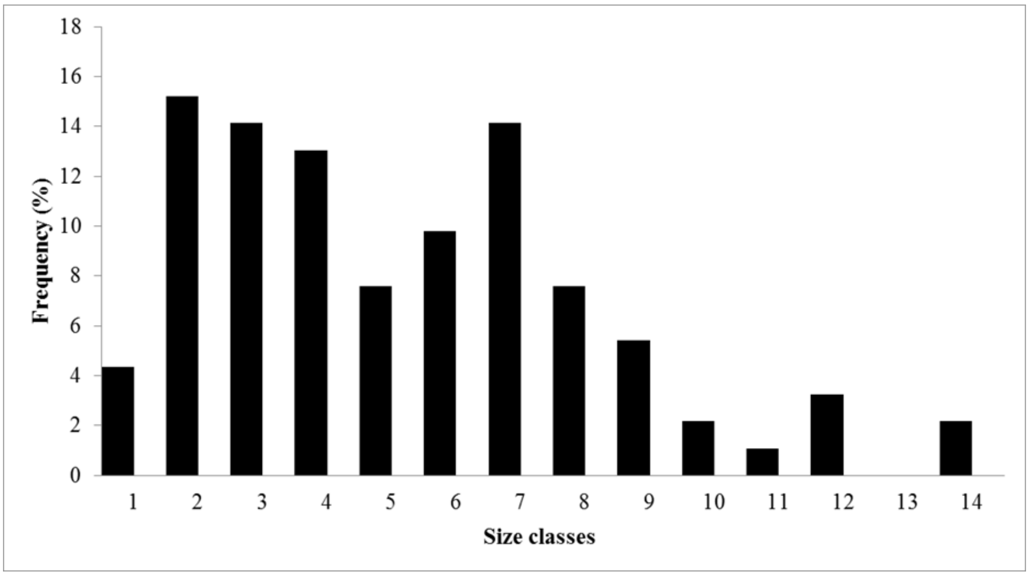

Figure 11: Size class frequency distribution of *Treptacantha elegans* grouped in 1 cm intervals (n=92).

Relationship between *Cystoseira sensu lato* densities and *Cladocora caespitosa* abundance

The two methodological approaches to estimate *Cladocora caespitosa* abundance (see Material and Methods section) give similar results (r=0.90, p<0.0001). Therefore, we have selected the approach (a) (number of subquadrats where *Cladocora caespitosa* is present) to estimate *Cladocora* abundance in the quadrats because the values obtained with this approach are more objective. *Treptacantha ballesterosii*, the most abundant species, shows a slight but very significant positive relationship with *Cladocora caespitosa* abundance (p=0.0005, n=202) (Figure 12A). In contrast, densities of *Carpodesmia brachycarpa* decline when *Cladocora caespistosa* abundance increases (p=0.02, n=65) (Figure 12C). No significant relationship is found between *Treptacantha elegans* densities and *Cladocora caespitosa* abundance (p=0.64, n=52) (Figure 12B).

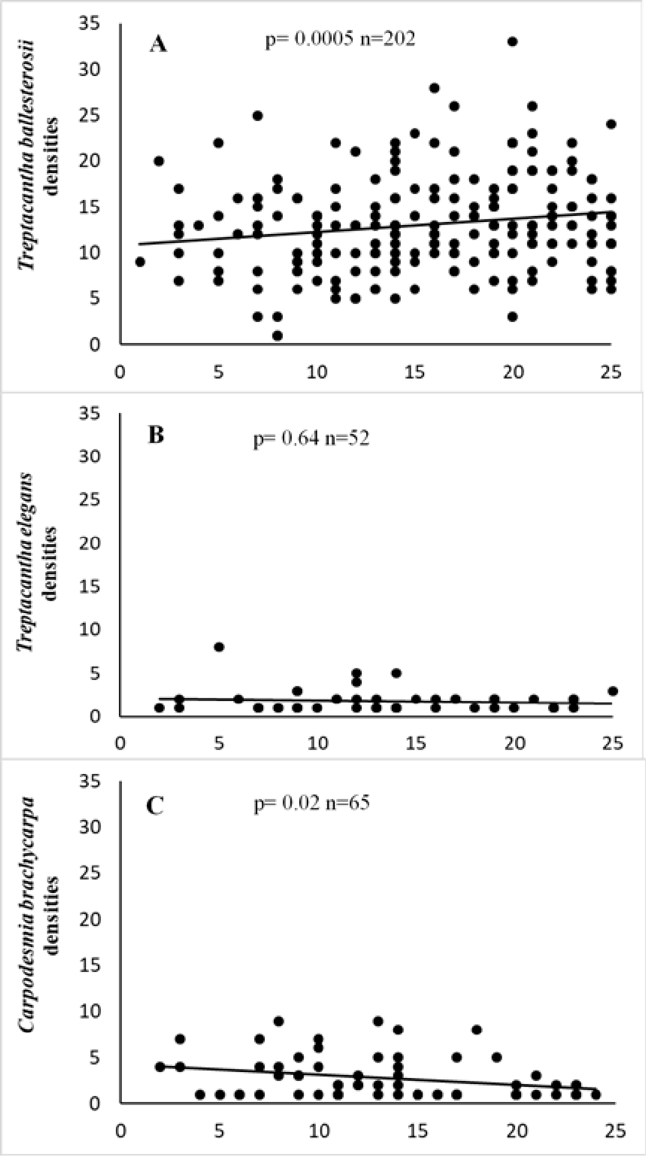

Figure 12: Relationship between the different species of *Cystoseira s. l.* densities and *Cladocora caespitosa* abundance: *Treptacantha ballesterosii* (A), *Treptacantha elegans* (B) and *Carpodesmia brachycarpa.* (C).

Discussion

We have identified and characterized a new Mediterranean habitat constituted by a mixture of *Cladocora caespitosa* colonies and *Cystoseira s. l.* (mainly *Treptacantha ballesterosii*) stands. This kind of habitat is not reported in the Spanish Marine Habitats List (Templado et al. 2012), which only lists two habitats with *Cladocora caespitosa* (i.e. 0301041408 "Infralittoral rock, moderately illuminated, without Fucales with *Cladocora caespitosa*", and 0301041607 "Infralittoral rock with low hydrodynamism, poorly lit dominated by invertebrates with *Cladocora caespitosa*") harbouring *Cladocora caespitosa*. Banks and/or beds of *Cladocora caespitosa* are known from several Mediterranean sites (reviewed by Casado-Amezúa et al. 2015) and have been poorly described in terms of cover, distribution and health status except those of Jiménez et al. (2016) and Kersting et al. (2017), which report a coexistence between *Cladocora* and *Cystoseira s. l.*. However, neither Jiménez et al. (2016) nor Kersting et al. (2017) make a particular description of the seaweed stands.

The population and individual sizes estimated in this study are very remarkable, for both the coral and the seaweeds. For the coral, in Es Banc, we estimated a total area of *Cladocora caespitosa* of 387.5 m^2, which is rather outstanding considering the 650 m^2 reported from Veliko Jezero lake (Mljet National Park) which hosts the best reef of *Cladocora* known to date (Kružic & Požar-Domac 2003). 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 Columbretes islands (Kersting & Linares 2012).

Mean colony diameter is also higher than other sites reported such as Bay of Piran, La Spezia and Espardelló islet (Schiller 1993; Peirano et al. 2001; Kersting et al. 2017). However, Columbretes has twice the mean colony size of Es Banc (31.48 cm average diameter) (Kersting & Linares 2012), which may be related to the highest depth, since water motion and other disturbances related to exceptional storms are minimized with depth (Schiller 1993). In fact, Es Banc and Columbretes show different types of spatial coral colony development. In Columbretes, coral colonies are big but their distribution is patchy, with big areas almost devoid or with very low density of colonies. In contrast, coral colonies in Es Banc form a wide irregular carpet that covers the rocky bottom. Es Banc holds some very big colonies (>100 cm diameter), similar to Columbretes (Kersting & Linares 2012) but these are present in reduced numbers. Large *Cladocora caespitosa* colonies are almost absent in Piran and La Spezia (Schiller 1993; Peirano et al. 1998, 2001). Small colonies are very abundant, in agreement with other localities (Schiller 1993; Peirano et al. 1998, 2001; Metalpa et al. 2005; Kersting & Linares 2012; Kersting et al. 2017).

The population of *Treptacantha ballesterosii* from Es Banc is also outstanding. Mean density reaches 206 individuals m^{-2}, which is very high when compared to densities reported from Scandola Marine Reserve (Parc Naturel Régional de Corse, France), where *Treptacantha ballesterosii* (as *Cystoseira spinosa* var. *compressa*) shows densities of 28 individuals m^{-2} at 26-29 m depth decreasing to 3 plants 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 length of 7 to 16 cm have been reported (Ballesteros et al. 1998; Hereu et al. 2009). The shape of the size class length distribution of *T. ballesterosii* populations in Es Banc is close to a negative exponential function, which has been associated with populations at equilibrium (Lorimer 1980, 1985; Edmond et al. 1992; Berg & 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 *Treptacantha ballesterosii* 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 has to be related either to unpredictable episodes of recruitment or to the dense canopy of large plants that should inhibit the recruitment of new individuals.

In Es Banc, the shape distribution of size classes in *Treptacantha elegans* population showing two peaks might indicate uneven recruitment events depending on the year, which has been already reported in *Cystoseira s. l.* populations (e.g. Ballesteros et al. 1998; Hereu et al. 2009; Ballesteros et al. 2009) and other fucoids (e.g. Deysher & Norton 1982; Dayton et al. 1984; Fernández et al. 1990).

An important result of this study is the discovery of a positive relationship between *Cladocora caespitosa* cover and density of *Treptacantha ballesterosii*, which challenges the predicted competition for space between corals and macroalgae (McCook et al. 2001). This contrasts with reports of growth limitation of *Cladocora* by soft algae (Peirano et al. 1998) or the competition between *Cladocora* and macroalgae (*Codium*) found in other localities (Kružić & Benković 2008; Kersting & Linares 2012). In fact, the positive interaction between *Cladocora* and *Treptacantha ballesterosii* points to a possible facilitation mechanism. We suggest the hypothesis that the recruitment or survival of *Treptacantha ballesterosii* might be enhanced by the presence of *Cladocora caespitosa* but the coral does not appear to be affected by the algae recruitment to this level. Indeed, many *T. ballesterosii* individuals are completely surrounded by or placed above living *Cladocora caespitosa* colonies, suggesting a recruitment facilitation. *Treptacantha elegans* shows a neutral relationship while the relationship with *Carpodesmia balearica* 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 several endemic canopy-forming algae. Both the coral and the macroalgae show large cover and abundance, challenging the theory of competitive exclusion between these two functional groups (photosyntethic organisms versus photo-suspension feeders) in the marine benthos. Moreover, this habitat being 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.

Chapter II

Introduction

Members of the order Fucales rank amongst the main canopy-forming species of marine macroalgae in temperate regions (Schiel & Foster 1986; Graham & Wilcox 2000). Communities dominated by *Carpodesmia* spp., *Treptacantha* spp. and *Cystoseira* spp. (=*Cystoseira sensu lato*, =*Cystoseira s. l.*) characterize Mediterranean infralittoral hard bottoms from unspoiled locations (Feldmann 1937; Giaccone 1973; Rodríguez-Prieto et al. 2013). Although zooxanthellate, reef-building corals do not thrive in the Mediterranean due to the high seasonal variability in environmental factors (e.g. light, nutrients, temperature) (Zabala & Ballesteros 1989), colonies of the coral *Cladocora caespitosa*, can create habitat in particular environments (Chintiroglou 1996; Koukouras et al. 1998; Pittaco et al. 2014). *Cladocora caespitosa* seems to be adapted to the Mediterranean seasonality by combining autotrophic and heterotrophic strategies (Hoogenboom et al. 2010; Ferrier-Pagés et al. 2011), deriving a large fraction of their energy from heterotrophic feeding in the winter.

While species of *Cystoseira s. l.* are usually dominant in the seascape of shallow water unspoiled Mediterranean environments, *Cladocora caespitosa* usually appears as a few colonies interspersed amongst macroalgal stands, coralligenous or detritic bottoms (Peirano et al. 1998; Gerovasileiou et al. 2009; Pittaco et al. 2014). This was not the case in other periods of time, when large *Cladocora caespitosa* beds and banks covered large extensions of sea bottom (Kühlmann 1996; Peirano et al. 1998; Aguirre & Jiménez 1998). However, there still are a few exceptional sites where high densities of these coral colonies can still be found, like those at Veliko Jezero Lake in Mjlet (Kružić & Benković 2008), the bay of Piran (Schiller 1993), Illa Grossa in Columbretes islands (Kersting & Linares 2012) and s'Espardelló in the Balearic Islands (Kersting et al. 2017).

Both reef-building corals and canopy-forming macroalgae are habitat formers, corals being dominant in tropical seas and macroalgae in temperate seas (Zabala & Ballesteros 1989). Although macroalgae can replace corals in tropical environments due to eutrophication and reduced herbivory caused by overfishing and sea urchin die-offs

(Lessios 1988; Hughes 1994; Lapointe 1997; Szmant 2002; Sandin et al. 2008; Bruno et al. 2009), they are usually spatially segregated in unspoiled locations (i.e. Vergés et al. 2016). Thus, a spatial segregation between *Cladocora* and Mediterranean canopy-forming algae would be expected, as both compete for space. In fact, the recent expansion of the zooxanthellate coral *Oculina patagonica* 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, the recent discovery of a mixed *Cladocora-Cystoseira s. l.* bed in Es Banc (Formentera) (Chapter I) calls into question the universality of the competitive exclusion between corals and macroalgae. In Es Banc, we have shown that neutral and even positive relationships between *Cladocora caespitosa* cover and *Cystoseira s. l.* density exist (see Chapter I). The positive relationship between *Treptacantha ballesterosii* density and *Cladocora* cover suggests that, in some way, *Cladocora caespitosa* facilitates the recruitment and/or persistence of individuals of *Treptacantha ballesterosii* (see Chapter I). Since this feature was totally unexpected, here we want to explore the consistency of the results found in Chapter I by looking for the kind of relationship existing between *Cladocora* cover and *Cystoseira s. l.* densities in other Mediterranean sites where they appear together. Therefore, we aim at using empirical distribution data to assess the hypothesis that there is no competitive exclusion between *Cladocora caespitosa* cover and the density of different species of *Cystoseira s. l.* that can coexist with *Cladocora*. This study also contributes to a growing body of knowledge on the competitive interactions between corals and canopy-forming macroalgae.

Material & Methods

Study sites

Sampling was performed in July 2019 at three sites: Es Banc (38°43'19.2’’N 1°23'09.2’’E), located in the western part of Formentera (Balearic Islands), S’Espardelló (38º47’14.2”N, 1º28’59.7”E), an islet placed on the northeast side of Formentera, and Columbretes islands (39º53.825’N, 0º41.214’E) which are a set of four groups of volcanic islands located 56 km off the Spanish coast, in the northwestern of Mediterranean (Figure 13). S’Espardelló and Columbretes are no-take zones or fully protected marine areas

(MPAs) and Es Banc is included in a MPA where artisanal fishing is allowed. The three sites harbor *Cladocora caespitosa* colonies together with relatively high densities of fucoid algae (*Cystoseira s. l.*) (Kersting & Linares 2012 in Columbretes; Kersting et al., 2017 in S'Espardelló; present work in Es Banc).

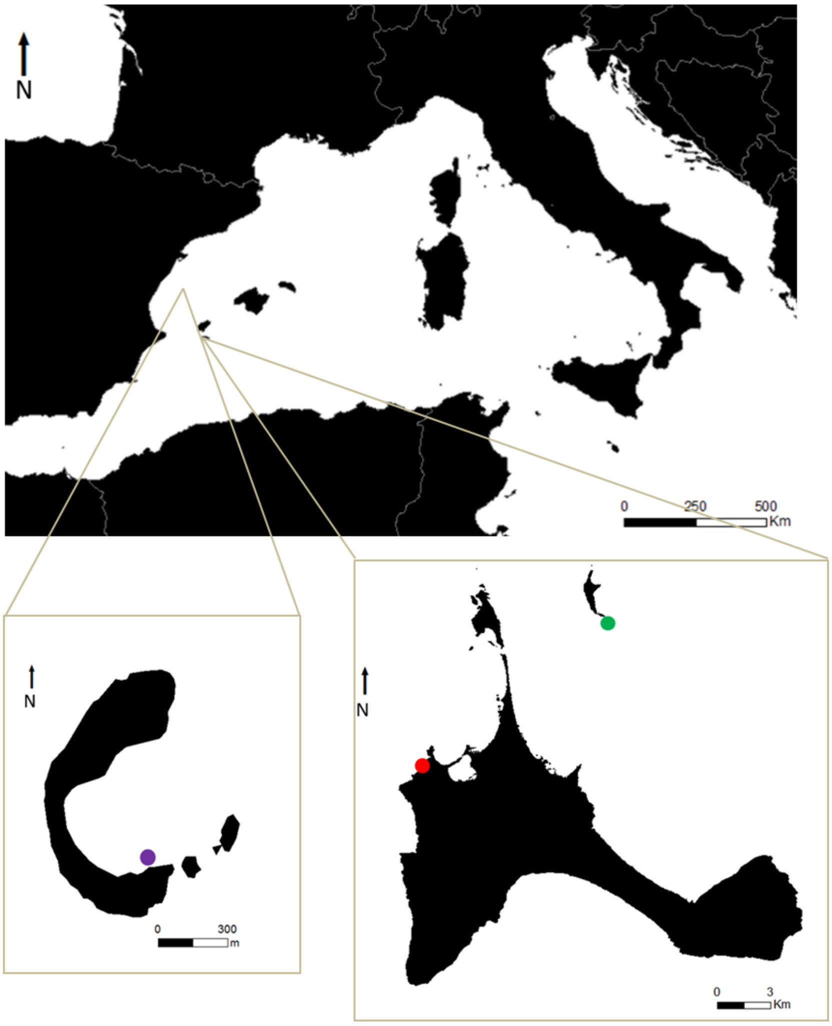

Figure 13: Sampling sites at Columbretes (purple dot), S'Espardelló (green dot) and Es Banc (red dot).

Sampling methods

The methodology explained in chapter I is the same for all the sites (Chapter I, Material and Methods). In summary, *Cystoseira s. l.* densities were estimated fusing 625 cm^2 quadrats divided into 25 (5 cm x 5 cm) subquadrats (Figure 5). *Cystoseira s. l.* were identified morphologically. The size of individuals was measured using a ruler, the length of the primary axis (Ballesteros et al. 1998, 2009), for *Treptacantha* species. On the contrary, species of *Carpodesmia* and *Cystoseira* (except *C. zosteroides*) do not have a prominent main axis but several branches arising from a basal disc (holdfast). Thus, these were just counted as number of basal discs. *Cladocora caespitosa* abundance was quantified at the same quadrats using two different strategies: (a) number of subquadrats where *Cladocora caespitosa* was present; and (b) visual estimation of *Cladocora caespitosa* cover (Figure 6).

Data analysis

Kolmogorov-Smirnov tests were performed to test normality of the size class frequency distributions of coral and seaweed populations. Descriptive statistics were calculated as: minimum, maximum, mean, standard deviation, skewness and kurtosis (Sokal & Rohlf 1995). Linear regression analyses were used to determine the relationship between seaweed and coral abundances (0.05 significance level). Student's t-test were used to compare mean *Cystoseira s. l.* densities in sites with and without *Cladocora caespitosa* colonies (0.05 significance level) in order to reconfirm the type of relationship. Statistical analyses were performed using Systat 11.0 (SPSS Inc. 2004).

Results

Comparisons of *Cladocora caespitosa* cover and *Cystoseira sensu lato* diversity from the three sites

Es Banc site description has been already performed in Chapter I, Results. The cover of *Cladocora caespitosa* colonies reaches ≈ 34% in average (Chapter I, Results). S’Espardelló islet sea bottom at 6-13 m depth has a moderate rugosity and *Cladocora caespitosa* colonies are more fragmented due to a moderate to high water motion. Indeed, a higher occurrence of free-living coral nodules or coralliths is present (as noted by Kersting et al. 2017) and the cover of *Cladocora caespitosa* colonies is ≈ 20% in average (Kersting et al. 2017). On Columbretes islands the sea bottom presents the highest roughness, and *Cladocora caespitosa* colonies, which attain ≈ 7% in coverage, are found spread on the rock crests and blocks between 15 and 18 m depth (Kersting & Linares 2012). All the sites show a different *Cystoseira s. l.* species composition although *Cystoseira compressa* and *Carpodesmia brachycarpa* are found in the three sites (Table 1). Columbretes hosts the highest diversity with six species and S'Espardelló the lowest with three species; the sciaphilous green alga *Halimeda tuna* is also regularly found around or growing on the surface of *Cladocora caespitosa* colonies (Figure 14).

Table 1: *Cystoseira s. l.* species composition from the three sampled sites.

Cystoseira sensu lato	**Es Banc**	**S'Espardelló**	**Columbretes**
Treptacantha ballesterosii	+	+	
Treptacantha elegans	+		
Treptacantha sauvageauana			+
Treptacantha ballesterosii var. *compressa*			+
Carpodesmia brachycarpa	+	+	+
Carpodesmia zosteroides			+
Cystoseira compressa	+	+	+
Cystoseira foeniculacea var. *latiramosa*			+

Figure 14: High abundance of *Halimeda tuna* within a huge *Cladocora caespitosa* colony, in Columbretes.

Cystoseira sensu lato populations from the three sites

Data from Es Banc has already been reported and will not be presented here again (see Results of Chapter I). In S'Espardelló, the most common species is *Treptacantha ballesterosii,* which accounts for the 72% of all the specimens of *Cystoseira s. l.* found, followed by *Cystoseira compressa* with 18% and *Carpodesmia brachycarpa* with less than 10% (Figure 15). The size frequency distribution of *Treptacantha ballesterosii* population is unimodal and no normal (the values are right skewed; K-S, d=0.694 p<0.0001) (Figure 16). Almost 50% of the total population measures from 0.5 to 3 cm of the length of the main axis. The mean length of the main axis is 4.1±2.4 cm (±SD, n=1502) with a maximum length of 14 cm.

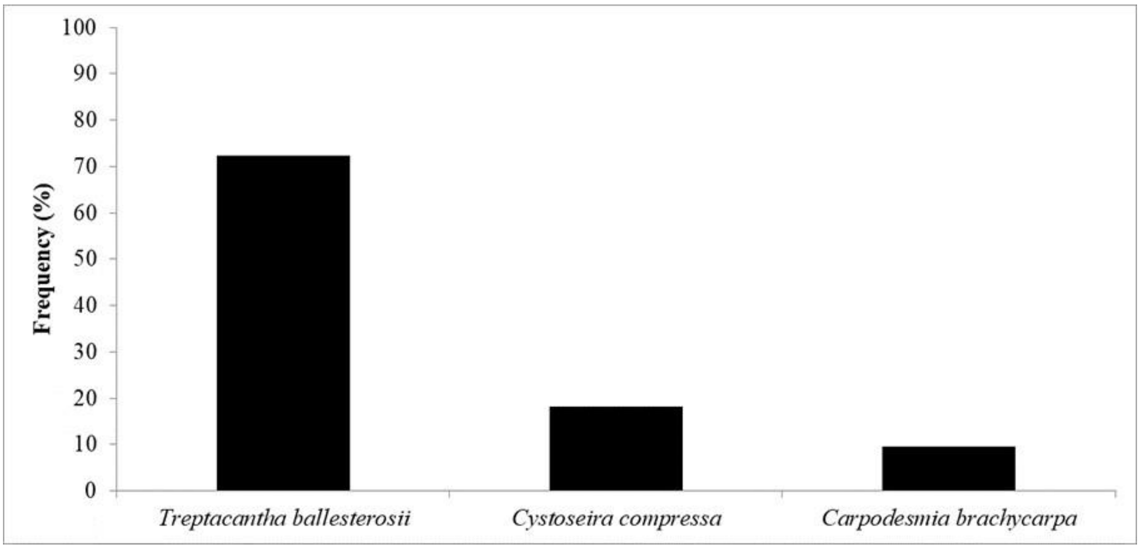

Figure 15: Density-frequency distributions of *Cystoseira s. l.* species in the mixed habitat with *Cladocora caespitosa* colonies (n=2078) in S'Espardelló.

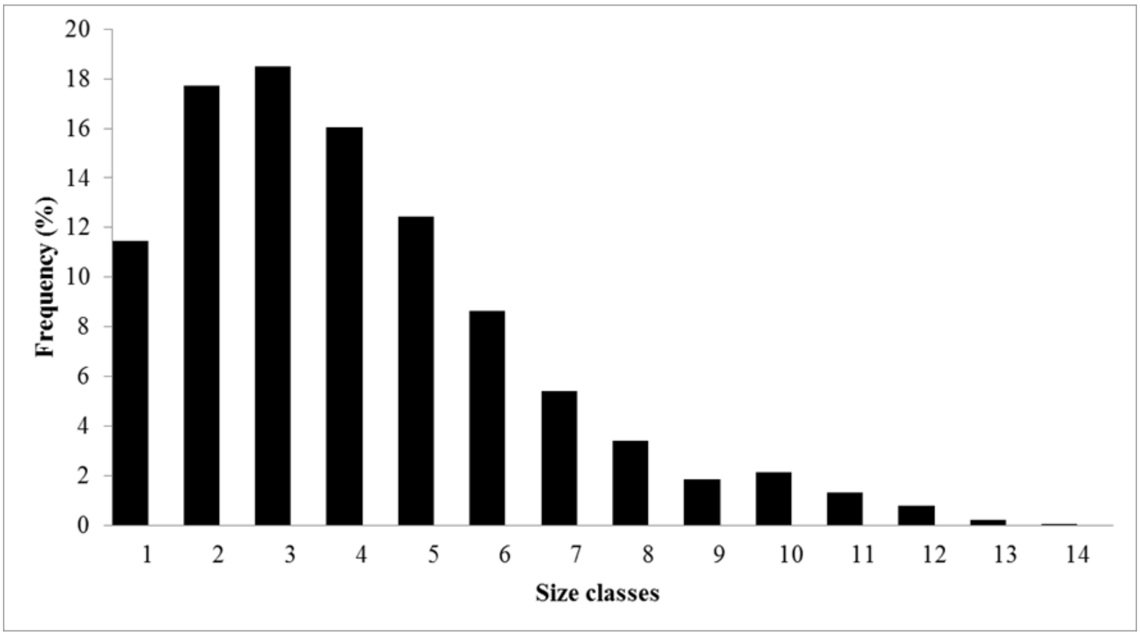

Figure 16: Size class-frequency distribution of *Treptacantha ballesterosii*, grouped in 1 cm intervals in S'Espardelló (n=1502).

In Columbretes, *Treptacantha sauvageauana* and *Cystoseira compressa* are the most frequent species (38% abundance each one) (Figure 17) while *Treptacantha ballesterosii* var. *compressa* is present in 19% of the quadrats. *Carpodesmia brachycarpa*, *Carpodesmia zosteroides* and *Cystoseira foeniculacea* var. *latiramosa* only represent a

5% of the total population. *Treptacantha sauvageauana* population exhibits a non-normal distribution (K-S, d=0.519 p<0.0001) peaking within the size classes between 3 and 10 cm, and showing a continuous decline for larger specimens (Figure 18). The mean length of the main axis is 7±3.3 cm (± SD, n=356) with the maximum length of 23 cm. The population of *Treptacantha ballesterosii* var. *compressa* shows a non-normal distribution (K-S, d=0.670, p<0.0001) with a peak within the size classes situated between 3 and 5 cm (Figure 19). The mean length of the main axis is 4.8±2.4 cm (± SD, n=176) with the maximum length being 14 cm.

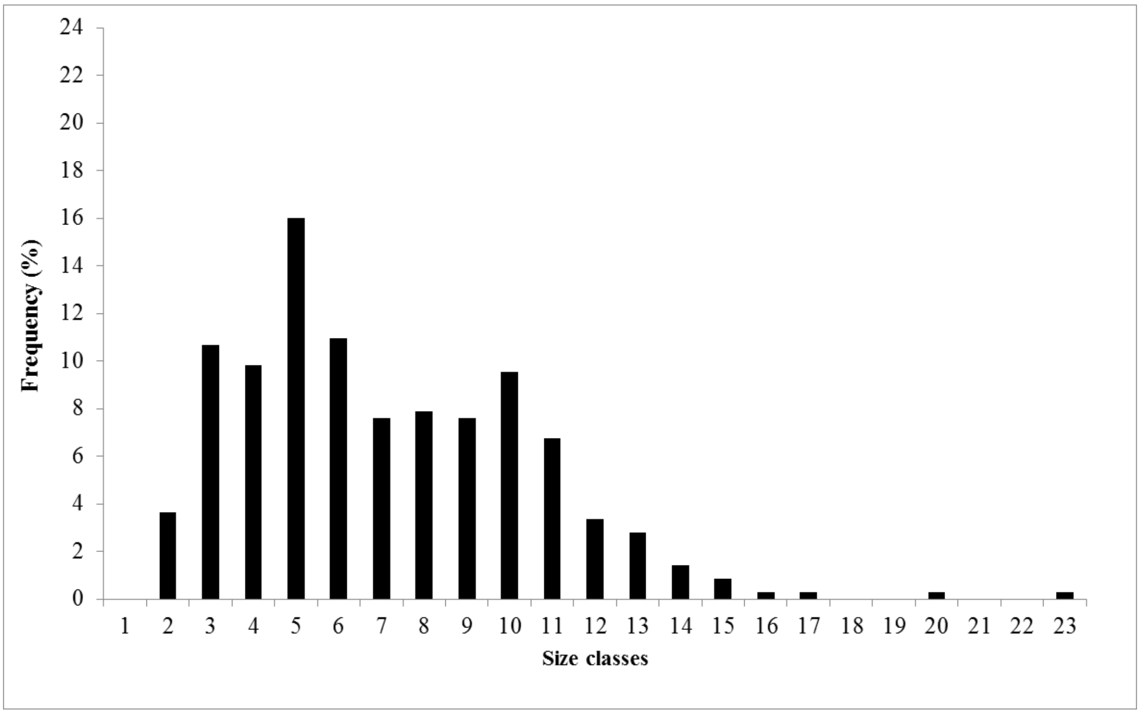

Figure 18: Size class-frequency distribution of *Treptacantha sauvageauana*, grouped in 1 cm intervals, in Columbretes (n=356).

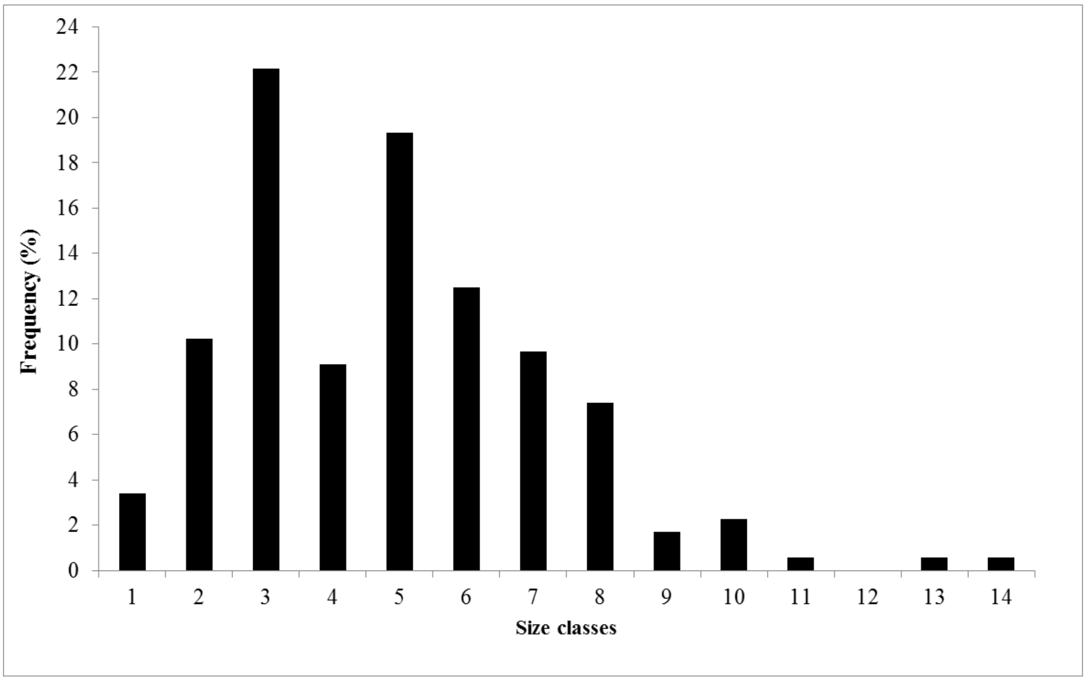

Figure 19: Size class-frequency distribution of *Treptacantha ballesterosii* var. *compressa*, grouped in 1 cm intervals, in Columbretes (n=176).

Relationship between *Cystoseira sensu lato* densities and *Cladocora caespitosa* abundance

In Es Banc, *Treptacantha ballesterosii* densities are higher when *Cladocora caespitosa* abundance increases (p=0.0005, n=202) while *Carpodesmia brachycarpa* densities decrease at high abundances of *Cladocora caespitosa* **(**p=0.02, n=65). *Treptacantha elegans* densities do not show any trend (Results table of the regression analysis in ANNEX). The corresponding linear regressions between the different *Cystoseira s. l.* densities and *Cladocora caespitosa* abundance in Es Banc have been already presented (see Results in Chapter I, p.21 and in Figure 20).

In S'Espardelló, *Treptacantha ballesterosii* and *Carpodesmia brachycarpa* densities do not show any trend (p=0.14 and p=0.09) (Results table of the regression analysis in ANNEX). On the contrary, *Cystoseira compressa* densities are statistically higher when *Cladocora caespitosa* abundance increases (p=0.02, n=97). The corresponding linear regressions between the different *Cystoseira s. l.* densities and *Cladocora caespitosa* abundance are shown in Figure 20.

In Columbretes, *Treptacantha sauvageauana* densities are statistically lower at increasing abundances of *Cladocora caespitosa* (p=0.0001, n=159). *Cystoseira compressa* and

Treptacantha ballesterosii var. *compressa* do not show any significant trend (p=0.62 and p=0.83) (Results table of the regression analysis in ANNEX). The corresponding linear regressions between the different *Cystoseira s. l.* densities and *Cladocora caespitosa* abundance are shown in Figures 20. Only a few individuals of *Carpodesmia brachycarpa*, *Carpodesmia zosteroides* and *Cystoseira foeniculacea* were sampled (n=21, n=6 and n=8, respectively) and therefore, we have not made any analysis with this data. The comparisons of *Cystoseira s. l.* densities in sites with and without *Cladocora caespitosa* colonies agree with the results of the linear regression, except for *Treptacantha ballesterosii* which, in Espardelló, shows significant higher densities in sites where *Cladocora caespitosa* colonies are present. The sample sizes, means and variances are presented in the Results table of the t- test analysis in ANNEX. *Carpodesmia brachycarpa, Carpodesmia zosteroides* and *Cystoseira foeniculacea* were not analyzed due to the small densities found for these species.

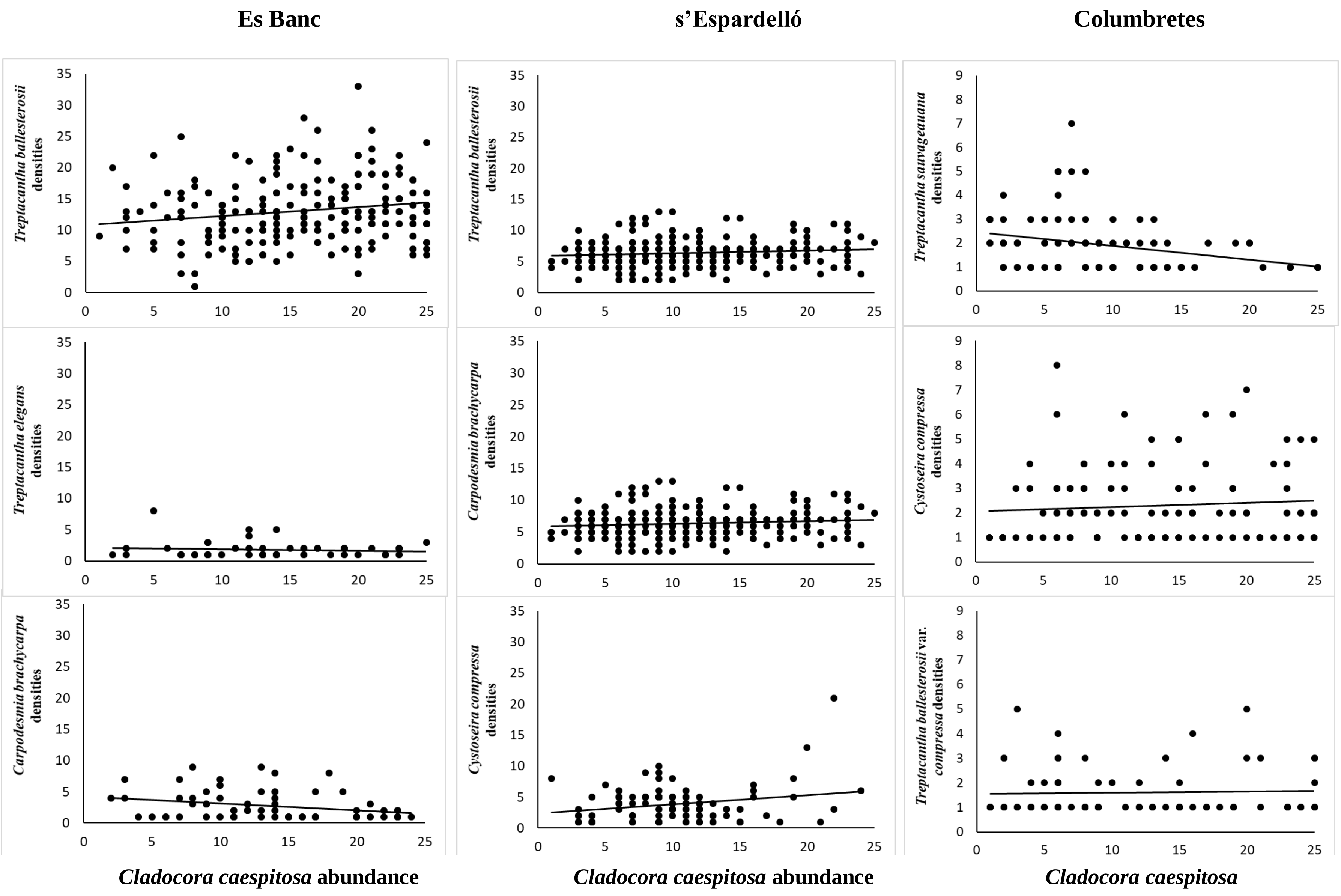

Figure 20: Relationships between the different species of *Cystoseira s. l.* and *Cladocora caespitosa* at the three sites.

Discussion

Competition between corals and benthic algae is recurrent on tropical to subtropical reefs worldwide (e.g. Zabala & Ballesteros 1989; Miller 1998; McCook et al. 2001) because they are both light- and space-dependent. Corals and algae use different physical (e.g. sweeper tentacles, overtopping, abrasion) and chemical (allelopathy) mechanisms to compete for space and suitable light levels. It is known that the competitive effects of algae on corals largely depend on the morphology of involved algae –filamentous, turf, fleshy or encrusting-. Turf and fleshy macroalgae have several detrimental effects on corals causing hypoxia on the neighboring coral tissue as well as severe damage, such as bleaching and necrosis (Hughes 1994; Tanner et al. 1995; Titlyanov et al. 2007; Barott et al. 2009, 2012). Coral overgrowth by turf algal mats or canopy-forming algae can also inhibit coral recruitment, growth of recruits and adults, as well as 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 of coral growth by algal overgrowth is also the result of the reduced photosynthetic efficiency of zooxanthellae (Lirman 2001; Vermeij et al. 2010). In addition, many macroalgae produce allelochemical compounds that can also lead to reduce the coral fitness (e.g. Titayanov et al. 2007; Rasher & Hay 2010, Rasher et al. 2011). Indirectly, the exudation/release of these secondary metabolites and dissolved organic compounds (DOC) from the macroalgae can increase the abundance of potentially pathogenic bacteria and thereby, alter the microbial communities associated with corals (e.g. Smith et al., 2006; Dinsdale et al. 2008; Barott et al., 2011). For instance, Nugues et al. (2004) showed that the fleshy macroalga *Halimeda opuntia* can carry virulent bacteria (White plague type II) which is able to cause extensive mortality on most Caribbean coral species. In contrast, crustose coralline algae (CCA) are less harmful to corals than turf and fleshy macroalgae (Barott et al. 2009, 2012; Vermeij et al. 2010). CCA can even be advantageous for corals by providing available substrate for coral recruits, settlement cues (Morse et al. 1988; Negri et al. 2001; Price 2010; Vermeij et al. 2011) and increasing benign microbial communities (Barott & Rohwer 2012).

Despite most evidence pointing to negative effects of algae on corals, coral and algal interactions are not one-sided, since some studies have reported inhibition of algal growth by corals or even overgrowth of algae by corals (McCook 2001, Jompa & McCook 2002). Regarding coral-algae competition, the most frequently studied type of algae is fleshy macroalgae (Chadwick & Morrow 2011) since they show a wide range of unflavored effects on corals (e.g. Smith et al. 2006), which sometimes corals can cope with. For instance, Jompa & McCook (2002) and Titlyanov et al. (2007) reported that despite the potential ability of large canopies of macroalgae (e.g. *Lobophora* spp. and *Dictyota* spp.) cause coral tissue mortality, scleractinian corals *Porites* spp. are able to inhibit algal overgrowth and, thus, competitive inhibition is mutual (Jompa & McCook 2002; Titlyanov et al. 2007).

Our results do not agree with the overall negative outcomes of fleshy macroalgae on scleractinian corals since *Cystoseira s. l.* species mainly showed neutral or positive relationships with *Cladocora caespitosa* (Table 2).

Table 2: Summary of the calculated probability or p-values from the simple linear regression (a) and t-tests (b). Positive regressions are written in italics, negative regressions in bold and non-significant interactions without any font. The (+) means that there were not enough samples outside of the target site (without *Cladocora caespitosa*) to perform the t-test.

(a) Relationship between *Cystoseira s. l.* densities and *Cladocora caespitosa* abundance.

	Es Banc	**Espardelló**	**Columbretes**
Treptacantha ballesterosii	*0.0005*	0.14	
Treptacantha elegans	0.64		
Carpodesmia brachycarpa	**0.02**	0.09	0.29
Cystoseira compressa		*0.02*	0.62
Treptacantha sauvageuana			**0.0001**
Treptacantha ballesterosii* var. *compressa			0.83

(b) Comparison between *Cystoseira s. l.* densities with/without *Cladocora caespitosa* abundance.

	Es Banc	**Espardelló**	**Columbretes**
Treptacantha ballesterosii	*0.0001*	*0.0001*	
Treptacantha elegans	0.10		
Carpodesmia brachycarpa	**0.0002**	0.56	
Cystoseira compressa		+	0.8
Treptacantha sauvageuana			**0.0004**
Treptacantha ballesterosii* var. *compressa			1

There are no studies on the competition between corals and *Cystoseira s. l.* macroalgae, but it is known that these macroalgae produce allelopathic compounds (mainly terpenoids) that act as chemical defense mechanisms used against herbivory (Amico 1995; Vergés et al. 2009) bacteria and fungi (Gouveia et al. 2013). However, these alellochemicals seem no to be affecting the interaction between *Cladocora caespitosa* and most *Cystoseira s. l.* species. In turn, Kersting et al. (2014a) found that *Cladocora caespitosa* has allelochemical mechanisms to avoid overgrowth by macroalgae but again this seems not to be playing here any effect. Indeed, some studies reported that the type of interaction is species specific (Nugues & Bak 2006; Titlyanov et al. 2007; Barott et al. 2011; Bonaldo & Hay 2014) and therefore, the interactions among *Cystoseira* and *Cladocora caespitosa* even though they are uncommon can be feasible under still uncharted mechanisms. Brown macroalgae of the genus *Sargassum*, belonging also to the order Fucales, may have also minor or no competitive effects on understory corals and even the shading effect by the algal canopies apparently is beneficial by mitigating the radiation exposure and the high temperatures (Jompa & McCook 1998; McCook 1999). We also found that the relationship between *Cladocora caespitosa* and *Cystoseira* spp. (*s. l.*) is site-specific (Table 2), in agreement with results by Brown et al. (2018).

Cladocora caespitosa shows a fast recovery after being exposed to damage on coral tissues and skeletons in an experimental aquarium (Casado et al. 2015), which may be very advantageous when competing with *Cystoseira s. l.* and other colonizing algae. A rapid recovery capacity from disturbances (e.g. storms, bleaching events, algal blooms) have been observed in other scleractinian corals (e.g. *Acropora* spp.) (Diaz-Pulido et al. 2009; Johns et al. 2014).

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 into the Mediterranean Sea (Oliveras Plá & Gómez Garreta 1989). *Cladocora caespitosa* also originated after the Messinian salinity crisis (Aguirre & Jiménez 1998). Thus, both *Cystoseira s. l.* and *Cladocora caespitosa* have been into close contact since long time ago and have been competing between them and other shallow benthic organisms like other algae and sessile invertebrates for the limiting resources (e.g. light and space). We contend that the close and lasting relationships that were formed by *Cystoseira s. l.* species and the coral *Cladocora caespitosa* include a variety of positive, negative and neutral effects that are species and site-specific. In fact, they live in the same habitats, and must have overlapping ecological roles and requirements to survive, grow and reproduce, which has probably fostered adaptations or mechanisms in order to allow their coexistence.

In summary, we have demonstrated that coral *Cladocora caespitosa* and perennial canopy-forming macroalgae (*Cystoseira sensu lato*) are able to coexist in Mediterranean shallow assemblages. The relationship between corals and macroalgae is species and site-specific, and although most of the species show neutral effects, in some of them (*Treptacantha ballesterosii*) it seems to be a facilitation effect of the coral on the macroalgae. Although the mechanisms that allow coexistence are far to be understood, description of these kind of relationships is an excellent starting point for future studies addressing competition and facilitation mechanisms between these Mediterranean endemic and highly vulnerable habitat-forming species.

Concluding remarks

The photosynthetic hermatypic coral *Cladocora caespitosa* and the perennial erect seaweeds *Cystoseira s. l.* in Es Banc coexist in mixed and conspicous coral-algal assemblages, with an average coral cover of 34% and densities of 206 individuals m^{-2} for the most abundant species (*Treptacantha ballesterosii*). Furthermore, there is evidence of a positive relationship between *Cladocora caespitosa* abundance and *Treptacantha ballesterosii* densities

At a regional level, the interactions among *Cladocora caespitosa* abundance and the densities of *Cystoseira s. l.* are species- and site-specific. Globally, most of the relationships between the abundance or presence of *Cladocora caespitosa* and the densities of *Cystoseira s. l.* species are neutral or positive. Therefore, these results highlight there is no always competitive exclusion between these dominant long-lived benthic organisms even when high abundances and lasting interactions are ongoing.

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Annexes

Outcomes of the Regression analysis

Site: Es Banc

	n	r	R^2	p-value
Treptacantha ballesterosii	202	0.24	0.06	**0.0005**
Carpodesmia brachycarpa	65	-0.29	0.08	**0.02**
Treptacantha elegans	52	-0.07	0.004	0.64

Site: S'Espardelló

	n	r	R^2	p-value
Treptacantha ballesterosii	232	0.1	0.01	0.14
Carpodesmia brachycarpa	90	-0.18	0.03	0.09
Cystoseira compressa	97	0.23	0.05	**0.02**

Site: Columbretes

	n	r	R^2	p-value
Treptacantha sauvageauana	159	-0.35	0.12	**0.0001**
Cystoseira compressa	154	0.04	0.002	0.62
Treptacantha ballesterosii var. ***compressa***	110	0.02	0	0.83
Carpodesmia brachycarpa	21	-0.24	0.06	0.29

Outcomes of the T test analysis

Site: Es Banc

Species: *Treptacantha ballesterosii*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	198	82
x̄	13.1	7.4
s^2	30.5	15.6

Monte Carlo permutation: p (same mean): **0.0001**

Species: *Carpodesmia brachycarpa*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	64	72
x̄	2.8	4.5
s^2	5.2	6.1

Monte Carlo permutation: p (same mean): **0.0002**

Species: *Treptacantha elegans*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	51	70
x̄	3.2	3.4
s^2	3.7	5.4

Monte Carlo permutation: p (same mean): **0.10**

Site: S’Espardelló

Species: *Treptacantha ballesterosii*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	233	99
x̄	6.4	4.0
s^2	4.6	2.8

Monte Carlo permutation: p (same mean): **0.0001**

Species: *Carpodesmia brachycarpa*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	90	44
x̄	2.2	2.0
s^2	0.6	1.2

Monte Carlo permutation: p (same mean): 0.56

Species: *Cystoseira compressa*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	97	2
x̄	3.9	-
s^2	8.6	-

Monte Carlo permutation: p (same mean): **-**

Site: Columbretes

Species: *Treptacantha sauvageauana*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	93	66
x̄	1.9	2.6
s^2	1.3	1.7

Monte Carlo permutation: p (same mean): **0.0004**

Species: *Treptacantha ballesterosii* var. *compressa*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	75	35
$\bar{x}$	1.6	1.6
s^2	1.0	1.2

Monte Carlo permutation: p (same mean): 1

Species: *Cystoseira compressa*

Parameters	With *Cladocora caespitosa*	Without *Cladocora caespitosa*
n	59	35
$\bar{x}$	2.3	2.4
s^2	2.1	2.2

Monte Carlo permutation: p (same mean): 0.8