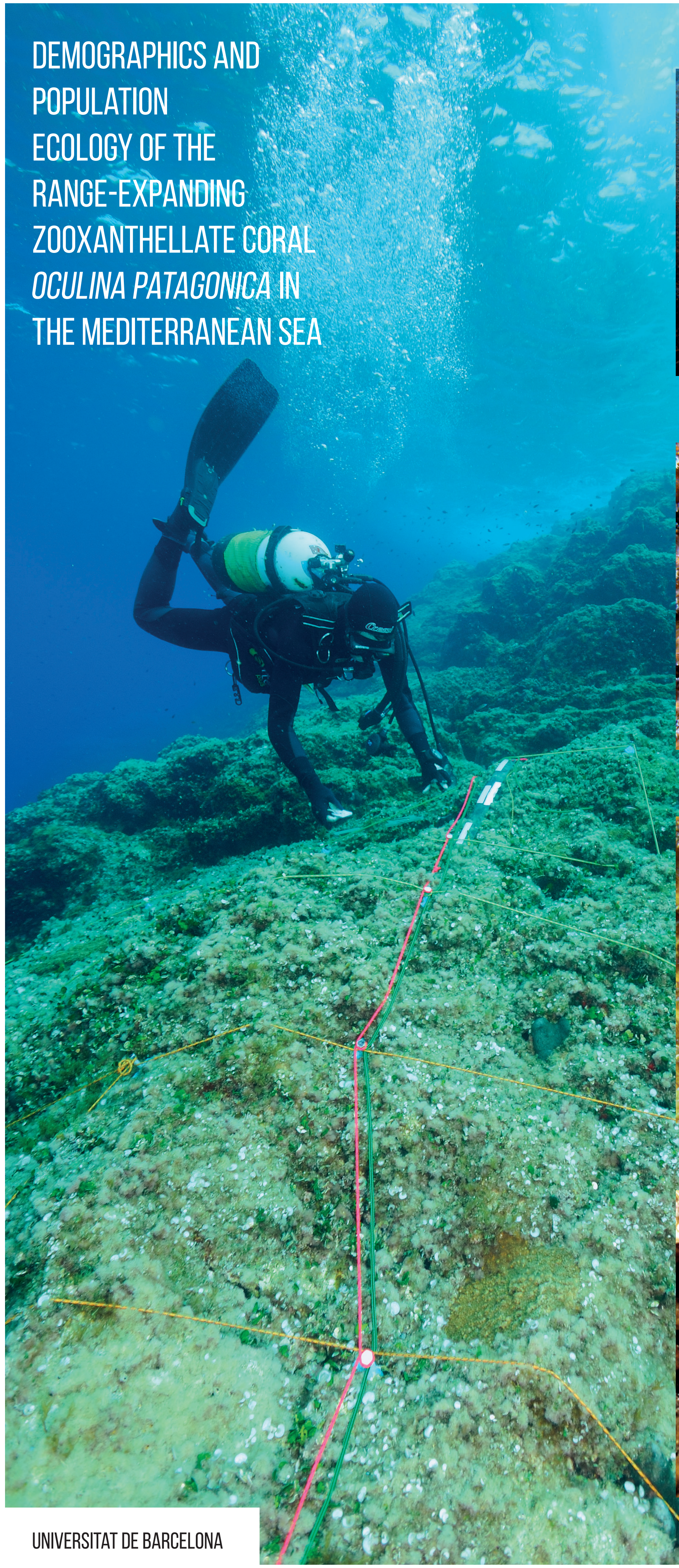

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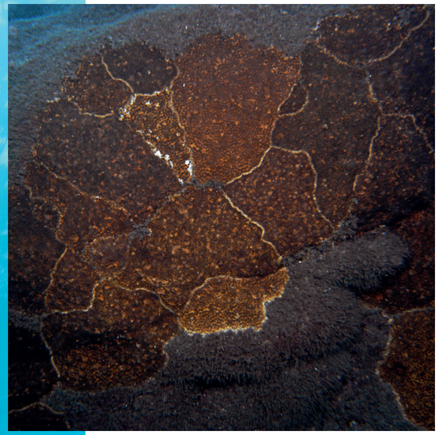

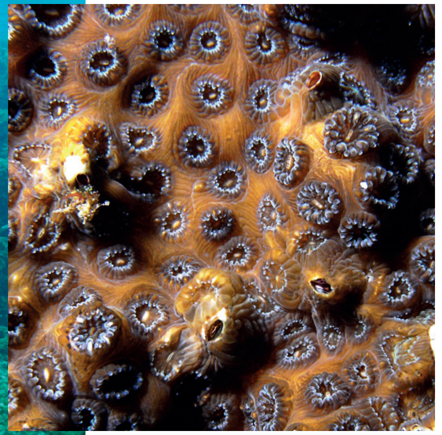

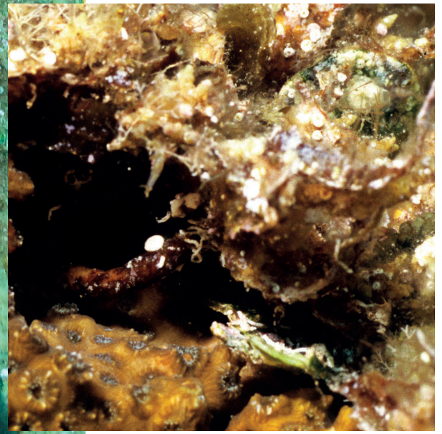

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EDUARD
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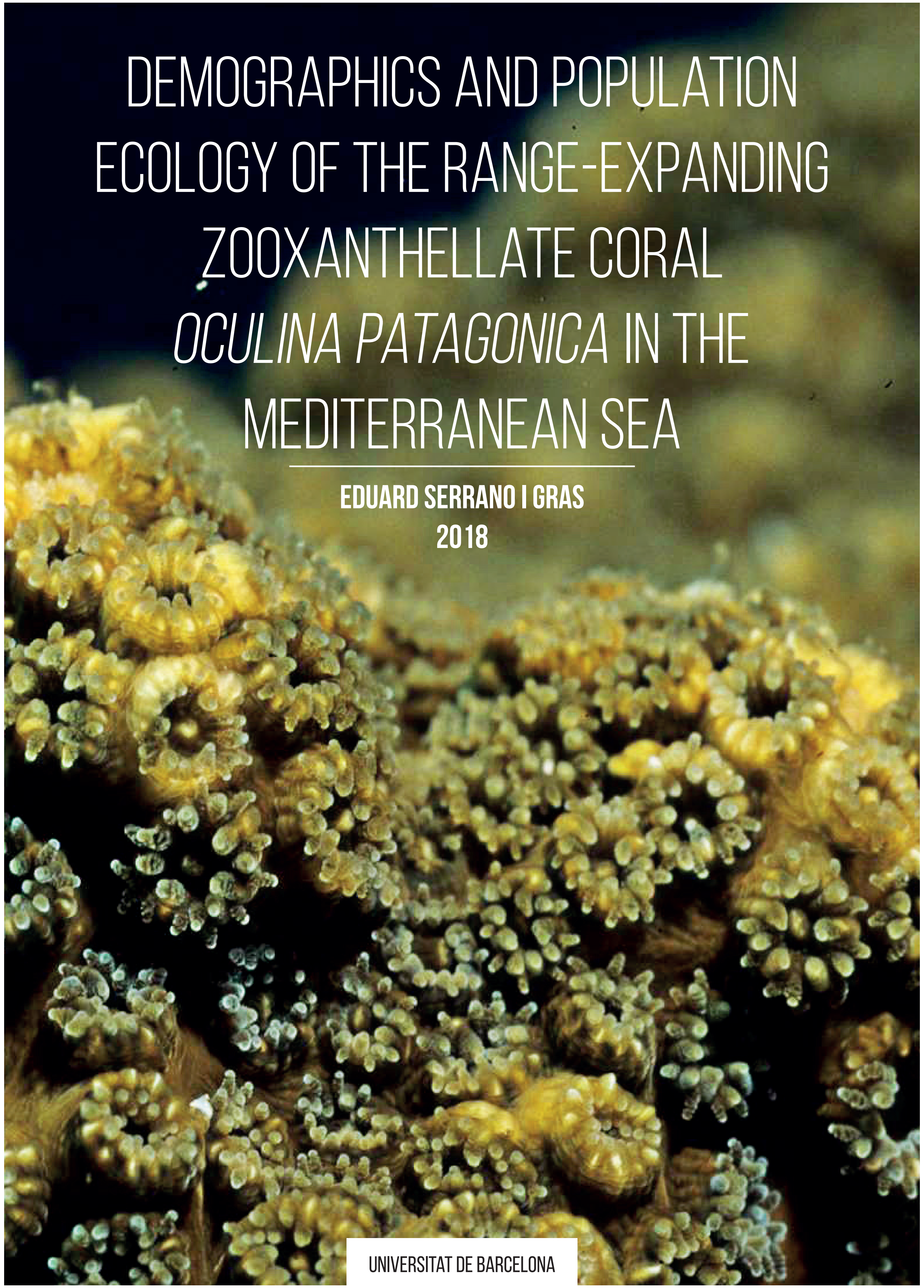

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EDUARD SERRANO I GRAS

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Universitat de Barcelona
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Demographics and population ecology of the range-expanding zooxanthellate coral *Oculina patagonica* in the Mediterranean Sea

Eduard Serrano i Gras

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Demographics and population ecology of the range-expanding zooxanthellate coral *Oculina patagonica* in the Mediterranean Sea

Memòria presentada per Eduard Serrano i Gras per optar al títol de Doctor per la Universitat de Barcelona, sota la direcció del Dr. Rafel Coma i Bau, i la Dra. Marta Ribes i Llordés, i la tutoria del Dr. Joan Lluís Pretus i Real.

Eduard Serrano i Gras

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El director:	La directora:	El tutor:
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All photographs in this PhD Thesis performed by Eduard Serrano in the Mediterranean coast of the Iberian Peninsula, unless otherwise specified.

Als meus pares,

al meu germà

i a l'Agnès

Agraïments

Després d'uns quants anys d'investigació, per fi he obtingut el premi final a tot l'esforç, que és aquesta Tesi Doctoral. Durant aquesta etapa de la meva vida he viscut nombroses experiències que no oblidaré mai, en companyia de moltíssimes persones que d'una manera o altra han contribuït a què arribés a bon port, a totes elles vull agrair sincerament haver compartit aquest viatge.

El meu interès per la ciència va començar el dia que vaig escollir fer les pràctiques de la Llicenciatura de Biologia a l'Institut de Ciències del Mar de Barcelona, de tota la oferta que hi havia em va cridar especialment l'atenció una proposta per estudiar la reproducció de la gorgònia vermella... Sí, justament la gorgònia que viu a més profunditat, però també la més bonica... Feia poc temps que m'havia tret el títol d'immersió, després d'haver anat en apnea des de ben petit, i sempre que en teníem la oportunitat anàvem a visitar aquells llocs desconeguts on n'hi havia, amb mon germà i els amics, de manera que no vaig dubtar al moment d'escollir. A l'Institut vaig conèixer na Marta Ribes i en Rafel Coma, el meu primer contacte amb el món científic i els directors d'aquesta tesis. Va ser una etapa que vaig viure amb la il·lusió del primer dia, combinant les feines de laboratori amb les desitjades sortides al camp per fer el seguiment de les gorgònies de les Illes Medes i el Cap de Creus. Però un dia va sorgir la possibilitat de realitzar el meu treball de Màster estudiant un corall que viu a poca profunditat... bé, no eren les gorgònies, però també era una espècie desconeguda per mi ja que només vivia al sud de la Península. Com us podreu imaginar, era una tal *Oculina patagonica*, amb una història molt rara però alhora molt interessant. I va arribar la primera campanya d'Oculina amb en Rafel, justament en un dels llocs més encantadors que he conegut, les Islas Hormigas al Cabo de Palos, no podia fallar. Encara recordo el primer cop que vaig conèixer la Oculina, va ser després d'ancorar la zodiac en un dels illots a mar obert, quan vaig submergir-me per assegurar l'àncora en uns blocs, i allí estava..., una colònia incrustada damunt d'una pedra que vaig contemplar encuriosit uns segons... i així es va iniciar aquesta tesis. Vull agrair sincerament a en Rafel i na Marta haver-me brindat l'oportunitat d'endinsar-me en aquest món científic i gaudir dels vostres amplis coneixements i bon fer, de la vostra dedicació, suport i ajut incondicionals, i de l'amistat i dels bons moments que hem viscut junts, aquesta tesis és també vostra.

Una tesis com aquesta ha necessitat de molta feina de camp, i això només ha estat possible gràcies a la col·laboració de molta gent que m'ha acompanyat a mar. En primer lloc en Rafel, amb qui he compartit centenars, probablement més de mil hores d'immersió al llarg d'aquests anys, i de qui he après moltíssim. També vull agrair a tots els amics que han estat companys d'immersió i/o que en algun moment m'han ajudat a dur a terme les tasques d'aquest treball, pel seu inestimable ajut i per totes les aventures i alegries que hem viscut junts. Els entranyables Boris Weitzmann i Maria García varen ser els meus primers companys de viatge i un duet amb una felicitat contagiosa. Vull agrair també a na Cristina Linares per totes les campanyes i moments que vàrem passar junts durant els meus inicis, i a en David Díaz, tots dos coautors d'un dels capítols d'aquesta tesis. També a tots aquells amb qui he fet campanyes voltant per la Península Ibèrica: Maria Elena Cefali, Eduard Llorente, Adriana Villamor, Ariadna Arnau, Marc Terrades, Alfredo García, Laura Navarro, Roger Ricart, Elia Vallejo i l' Isaac Gállego. Els estudiants de pràctiques universitàries i de treballs de Grau i Màster que m'han acompanyat també han estat de gran ajuda en aquesta tesis i en treballs en curs: Carla Pérez, Anna Bohigas, Eduard Bonmatí, Miquel Correa, Anna Peris i Blanca Pairó. Moltíssimes gràcies a tots!

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Aquests anys he tingut l'oportunitat de compartit nombroses hores d'immersió amb en Juan Carlos Calvín, un gran coneixedor de la biodiversitat del mar Mediterrani a qui és difícil submergir sense la seva càmera fotogràfica, i és que les seves fotografies de les Oculines de les Islas-Hormigas són un gran regal per aquesta tesis, muchas gracias! En Juancho Movilla, n'Eva Calvo i en Carles Pelejero han estat uns grans companys durant les meves estades als aquaris experimentals de l'ICM, moltes gràcies per brindar-me l'oportunitat de col·laborar amb els vostres experiments acidificats i per l'alegria que m'heu transmès sempre. També vull agrair a en Mikel Zabala els coneixements i l'interès conservacionista de la natura que m'ha brindat, i a en Miguel Ángel Mateo per donar-me l'oportunitat de participar en els seus estudis i el seu suport. Moltes gràcies també a en Joan Lluís Pretus per ser el tutor d'aquesta tesis i un professor referent durant la meva etapa universitària. A en Miquel Canals i n'Antoni Calafat els vull agrair el seu ajut com a coordinadors del meu Programa de Doctorat en Ciències del Mar, agrair també als membres del Tribunal que han avaluat aquesta tesis: Josep Maria Gili, José Templado, Creu Palacín, i als vocals de reserva Emma Cebrian i Andrea Gori.

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Per últim, agrair de tot cor als meus pares per estimar-me i recolzar-me sempre, i per apropar-me a la natura en un sentit ampli, us estimo. També a la resta de la meva família, als meus avis, als meus tiets i cosins, a na Lluïsa, en Xavi i na Karina, i a la meva família política, moltes gràcies per ser casa meva! Aquesta tesis li dedico especialment al meu germà, per ser la meva mà dreta i company de vida, i a l'Agnès per tot el que hem viscut i viurem junts, ambdós sou el pilar que ha permès aquesta tesis en el sentit personal, i també m'heu ajudat moltíssim en molts aspectes del seu dia a dia.

A tots ells, i als qui havent col·laborat en alguns aspectes d'aquest treball no he mencionat, vull expressar el meu sincer agraïment.

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Appendix II. Published manuscript of Chapter 4.2

Appendix III. Published manuscript of Chapter 4.3

Appendix IV. Published manuscript of Chapter 4.4

ABSTRACT

Shallow-water rocky ecosystems in temperate areas are dominated by macroalgae, whilst zooxanthellate corals are extremely rare. In an era of global change, sea warming plays a crucial role in the widespread phase shifts from coral- to algal-dominance in tropical coral reef ecosystems, and in the poleward spread and increase in abundance of some tropical and subtropical zooxanthellate corals into algal-dominated temperate areas. In the Mediterranean Sea, some evidences suggest that the zooxanthellate coral *Oculina patagonica* (Scleractinia, Oculinidae) is experiencing a range-expanding process, providing a good case study to examine how zooxanthellate corals can affect the algal-dominated structure of shallow-water ecosystems in temperate areas. However, the characterization, relevance and the mechanisms of this expansion process had not been established.

In this PhD Thesis, different field studies were performed along the Iberian coast in the western Mediterranean, using descriptive and long-term experimental approaches, to examine the demographics and population ecology of *O. patagonica* and contribute understanding the interaction among the main intrinsic and extrinsic factors in modulating the species' dynamics under current global change. First, we document that *O. patagonica* is experiencing an invasive behavior that challenges the current conceptual framework of shallow-water rocky ecosystems, by providing evidence that the species is able to: i) form encrusting bioconstructions and drive a phase shift from macroalgal- to coral-dominated states in the natural rocky ecosystems (Chapter 4.1), and ii) experience an invasive behavior at both population outbreak (i.e., a yearly monitoring of four populations of the species over 2002-2010, showing a 3-fold increase in species' abundance; Chapter 4.2) and geographical distribution range levels (i.e., a species-specific monitoring of 233 locations over 1992-2010, documenting a northward distributional range shift along ~400 km of the north-eastern Iberian coast; Chapter 4.3). Second, over a ~4-yr field experiment (2008-2012) we document that a severe and recurrent pattern of partial mortality on *O. patagonica* colonies occurs under low seawater temperature (ST) conditions during winter, which appears to play a crucial role in constraining the growth dynamics of the species at the high-latitude area in the north-eastern Iberian coast (Chapter 4.4). Third, we document the spatial variation in the demographics of *O. patagonica* (occurrence, density, cover, colony partial mortality and size-structure) by examining 314 locations along ~1300 km Iberian coast that provides a detailed baseline quantitative dataset, including natural and artificial locations (Chapters 4.1, 4.3, 4.5). We found that the colony size-structure of coral populations in natural locations were unimodal and positively skewed, indicative of non-stable and growing populations. However, the species' demographics showed a marked 'abundant-center' pattern that is not only related to the time of establishment but also to the relevant role of differences in coral population growth that correlate with key environmental variables.

Finally, we layered our broad spatial scale observations on the demographics of *O. patagonica*, together with our and previous empirical and experimental studies on the interaction between biological traits and key environmental factors modulating coral performance, to identify the potential causes of the geographic range structure and invasion behavior of this species within the Iberian coast. The success of *O. patagonica* colonies and populations on natural locations appear to be generally constrained by low ST and light conditions, with thresholds that limit coral growth of mean annual photosynthetic active radiation at 3 m depth <30 mol photons m^{-2} d^{-1}, mean ST <19ºC, percentile 10th-ST <14ºC and percentile 90th-ST <25ºC, but without severe high-ST periods (percentile 90th-ST >27ºC). In addition, the high availability of open space for *O. patagonica* to colonize (i.e., mean of 33% cover of algal-depleted reefs and barren grounds; Chapter 4.5), and the positive effects of sand scouring (Chapter 4.1) and sea urchins herbivory (Chapter 4.2) on coral population growth, indicate that open space availability is a crucial factor enhancing the proliferation of the species within the Iberian coast. We also found that artificial reefs foster the population growth and the expansion of the distributional range of this coral species (Chapters 4.3, 4.5). This knowledge is fundamental to understand the drivers of expansion under past and present environmental scenarios, and to predict whether its invasive behavior may substantially impact macroalgal-dominated ecosystems in the temperate Mediterranean Sea. The broad spread of *O. patagonica* across the Mediterranean Sea, and its invasive behavior at both distributional range shift and population outbreak levels, able to drive phase shifts from macroalgae to coral dominance in natural and artificial reefs, is consistent with the ongoing process of zooxanthellate coral-mediated tropicalization of shallow-water rocky ecosystems documented in other subtropical and temperate areas under current global change.

RESUM

Els ecosistemes rocosos d'aigües superficials en àrees temperades estan dominats per macro-algues, mentre que els coralls zooxantel·lats són extremadament rars. En una època de canvi global, l'escalfament de l'aigua del mar juga un paper crucial en els desplaçaments de fase que s'estan produint de manera generalitzada en els ecosistemes tropicals d'esculls de corall, des de la dominància dels coralls cap a la dominància d'algues, i en l'expansió cap als pols i l'augment en abundància d'alguns coralls zooxantel·lats tropicals i subtropicals en àrees temperades dominades per macro-algues. Al mar Mediterrani, algunes evidències suggereixen que el corall zooxantel·lat *Oculina patagonica* (Scleractinia, Oculinidae) està experimentant un procés d'expansió, oferint un bon cas d'estudi per examinar com els coralls zooxantel·lats poden afectar l'estructura dominada per algues dels ecosistemes d'aigües superficials en àrees temperades. Tanmateix, no s'ha establert la caracterització, rellevància ni els mecanismes d'aquest procés d'expansió.

En aquesta Tesi doctoral, es varen realitzar diferents estudis de camp al llarg de la costa Ibèrica a la Mediterrània occidental, utilitzant enfocaments descriptius i experiments a llarg termini, per examinar la demografia i l'ecologia de poblacions de l'*O. patagonica* i contribuir a comprendre la interacció entre els principals factors intrínsecs i extrínsecs en la modulació de la dinàmica de l'espècie sota el canvi global actual. En primer lloc, documentem que l'*O. patagonica* està experimentant un comportament invasiu que desafia el marc conceptual actual dels ecosistemes rocosos d'aigües superficials, aportant evidència de què l'espècie és capaç de: i) formar bioconstruccions incrustants i impulsar un desplaçament de fase en els ecosistemes rocosos naturals, des de la dominància de les macro-algues cap a la dominància d'aquest corall (Capítol 4.1), i ii) experimentar un comportament invasiu tant a nivell de proliferacions poblacionals (és a dir, un seguiment anual de quatre poblacions de l'espècie al llarg de 2002-2010, que mostra un augment de 3 vegades en l'abundància de l'espècie; Capítol 4.2) com a nivell del rang de distribució geogràfica (és a dir, un seguiment específic de l'espècie a 233 localitats al llarg de 1992-2010, que documenta un canvi de distribució cap al nord al llarg de ~400 km del nord-est de la costa Ibèrica; Capítol 4.3). En segon lloc, en un experiment de camp de ~4 anys (2008-2012) documentem que un patró sever i recurrent de mortalitat parcial en les colònies de l'*O. patagonica* es produeix sota les condicions de baixa temperatura de l'aigua de mar (ST) durant l'hivern, el qual sembla jugar un paper crucial en restringir la dinàmica de creixement de l'espècie a l'àrea d'alta-latitud de la costa Ibèrica del nord-est (Capítol 4.4). En tercer lloc, documentem la variació espacial en la demografia de l'*O. patagonica* (ocurrència, densitat, cobertura, mortalitat parcial i estructura de mida de les colònies) examinant 314 localitats al llarg de ~1300 km de la costa Ibèrica, que proporciona una base de dades quantitativa i detallada com a línia de base, incloent localitats naturals i artificials (Capítols 4.1, 4.3, 4.5). Es va determinar que les estructures de

mida de les colònies a les poblacions del corall en localitats naturals eren asimètriques i esbiaixades positivament, indicant poblacions no estables i creixents. Tanmateix, la demografia de l'espècie va mostrar un patró marcat de 'centre-abundant' que no només es relaciona amb el temps d'establiment, sinó també amb el paper rellevant de les diferències en el creixement poblacional del corall que es correlacionen amb les variables ambientals clau.

Finalment, hem superposat les nostres àmplies observacions a escala espacial sobre les dades demogràfiques de l'*O. patagonica*, juntament amb els nostres i els anteriors estudis empírics i experimentals sobre la interacció entre els trets biològics i els factors ambientals clau que modulen la proliferació de l'espècie, per identificar les causes potencials de l'estructura del rang geogràfic i el comportament invasiu d'aquesta espècie dins de la costa Ibèrica. L'èxit de les colònies i de les poblacions de l'*O. patagonica* en localitats naturals sembla estar generalment limitat per condicions de baixa ST i llum, amb llindars que limiten el creixement del corall de mitjana anual de radiació activa fotosintètica a 3 m de profunditat <30 mol fotons m^{-2} d^{-1}, mitjana ST <19ºC, percentil 10th-ST <14ºC i percentil 90th-ST <25ºC, però sense períodes severs de ST alta (percentil 90th-ST >27ºC). A més, la gran disponibilitat d'espai obert per *O. patagonica* per colonitzar (és a dir, esculls rocosos desproveïts d'algues i amb blancalls, amb una cobertura mitjana del 33%; Capítol 4.5), i els efectes positius de l'abrasió produïda per la sorra (Capítol 4.1) i de l'herbivorisme dels eriçons de mar (Capítol 4.2) sobre el creixement poblacional d'aquest corall, indiquen que la disponibilitat d'espai obert és un factor crucial que afavoreix la proliferació de l'espècie dins de la costa Ibèrica. També vàrem constatar que els esculls artificials afavoreixen el creixement de les poblacions i l'expansió del rang de distribució d'aquesta espècie de corall (Capítols 4.3, 4.5). Aquest coneixement és fonamental per comprendre els conductors de l'expansió sota els escenaris mediambientals passats i presents, i per predir si el seu comportament invasiu podria afectar substancialment els ecosistemes temperats dominats per macro-algues del mar Mediterrani. L'àmplia proliferació de l'*O. patagonica* a través del mar Mediterrani, i el seu comportament invasiu tant a nivell de canvis en el rang de distribució com a nivell de proliferacions poblacionals, capaç d'impulsar desplaçaments de fase des de la dominància de les macro-algues cap a la dominància d'aquest corall en esculls naturals i artificials, és coherent amb el procés en curs de tropicalització conduit per coralls zooxantel·lats dels ecosistemes rocosos d'aigües superficials documentats en altres àrees subtropicals i temperades sota el canvi global actual.

RESUMEN

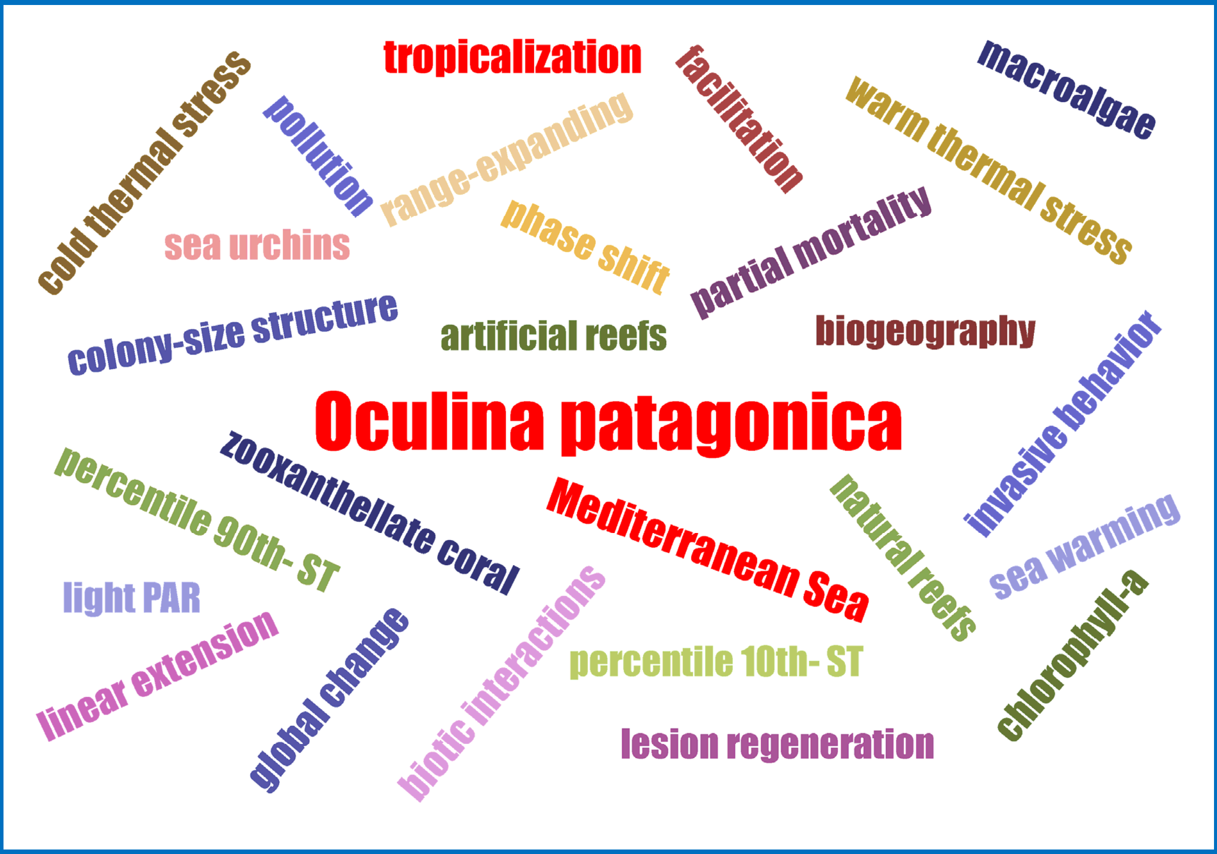
Los ecosistemas rocosos de aguas superficiales en áreas templadas están dominados por macro-algas, mientras que los corales zooxantelados son extremadamente raros. En una época de cambio global, el calentamiento del agua del mar juega un papel crucial en los desplazamientos de fase que se están produciendo de manera generalizada en los ecosistemas tropicales de arrecifes de coral, desde la dominancia de los corales hacia la dominancia de algas, y en la expansión hacia los polos y el aumento en abundancia de algunos corales zooxantelados tropicales y subtropicales en áreas templadas dominadas por macro-algas. En el mar Mediterráneo, algunas evidencias sugieren que el coral zooxantelado *Oculina patagonica* (Scleractinia, Oculinidae) está experimentando un proceso de expansión, ofreciendo un buen caso de estudio para examinar cómo los corales zooxantelados pueden afectar la estructura dominada por algas de los ecosistemas de aguas superficiales en áreas templadas. Sin embargo, no se ha establecido la caracterización, relevancia ni los mecanismos de este proceso de expansión.

En esta Tesis doctoral, se realizaron diferentes estudios de campo a lo largo de la costa Ibérica en el Mediterráneo occidental, utilizando enfoques descriptivos y experimentos a largo plazo, para examinar la demografía y la ecología de poblaciones de *O. patagonica* y contribuir a comprender la interacción entre los principales factores intrínsecos y extrínsecos en la modulación de la dinámica de la especie bajo el cambio global actual. En primer lugar, documentamos que *O. patagonica* está experimentando un comportamiento invasivo que desafía el marco conceptual actual de los ecosistemas rocosos de aguas superficiales, aportando evidencia de que la especie es capaz de: i) formar bioconstrucciones incrustantes e impulsar un desplazamiento de fase en los ecosistemas rocosos naturales, desde la dominancia de las macro-algas hacia la dominancia de este coral (Capítulo 4.1), y ii) experimentar un comportamiento invasivo tanto a nivel de proliferaciones poblacionales (es decir, un seguimiento anual de cuatro poblaciones de la especie a lo largo de 2002-2010, que muestra un aumento de 3 veces en la abundancia de la especie; Capítulo 4.2) como a nivel del rango de distribución geográfica (es decir, un seguimiento específico de la especie en 233 localidades a lo largo de 1992-2010, que documenta un cambio de distribución hacia el norte a lo largo de ~400 km del noreste de la costa Ibérica; Capítulo 4.3). En segundo lugar, en un experimento de campo de ~4 años (2008-2012) documentamos que un patrón severo y recurrente de mortalidad parcial en las colonias de *O. patagonica* se produce bajo las condiciones de baja temperatura del agua de mar (ST) durante el invierno, el cual parece jugar un papel crucial en restringir la dinámica de crecimiento de la especie en el área de alta-latitud de la costa Ibérica del noreste (Capítulo 4.4). En tercer lugar, documentamos la variación espacial en la demografía de *O. patagonica* (ocurrencia, densidad, cobertura, mortalidad parcial y estructura de tamaño de las colonias) examinando 314 localidades a lo largo de ~1300 km de

la costa Ibérica, que proporciona una base de datos cuantitativa y detallada como línea de base, incluyendo localidades naturales y artificiales (Capítulos 4.1, 4.3, 4.5). Se determinó que las estructuras de tamaño de las colonias en las poblaciones del coral en localidades naturales eran asimétricas y sesgadas positivamente, indicando poblaciones no estables y crecientes. Sin embargo, la demografía de la especie mostró un patrón marcado de 'centro-abundante' que no sólo se relaciona con el tiempo de establecimiento, sino también con el papel relevante de las diferencias en el crecimiento poblacional del coral que se correlacionan con las variables ambientales clave.

Finalmente, hemos superpuesto nuestras amplias observaciones a escala espacial sobre los datos demográficos de *O. patagonica*, junto con los nuestros y los anteriores estudios empíricos y experimentales sobre la interacción entre los rasgos biológicos y los factores ambientales clave que modulan la proliferación de la especie, para identificar las causas potenciales de la estructura del rango geográfico y el comportamiento invasivo de esta especie dentro de la costa Ibérica. El éxito de las colonias y de las poblaciones de *O. patagonica* en localidades naturales parece estar generalmente limitado por condiciones de baja ST y luz, con umbrales que limitan el crecimiento del coral de media anual de radiación activa fotosintética a 3 m de profundidad <30 mol fotones m^{-2} d^{-1}, media ST <19ºC, percentil 10^{th}-ST <14ºC y percentil 90^{th}-ST <25ºC, pero sin períodos severos de ST alta (percentil 90^{th}-ST >27ºC). Además, la gran disponibilidad de espacio abierto para *O. patagonica* para colonizar (es decir, arrecifes rocosos desprovistos de algas y con blanquizales, con una cobertura media del 33%; Capítulo 4.5), y los efectos positivos de la abrasión producida por la arena (Capítulo 4.1) y de la herbivoría de los erizos de mar (Capítulo 4.2) sobre el crecimiento poblacional de este coral, indican que la disponibilidad de espacio abierto es un factor crucial que favorece la proliferación de la especie dentro de la costa Ibérica. También constatamos que los arrecifes artificiales favorecen el crecimiento de las poblaciones y la expansión del rango de distribución de esta especie de coral (Capítulos 4.3, 4.5). Este conocimiento es fundamental para comprender los conductores de la expansión bajo los escenarios medioambientales pasados y presentes, y para predecir si su comportamiento invasivo podría afectar sustancialmente los ecosistemas templados dominados por macro-algas del mar Mediterráneo. La amplia proliferación de *O. patagonica* a través del mar Mediterráneo, y su comportamiento invasivo tanto a nivel de cambios en el rango de distribución como a nivel de proliferaciones poblacionales, capaz de impulsar desplazamientos de fase desde la dominancia de las macro-algas hacia la dominancia de este coral en arrecifes naturales y artificiales, es coherente con el proceso en curso de tropicalización conducido por corales zooxantelados de los ecosistemas rocosos de aguas superficiales documentados en otras áreas subtropicales y templadas bajo el cambio global actual.

1. GENERAL INTRODUCTION



Chapter 1

1. GENERAL INTRODUCTION

1.1. Marine ecosystems facing anthropogenic global change

The history of life' distribution on Earth is dynamic and closely associated with environmental change at multiple spatial and temporal scales (Davis and Shaw 2001; Lawing and Polly 2011; Bernhardt and Schlesinger 2013). Anthropogenic greenhouse gas emissions have resulted in accelerated environmental changes during the 21st century, which are comparable in magnitude to the largest global natural changes over the past 65 million years (Diffenbaugh and Field 2013; Poloczanska et al. 2013; Pörtner et al. 2014; Kemp et al. 2015; Pecl et al. 2017). The oceans have absorbed 93% of the extra energy arising from anthropogenic greenhouse gas emissions (1971-2010), resulting in an average rate of increase in global seawater temperature (ST) of ~0.15ºC decade^{-1} in the upper 75 m; although it is likely that the upper oceans may have experienced some warming between 1870s and 1971 (Hoegh-Guldberg et al. 2014; Pörtner et al. 2014; Gleckler et al. 2016). Examination of the Hadley Centre Interpolated Sea Surface Temperature 1.1 (HadISST1.1) data over 60 years (1950–2009) reveals significant warming trends in average surface ST for the three ocean basins: Indian, Atlantic and Pacific oceans (0.65ºC, 0.41ºC and 0.31ºC, respectively; Fig. 1.1), and in the warmest (0.64ºC, 0.55ºC and 0.28ºC) and coolest months of the year (0.78ºC, 0.36ºC and 0.26ºC, respectively; Rayner et al. 2003; Hoegh-Guldberg et al. 2014; Fig. 1.1). The oceans will continue warming under moderate to high greenhouse gas emission scenarios, such as Representative Concentration Pathway (RCP) 4.5 to RCP 8.5, and will only stabilize over the 2050s in the case of low range scenarios such as RCP 2.6 (Hoegh-Guldberg et al. 2014; Fig. 1.1).

Other global change-related physical and chemical changes include a decrease in ocean pH and changing of carbonate chemistry, light and nutrient concentrations, declines in dissolved oxygen concentrations and alteration of ocean circulation (Wu et al. 2012; Andrews et al. 2013; Hoegh-Guldberg et al. 2014; Pörtner et al. 2014; Gattuso et al. 2015). The picture is further complicated by the interaction of global climate change with many other human impacts at local and regional scales, such as habitat alteration, eutrophication, pollution, overfishing, coastal development and invasive species (Halpern et al. 2008). These decadal-scale anthropogenic changes, particularly when changes in biotic and abiotic interactions involve keystone or foundation species, have already altered the composition, structure and resilience of marine ecosystems worldwide; affecting ecosystem biogeography, biodiversity, function and services, human well-being, and the dynamics of climate change itself (Lotze et al. 2006; Zarnetske et al. 2012; Poloczanska et al. 2013; Pecl et al. 2017).

In front of this context, understanding and predicting the effects of accelerated global change is now a central theme in ecology of terrestrial, freshwater and marine ecosystems. Discriminating between natural and human-induced changes, cycles, and trends in the ecosystems is often difficult without an adequate time perspective (Willis and Birks 2006; Luo et al. 2011). For this reason, long, detailed and reliable time-series of data on relevant ecosystem structural and functional variables is of key significance for researchers and managers to identify shifting trends, detect potential impacts, and propose policy action strategies. Identifying and protecting spatial refuge is a common strategy for conservation of threatened species and ecosystems, but local interventions may have no discernible effect on securing future for global ecosystems if immediate global action to reduce greenhouse gas emissions is not actioned.

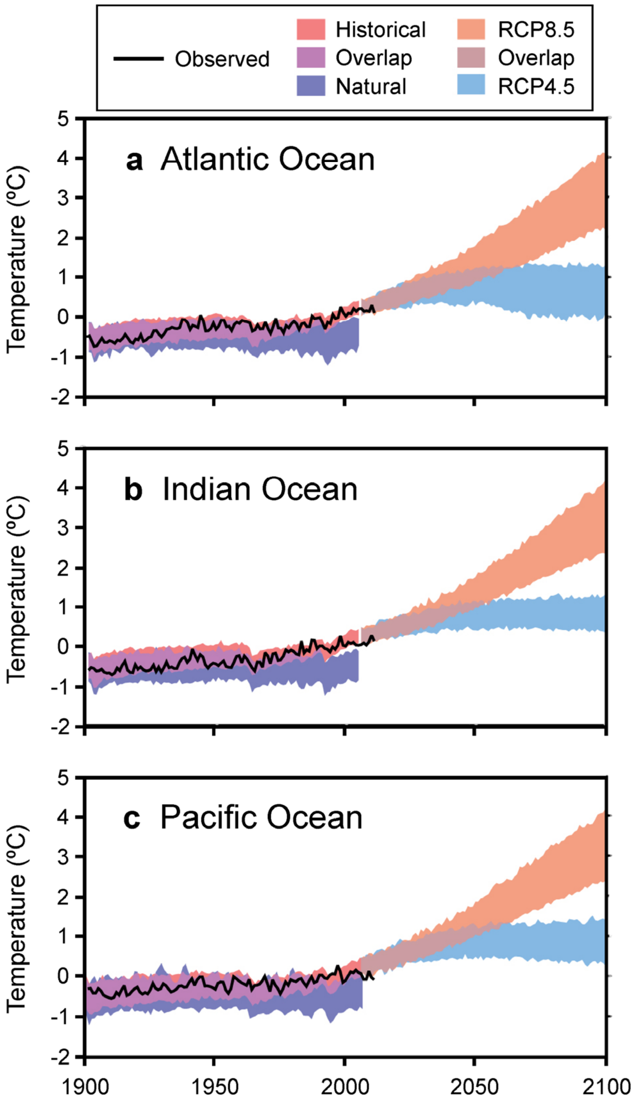


Fig. 1.1 Observed and simulated variations in past and projected future annual average surface sea temperature over three ocean basins: Atlantic Ocean, Indian Ocean and Pacific Ocean. The *black line* shows estimates from Hadley Centre Interpolated sea surface temperature 1.1 (HadISST1.1) observational measurements. *Shading* denotes the 5th to 95th percentile range of climate model simulations driven with ‘historical’ changes in anthropogenic and natural drivers (62 simulations), historical changes in ‘natural’ drivers only (25 simulations), and the Representative Concentration Pathways (RCPs) 4.5 and 8.5 scenarios. Data are anomalies from the 1986-2006 average of the HadISST1.1 data time series or of the corresponding historical all-forcing simulations. Adapted from Hoegh-Guldberg et al. (2014).

Two main phenomena, the spread of alien species (i.e., biological invasions) and climate change, appear to be increasing the rate of change in species distribution boundaries and abundances, making possible to examine the consequences of such impacts on ecosystem functioning over decadal time scales (Carlton 1999; Kinlan and Hastings 2005; Hawkins et al. 2009; Poloczanska et al. 2013, 2016). Biological invasions are a major component of global change, accelerating the redistribution of species at global scales (e.g., across oceans) and often causing negative effects on native biodiversity and ecosystem functioning, leading to ecological and human well-being impacts (Grosholz 2002; Blackeslee et al. 2011; Pyšek and Richardson 2010; Simberloff et al. 2013; Vergés et al. 2016). The main vectors of human-mediated introduction of marine organisms to a new area include fouling on hulls of ships, transport in ballast water, navigational canals, aquaculture and the aquarium trade (Carlton 1987; Zibrowius 1992; Hulme 2009; Katsanevakis et al. 2013). The rapid globalization and increasing trends of trade and travel in recent decades have accelerated the transport of species beyond their native range limits of distribution, and marine ecosystems remain one of the most affected (e.g., Grosholz 2002). High confidence expectations for biological and ecological responses (i.e., native and alien species) to sea warming include distributional range shifts (e.g., at local and regional scales), changes in relative abundances within species ranges, and changes in life-history, activity timing and microhabitat use (Williams et al. 2008; Bates et al. 2014; Poloczanska et al. 2016). The successive stages of a range-shifting native species (i.e., arrival, population outbreak and persistence) and their consequences on ecosystems are broadly comparable with the invasion pathway (Blackburn et al. 2011; Simberloff 2011; Madin et al. 2012; Valéry et al. 2013; Bates et al. 2014).

All species including marine ones have limited temperature ranges within which they live and function (Angilletta 2009; Chevin et al. 2010; Pörtner et al. 2014). Each species' performance (i.e., the establishment, survival, reproduction and increase in size as individuals and populations) is maximal at its optimum temperature, and becomes progressively constrained during cooling or warming (Fig. 1.2a). The distributional limits and abundances of marine species are closely related to their physiological limits of thermal tolerance, and are expected to range shift tracking the warming-related migration of suitable STs (e.g., Kleypas et al. 1999; Burrows et al. 2011, 2014; Sunday et al. 2012; Hoegh-Guldberg et al. 2014; Pörtner et al. 2014; Poloczanska et al. 2016; Fig. 1.2b,c). In fact, marine species are directly responding to sea warming (i.e., shifting ST means, and cold and warm extremes) by range shifting to colder waters (i.e., poleward or deeper locations) at the cooler extremes of their distributions, whereas range limits are contracting at the warmer range edge, where ST are no longer tolerable, typically resulting in a poleward shift of the biogeographic range (Fig. 1.2b).

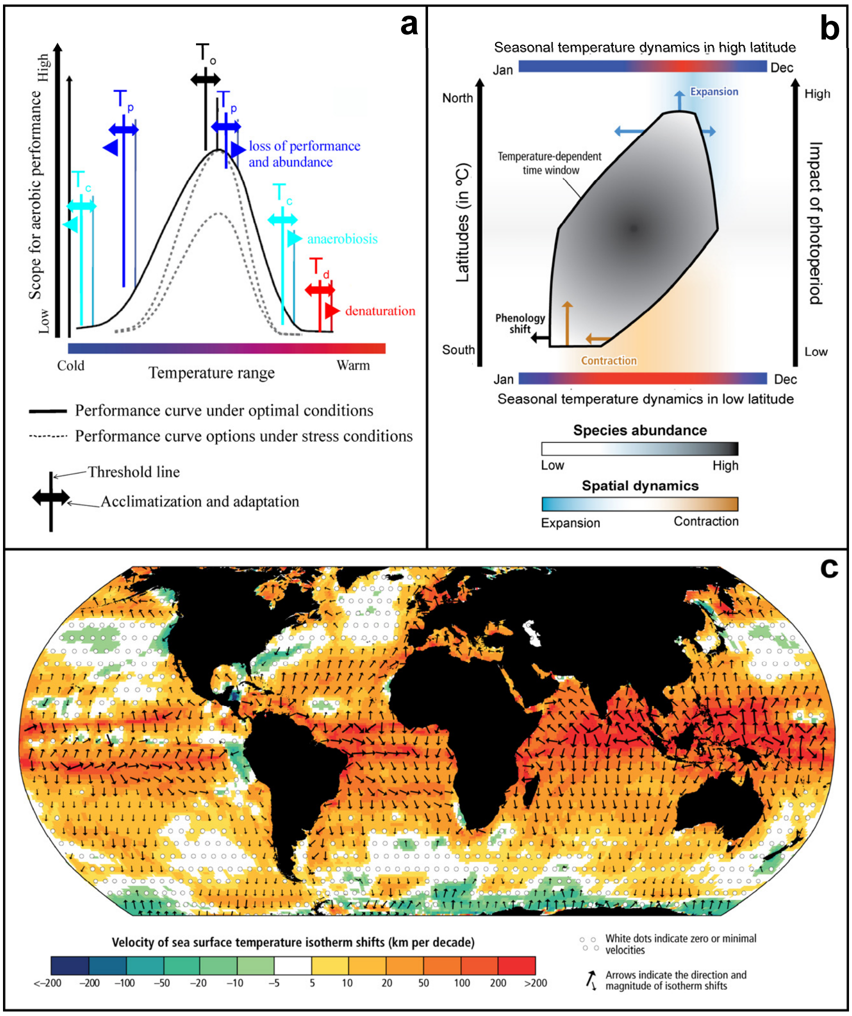


Fig. 1.2 Temperature specialization of species causes warming-induced abundance and distribution shifts. **a** The thermal tolerance range and performance levels of an organism are described by its performance curve and depend on species-specific physiology and ecology. Each performance is maximal at its optimum temperature (T_o), and becomes progressively constrained during cooling or warming. Surpassing the first low- and high-temperature thresholds (T_p: pejus temperatures: getting worse) means going into time-limited tolerance. Once further cooling or warming surpasses the next low or high thresholds (T_c: critical temperatures), oxygen availability becomes insufficient and an anaerobic metabolism begins. Denaturation temperatures (T_d) are even more extreme and characterized by the onset of damage to cells and proteins. *Horizontal arrows* indicate that thermal thresholds of an individual can shift, within limits, between summer and winter (seasonal acclimatization) or when the species adapts to a cooler or warmer climate over generations (evolutionary adaptation). The width of the thermal range also increase over time when an individual develops from egg to larva to adult and gains weight and size. Under other stress conditions (i.e., non-thermal), performance levels can decrease and thermal windows narrow (*dashed gray curves*). *Blue* to *red color gradients* illustrate the range between cold and warm temperatures. **b** Spatial dynamics for species during progressive warming. During climate warming, a species follows its normal temperatures as it moves or is displaced, typically resulting in a poleward shift of the biogeographic range (exemplified for the Northern Hemisphere). The *polygon* delineates the distribution range in space and seasonal time; the *level of gray* denotes abundance. **c** Velocity at which surface seawater temperature (SST) isotherms shifted (km per decade) over the period 1960–2009 calculated using Hadley Centre Interpolated SST 1.1, with *arrows* indicating the direction and magnitude of shifts. Velocity of climate change is obtained by dividing the temperature trend in °C per decade by the local spatial gradient °C km^{-1}. The direction of movement of SST isotherms are denoted by the direction of the spatial gradient and the sign of the SST trend: toward locally cooler areas with a local warming trend or toward locally warmer areas where temperatures are cooling. Adapted from Hoegh-Guldberg et al. (2014) and Pörtner et al. (2014).

Under increasing warming pressure, persistent changes in the distributions and abundances of keystone species affecting the structure, dynamics, function and services have increasingly documented in multiple, diverse ecosystems around the globe (Worm et al. 2006; Jiao 2009; Estes et al. 2011; Biggs et al. 2012; Poloczanska et al. 2013). Recording the arrival, progression, geographic distribution and impact of range-shifting species, together with the understanding of the main processes modulating their spread dynamics, has become a major concern in marine ecology research and ecosystem conservation management, and are crucial to develop strategies for predicting future changes in their impacts in the context of global environmental change (e.g., Ruiz et al. 1997; Zibrowius 1992; Streftaris and Zenetos 2006; Zenetos et al. 2010, 2012; Simberloff et al. 2013).

A striking consequence of cumulative human-related impacts is the occurrence of ecological regime shifts (synonymous with phase shifts), which are dramatic, abrupt changes between regimes/states of populations, communities and/or whole ecosystems that are persistent in time, encompass multiple variables, and include key structural species (Conversi et al. 2015). Regime shifts occur when an ecosystem reorganizes around a new set of self-reinforcing feedbacks in an alternative state and thus, can be difficult to reverse (Folke et al. 2004). Regime shifts in marine ecosystems are caused by multiple, interacting natural and anthropogenic disturbances, either bottom-up (e.g., abiotic factors such as temperature, nutrients, pollution or severe storms) and top-down (e.g., biotic factors such as changes in biotic interactions due to disease outbreaks, overharvesting or invasive species) that impact the endogenous trophic interactions of the food web and the overall resilience, state and function of the ecosystem, generally leading to depauperate ecosystem states (Scheffer et al. 2001; Scheffer 2009; Möllmann et al. 2015). The effects of multiple interacting factors in a changing environment may be synergistic or even antagonistic depending on species sensitivities and ecological processes. Because different species respond to human-related changes at varying degrees, native biotic interactions among species are often disrupted, and new interactions develop, which can result in novel communities and rapid changes in ecosystem functioning (Hughes et al. 2003; Didham et al. 2007; Hoegh-Guldberg and Bruno 2010; Zarnetske et al. 2012; Hoegh-Guldberg et al. 2014). Many marine ecosystems exhibit abrupt ecosystem responses to gradually increasing stressors and move towards a new and easily recognized equilibrium state when a critical threshold or tipping point is exceeded (Scheffer and Carpenter 2003; Andersen et al. 2009). However, transitions from one ecological regime to another often unfold in slow motion and imperceptibly over decades or centuries, with major consequences for our capacity to detect, avoid or reverse them (Scheffer and Carpenter 2003; Hughes et al. 2013). The detection of critical stressors (i.e., bottom-up and top-down processes) in modulating the key structuring species and attribution of critical ecological responses to environmental change is thus a challenging endeavor for research, management and policy actions to predict ecological regime shifts and protect the diversity, function and services provided by marine ecosystems.

A topical example of ecological regime shifts in marine ecosystems is found in shallow-water coral reefs from tropical regions, where the interaction of natural- and human-related impacts (e.g., sea warming, pollution, eutrophication, severe storms, a decrease in herbivore biomass of sea urchins and fishes, coral diseases and predation outbreaks) has led to widespread catastrophic phase shifts from coral- to turf algae- or macroalgal-dominance since the 1980s (e.g., Mumby and Steneck 2008; Bruno et al. 2009; De'ath et al. 2012; Graham et al. 2014, 2015; Jouffray et al. 2015; Spalding and Brown 2015; Heron et al. 2016; Fig. 1.3a). During warming-related marine heatwaves, thermal stress is the main trigger causing the disruption of the symbiotic relationship between reef-building scleractinian corals (Cnidaria, Anthozoa, Hexacorallia, Scleractinia) and their photosynthetic dinoflagellate microalgae symbionts (*Symbiodinium* spp., named vulgar zooxanthellae), causing corals to lose their color. Bleached corals are physiologically damaged (i.e., diminished resilience; Muscatine et al. 1990) and if prolonged, together with other interacting natural- and human-related impacts, often leads to severe mortality events pushing reefs beyond their stable coral-dominated state (Mumby et al. 2007; Bozec and Mumby 2015; Hughes et al. 2017). Dead coral skeletons provide open substrate for the settlement of macroalgae, which outbreak especially if the reef has high productivity (i.e., eutrophic) and/or the top-down control by herbivores is not efficient (Hughes et al. 2003, 2010; Graham et al. 2015). The persistence of algae in tropical ecosystems is further enhanced by the inhibition of coral survival, recruitment, growth and fecundity in algal-dominated substrates (Miller and Hay 1996; McCook et al. 2001; Nugues and Bak 2006), thereby intensifying the bottleneck in coral population dynamics and leading shifts difficult to reverse (Hughes et al. 2007; Mumby and Steneck 2008). The first reported cases were in coral reefs from the Caribbean during the 1980s, where following several disturbances including hurricanes, coral predator and coral disease outbreaks, the pathogen-induced mass mortality of a keystone grazer (i.e., the sea urchin *Diadema antillarum*) and a series of coral bleaching and mortality events, resulted in depleted coral cover and a phase shift in community structure and trophic group toward macroalgae domination (Hughes 1994; Gardner et al. 2003; Aronson and Precht 2001, 2006). Similarly, coral reefs have declined by at least 50% over the past decades in large parts of the world's tropical regions of the Pacific, Indian and Atlantic Oceans, indicating that the shift toward a non-coral dominated state is an ongoing phenomenon occurring in coral reefs at a global scale (Bruno and Selig 2007; De'ath et al. 2012; Hughes et al. 2017; Fig. 1.3b-d).

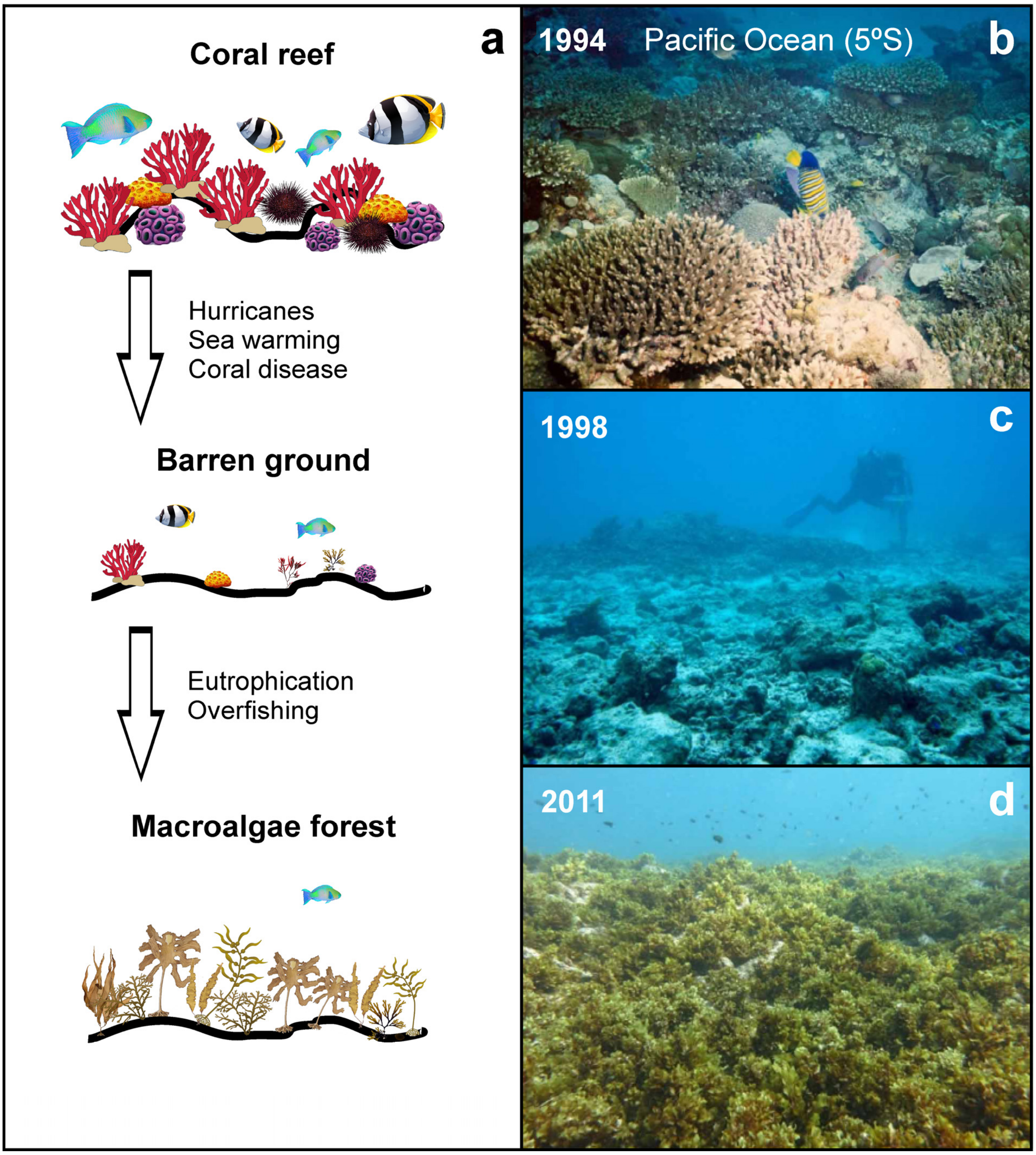


Fig. 1.3 Regime shift from coral reefs to macroalgae dominance in tropical marine ecosystems. a Schematic representation showing a phase shift from a healthy coral reef toward an unhealthy system lacking coral and structural complexity, ultimately leading to macroalgal-dominated communities. The main natural- and human-mediated impacts driving these shifts are indicated. **b-d** Case example from the inner Seychelles Islands in the Pacific Ocean (5ºS). **b** Benthic communities of the Seychelles were typified by high coral cover and low macroalgal cover in 1994. **c** The severe coral bleaching event in 1998 caused widespread coral loss and some reefs collapsed due to storm damage and bioerosion processes. **d** In 2011, many reefs had undergone a regime shift from coral to macroalgal dominance. Adapted from Graham et al. (2006, 2015).

Another dramatic example of regime shifts in marine ecosystems is found in shallow-water rocky reefs from temperate regions, where the interaction of natural- and human-related impacts has first led to widespread phase shifts from macroalgae- to barren-dominance, and lately the poleward shift of subtropical and tropical zooxanthellate corals is leading to coral-dominated assemblages, resulting in an ongoing net tropicalization of temperate ecosystems with a distinctive tropical fauna that challenges the dominant functional benthic group (Harley et al. 2012; Vergés et al. 2014a; Fig. 1.4a). Healthy marine ecosystems in temperate regions are generally dominated by large canopy-forming, fleshy macroalgae such as kelps and fucoids (Phaeophyceae), where they are among the most productive and diverse communities, whilst zooxanthellate corals are extremely rare (Dayton 1985; Zabala and Ballesteros 1989; Miller 1998; Steneck et al. 2002; Schiel and Foster 2006). However, a variety of human impacts are responsible, directly or indirectly, for the worldwide decline of canopy-forming macroalgae in temperate regions. Increasing temperatures typically have negative impacts on the resilience of macroalgae, and the distribution of cool-water macroalgae is already retracting poleward in response to warming (Harley et al. 2012; Smale and Wernberg 2013; Steneck and Johnson 2013; Wernberg et al. 2010, 2016). Sea warming can also indirectly affect temperate macroalgae-dominated ecosystems by altering biotic interactions, such as a temperature-mediated increase in the top-down control by herbivores (i.e., sea-urchins and fish herbivores), and the intrusion of tropical herbivores into warming temperate areas tracking the migration of suitable STs (O'Connor 2009; Steneck et al. 2002; Vergés et al. 2014a; Bennet et al. 2015). In addition, other human-related impacts at local and regional scales such as habitat alteration, pollution and the outbreak of herbivorous species due to overfishing of predators are further decreasing the resilience of the native macroalgal forests (Pinnegar et al. 2000; Thibaut et al. 2005; Ling et al. 2009, 2015; Filbee-Dexter and Scheibling 2014). A major consequence of these impacts in temperate systems is an ecosystem phase shift from a state with canopy-forming macroalgae to depauperate alternative states, ranging from less structurally complex macroalgae assemblages to barren grounds.

In turn, sea warming is enhancing the poleward expansion of coral habitats by lessening low-ST stress (Hoegh-Guldberg et al. 2005; Burrows et al. 2011, 2014; Freeman 2015), which drives an increase in the abundance and a poleward shift in the distributional range of some subtropical and tropical zooxanthellate corals into temperate areas, tracking the migration of suitable STs (reviewed in Vergés et al. 2014a). The population outbreak of these range-expanding corals is further facilitated by the ongoing decline of canopy-forming macroalgae in temperate rocky reefs (e.g., McCook et al. 2001; Harley et al. 2012). Regions with continuous tropical-temperate coastlines influenced by poleward currents (i.e., transport warm tropical water into temperate areas) facilitate the poleward dispersal of marine organisms *via* their pelagic stages and have warmed two to three times faster than the global ocean (Wu et al. 2012; Yang et al. 2016), and are thus potential hotspots for such ecosystem shift in response to gradual warming. The main regions with continuous tropical-temperate coastlines include

Japan and Korea, eastern North America, eastern Australia, western Australia, northern Brazil and south-eastern Africa. In fact, a decline in cool-water macroalgae and a poleward influx and/or increase in abundance of subtropical and tropical organisms (e.g., herbivorous sea urchins and fishes, and zooxanthellate corals) have been already described in most of these temperate regions, suggesting that the tropicalization of high-latitude ecosystems is an ongoing phenomenon occurring at a global scale (Vergés et al. 2014a). Tosa Bay in southern Japan (33ºN) provides one of the most well-known examples of these consecutive phase shifts, where a temperate macroalgae-dominated healthy ecosystem during the 1980s was first replaced by barrens in the 2000s, and now barrens have been colonized by zooxanthellate scleractinian corals such as reef-building *Acropora* species, resulting in a novel coral-dominated ecosystem (Serisawa et al. 2004; Yara et al. 2011; Mezaki and Kubota 2012; Denis et al. 2013; Takao et al. 2015; Fig. 1.4b-d).

Corals play a pivotal role in the primary production, habitat complexity, structure and functioning of coral reef ecosystems, and human communities derive many benefits from coral reefs including food, recreation, coastal protection and many other ecological goods and services (Hoegh-Guldberg et al. 2009; Costanza et al. 2014). Under even lower greenhouse gas emission scenarios such as RCP 4.5, most coral reefs in tropical and subtropical regions may enter a non-coral-dominant stage before the end of the century due to sea warming (Hoegh-Guldberg et al. 1999, 2014, 2017; Pandolfi et al. 2011; Frieler et al. 2013). The ongoing new records of several tropical corals at high latitudes appear necessary but not sufficient to support the notion that whole coral reef ecosystems (i.e., biodiversity, structure and function) will migrate successfully to higher latitudes and keep up with rapid ocean warming and other human impacts (Hoegh-Guldberg 2009, 2012; Hughes et al. 2010). Nonetheless, marginal habitats for coral reefs are predicted to expand poleward in future climate scenarios (Burrows et al. 2011; Freeman 2015), and small increases in ST in the past have resulted in the appearance of coral reefs at higher latitudes (Precht and Aronson 2004; Greenstein and Pandolfi 2008), which is consistent with the hypothesis and evidences that temperate regions may serve as a refuge for tropical corals in an era of global warming. In this context, understanding the ability of such tropical and subtropical zooxanthellate coral species to adapt to environmental conditions at high latitudes is crucial to predict future responses of marine organisms and ecosystem changes in response to human-mediated impacts.

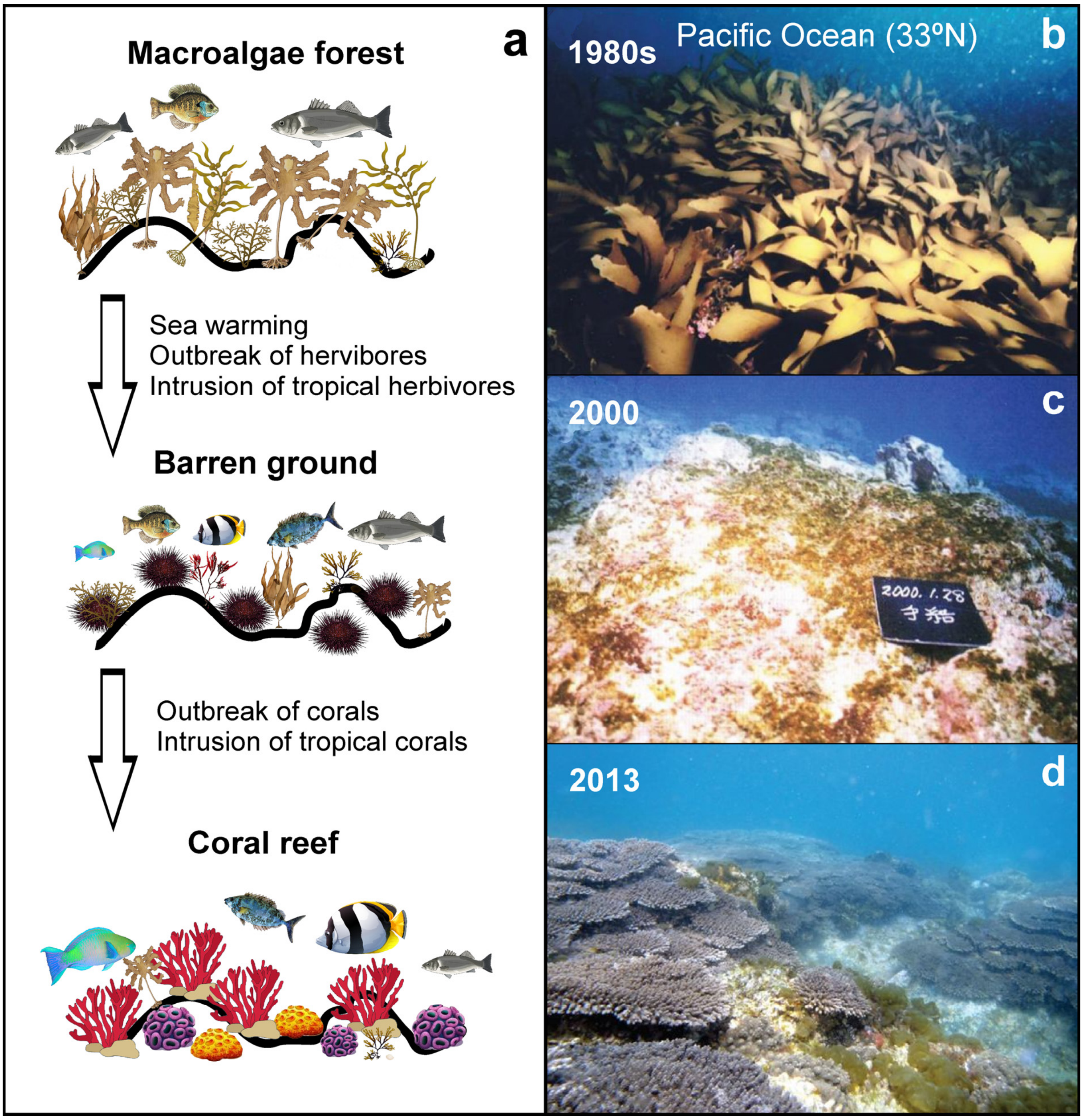


Fig. 1.4 Regime shift from macroalgae- to coral-dominance in temperate marine ecosystems. a Schematic representation showing a phase shift from a healthy macroalgae forest toward a depauperate ecosystem lacking macroalgae and structural complexity, and toward a coral reef ecosystem. The main natural- and human-mediated impacts driving these shifts are indicated. **b-d** Case example from Tosa Bay, southern Japan in the Pacific Ocean (33ºN). **b** Benthic communities of Tosa Bay were typified by high kelp *Ecklonia cava* cover and low coral cover in the early 1980s. **c** Increases in temperature and a rise in the abundance of tropical herbivorous fishes coincided with a widespread kelp loss and the formation of deforested barrens in 2000. **d** In 2013, rocky reefs had undergone a regime shift from macroalgal dominance to abundant coral communities dominated by *Acropora* species. Photographs (b-d) were taken from sites <50 m apart, by Zenji Imoto (b,c) and Yohei Nakamura (d). Adapted from Vergés et al. (2014a).

1.2. The Mediterranean Sea, a hotspot of global change

The Mediterranean is a semi-enclosed sea (i.e., a land-locked miniature ocean) that has been identified as an important hotspot of biological biodiversity with a high level of endemism, particularly in shallow-water coastal ecosystems (~20%; Margalef 1985; Bianchi and Morri 2000; Boudouresque 2004; Coll et al. 2010; Templado 2014). On the other hand, it can be considered one of the hotspots of human impacts on Earth, highly affected by historical overexploitation of marine resources, habitat loss and degradation, pollution, eutrophication, man-made infrastructures, invasive species and finally global climate change (Coll et al 2010, 2012; Lejeusne et al. 2010; Calvo et al. 2011; Katsanevakis et al. 2014; Marbà et al. 2015). The Mediterranean basin is an optimal study region for early detection and characterization of the effects of sea warming on the redistribution of marine species ranges and ecosystems for two main reasons. First, it is a semi-enclosed sea that has been warming 2 to 3-fold faster than the rate for the global ocean since at least the 1980s (Coma et al. 2009; Conversi et al. 2010; Vargas-Yáñez et al. 2008, 2010; Pecl et al. 2014; Hoegh-Guldberg et al. 2014). Second, it is a hotspot of biological invasions, with ~1,000 alien and/or cryptogenic species, and probably hosts the oldest and greatest pressure of introduction vectors in the oceans such as intense maritime traffic and aquaculture, and its connection through the Strait of Gibraltar to the Atlantic Ocean in the southwest, and through the Suez Canal (i.e., opened in 1869) to the tropical Red Sea and the Indian Ocean in the southeast (Halpern et al. 2008; Rilov and Galil 2009; Galil et al. 2015; Zenetos et al. 2010, 2017). Finally, these cumulative and interacting human-related impacts accelerated after 1980s and had already affected the biodiversity, structure and functioning of food webs and ecosystems, while these effects are expected to persist or escalate in the following years (Airoldi and Beck 2007; Coll et al. 2012; Conversi et al. 2010; Raitsos et al. 2010; Marbà et al. 2015).

Sea warming in the Mediterranean has already affected the distribution, abundance, survival, reproduction, phenology and migration of coastal marine species, enlarging the pool of alien species that could establish and enabling thermophilic species (native and alien) to expand their biogeographical range to colder waters to maintain their thermal niche (Fig. 1.2; Coll et al. 2010; Lejeusne et al. 2010; Burrows et al. 2011, 2014; Marbà et al. 2015). In fact, accelerated seawater warming after the 1980s was concomitant with the 90% of reported impacts since 1950s (Marbà et al. 2015). For instance, sea warming has increased the frequency of heat waves which have been linked to severe mass mortality events in native benthic invertebrates (e.g., sponges, cnidarians, mollusks and bryozoans) over broad geographical scales (Cerrano et al. 2000; Pérez et al. 2000; Coma et al. 2009; Garrabou et al. 2009; Crisci et al. 2011). These cold-water species may move northward to escape heat and restrict their distribution to the colder areas of the basin, but if warming intensifies these cold-water areas may act as a ‘cul de sac’. In turn, the cold isotherms during winter have shifted northward allowing the overwinter survival and driving the spread of warm-water species from southern areas into cooler northern areas (e.g., Bianchi and Morri 1993; Francour et al. 1994; Bianchi 2007; Coll et al. 2010; Raitsos et al. 2010; Calvo et al. 2011). Most alien species in the Mediterranean are shallow-water benthic or demersal species of invertebrates and fish, of tropical and subtropical origin, and therefore thermophilic (except for alien macroalgae, which most are cold-water species; Coll et al. 2010; Zenetos et al. 2017). The numbers of alien species have exponentially increased during the last decades and many have established permanent populations and extended their distributional range, showing an invasive behavior and causing severe impacts on fisheries economy, human health and displacing native species and ecosystems (Streftaris and Zenetos 2006; Galil 2007, 2009). The appearance of numerous alien species of tropical origin and the increased abundance of native thermophilic species is leading to what is called the 'tropicalization' of the Mediterranean Sea (Bianchi and Morri 2003).

Shallow-water rocky reefs in the temperate Mediterranean Sea are generally dominated by photosynthetic macrophytes such as assemblages of fleshy and coralline macroalgae (Fig. 1.5a,b) and meadows of the seagrass *Posidonia oceanica* (Fig. 1.5c). Macrophytes constitute highly biodiverse habitats of key importance, with engineer species that provide the primary source of energy and organic matter, and food and refuge to a large number of species (e.g., Ballesteros 1989,1991; Jones et al. 1994; Garcia-Rubies and Macpherson 1995; Sales and Ballesteros 2011; Sala et al. 2012; Cheminée et al. 2013). Long-lived animal species (i.e., macroinvertebrates such as sponges, cnidarians and bryozoans) with photo-suspension or suspension feeding strategies also inhabit the shallow rocky bottoms, but generally with low cover and a limited role as trophic group and as ecosystem engineers (Zabala and Ballesteros 1989). In very rare occasions, shallow rocky communities can also be dominated by bioconstructions formed by the aggregation of calcifying organisms (e.g., cnidarians, bryozoans, polychaetes and molluscs; Zibrowius 1980; Bianchi et al. 1995; Cocito 2004; Kružić and Benković 2008; Kersting and Linares 2012; Lombardi et al. 2014). The largest bioconstructions on Earth are coral reefs in tropical and subtropical regions, which are formed by a large number of reef-building, zooxanthellate scleractinian species (Kleypas et al. 1999; Veron 2000). In the Mediterranean, monospecific or oligospecific bioconstructions of native scleractinians can also constitute the dominant trophic group (Zibrowius 1980). For instance, shallow-water rocky assemblages can be dominated by bioconstructions of the azooxanthellate scleractinian *Astroides calycluaris* (Fig. 1.5d) or by dense 3-D aggregations of the reef-building zooxanthellate scleractinian *Cladocora caespitosa* (Fig. 1.5e). As addressed in this **PhD Thesis**, the zooxanthellate scleractinian *Oculina patagonica* can also form encrusting bioconstructions, being able to drive a regime shift from macroalgae- to coral-dominated states in the shallow rocky assemblages from the Mediterranean (Fig. 1.5f).

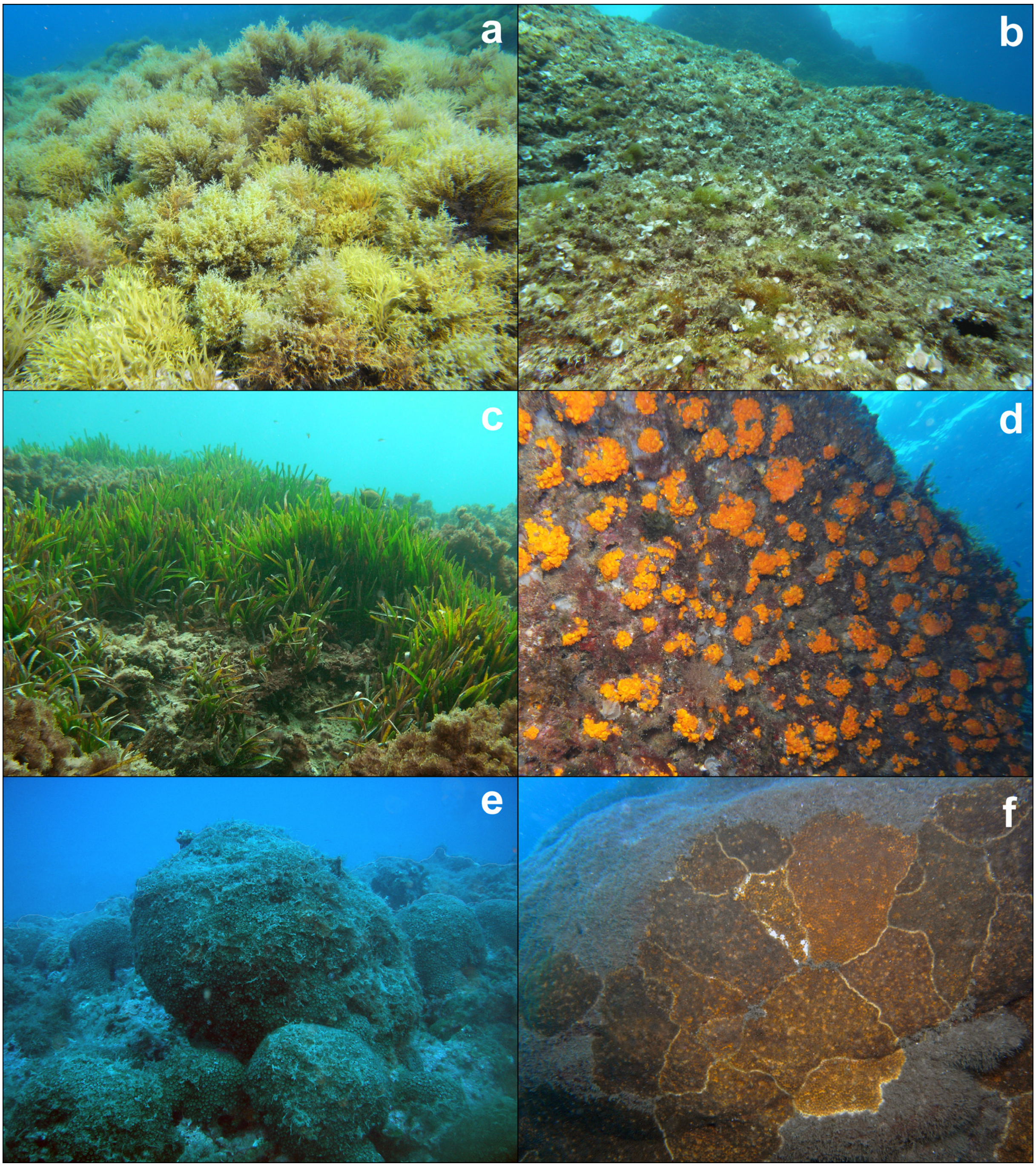


Fig. 1.5 Benthic community assemblages in shallow-water rocky reefs in the Mediterranean Sea. Community dominated by macrophytes such as **a** canopy-forming macroalgae, **b** less structured macroalgae assemblages and **c** the seagrass *Posidonia oceanica*. Community dominated by bioconstructions of calcifying organisms such as **d** the azooxanthellate scleractinian *Astroides calycularis*, and the zooxanthellate scleractinians **e** *Cladocora caespitosa* and **f** *Oculina patagonica*.

The present diversity of zooxanthellate scleractinians in the Mediterranean is very low and only five species exist (Zibrowius 1980; Hoeksema and Ocaña-Vicente 2014; see Box 1.1). However, the history of scleractinian corals in the Mediterranean is dynamic and has undergone several changes in both diversity, abundance, reef-building capacity and geographic distribution through time (e.g., the last 20 million years), particularly sensitive to the major environmental modifications on a global scale. The Early-Middle Miocene (i.e., 15-20 milion years ago) represents a flourishing time interval for shallow-water coral reefs in the Mediterranean, which nearly disappeared towards the end of the Miocene (i.e., ~5 million years ago), concomitant with the Messinian Salinity Crisis, the closure of marine seaways through the Middle East impeding the possible exchange with zooxanthellate coral faunas of the Indo-Pacific, and the decreasing STs linked with the gradual northward shift of the Mediterranean region outside the tropical belt (e.g., Bosellini and Perrin 2008; Vertino et al. 2014). Accelerated anthropogenic pressures during the last decades (e.g., sea warming, habitat alteration, pollution) appear as the main drivers for the present decline of the three native zooxanthellate corals in the Mediterranean (e.g., Kružić and Požar-Domac 2007; Kersting et al. 2013; Goffredo et al. 2008; Kružić and Popijač 2015; Kružić et al. 2016; Box 1.1), such as observed in their tropical counterparts (Fig. 1.3). In contrast, the zooxanthellate scleractinian *O. patagonica* (first recorded in the Mediterranean in 1966; Zibrowius 1974), appear to have benefited from such anthropogenic impacts, being able to abruptly increase its distribution range and abundance during the last decades (see 5.General Discussion). The spread of *O. patagonica* may affect the stability of algal assemblages as the dominant trophic group (Fig. 1.5f) and thus, challenges the present biodiversity, structure, trophic regime and function of shallow-water rocky ecosystems in the temperate Mediterranean Sea (Zabala and Ballesteros 1989), such as observed in other temperate marine ecosystems (Vergés et al. 2014a; Fig. 1.4). Given the ongoing spread and coral-mediated tropicalization of temperate macroalgae assemblages by the zooxanthellate *O. patagonica* in the Mediterranean Sea, there is an urgent need to understand the interactive effects of global change threats on the dynamics of its invasive behavior and impacts on the shallow rocky native ecosystems. Understanding of processes driving the coral-mediated tropicalization of temperate ecosystems should guide policymakers toward the best management approaches.

Box 1.1. Scleractinian corals in the Mediterranean: past, present and future trends

The present diversity of scleractinian corals in the Mediterranean is relatively low, with 26 genera and 34 species (Zibrowius 1980; Hoeksema and Ocaña-Vicente 2014), which strikingly contrast with the high diversity of reef-building corals found during the Early-Middle Miocene (i.e., 15-20 milion years ago), with over 80 genera and hundreds of species (Vertino et al. 2014). Towards the end of the Miocene (i.e., ~5 million years ago), almost all scleractinians and the tropical/subtropical coral reef province disappeared from the Mediterranean. The present assemblages of shallow-water scleractinian corals in the temperate Mediterranean are very similar to the old fossil remains found during warmer periods of the Pleistocene (i.e., from ~2.5 milion years to 10,000 years), although the geographic distribution and abundance of some species (e.g., *Astroides calycularis* and *Cladocora caespitosa*) appears to be highly reduced (Zibrowius 1995; Peirano et al. 1998; Bianchi 2007). On a global scale, the end of the Miocene corresponds to a strong decrease in the diversity of scleractinians, in particular for reef-building zooxanthellate scleractinians, and the establishment of the current latitudinal belt for the distribution of shallow-water coral reefs within tropical and subtropical regions comprised between ~35–40°N and 35°S (Perrin and Kiessling 2010).

Only five species of shallow-water zooxanthellate scleractinians currently exist in the temperate Mediterranean, two of which are considered of foreign or unknown origin (Zibrowius 1980; Hoeksema and Ocaña-Vicente 2014; Fig. 1.6). *Balanophyllia europaea* (Risso 1826) (Dendrophylliidae) is a solitary and obligatorily zooxanthellate scleractinian endemic to the Mediterranean Sea that inhabits illuminated rocky reefs up to ~50 m depth (Goffredo et al. 2007; Fig. 1.6a). *Cladocora caespitosa* (Linnaeus 1767) (family *incertae sedis*) is an obligatorily zooxanthellate scleractinian that forms globose to hemispherical colonies with phaseloid calices within illuminated rocky reefs up to ~50 m depth, being the sole endemic reef-builder in the Mediterranean (Morri et al. 1994; Peirano et al. 1998; Fig. 1.6b). Although it is a conspicuous species, *C. caespitosa* banks (3-D aggregation of large colonies up to 1 m in height, heaped and covering several square meters in surface area) and beds (groups of aggregated small colonies) are very scarce (Kersting and Linares 2012). *Madracis pharensis* (Heller, 1868) (Pocilloporidae) is a facultative zooxanthellate scleractinian native in the Mediterranean that forms small colonies (i.e., few cm in diameter and in height) with a knobby, nodular growth form (Fig. 1.6c). The zooxanthellate form of *M. pharensis* is present in relatively shaded habitats such as walls, overhangs and cave entrances, whereas the azooxanthellate form is found in obscure caves, up to ~50 m depth (Morri et al. 2000). *Oculina patagonica* de Angelis, 1908 (Oculiniidae) is a facultative zooxanthellate scleractinian that forms encrusting colonies up to 150 cm in diameter inhabiting illuminated rocky reefs within 10 m depth, and it is rarely found beyond 20 m depth (Zibrowius 1974; Fig. 1.6d). A single large colony of *O. patagonica* was first reported in the Ligurian Sea in 1966, and was considered an alien introduced species that probably arrived as a fouling organism on the hull of ships several decades ago (Zibrowius 1974), although its origin still remain unknown and it maintain a cryptogenic status (Carlton 1966; Zenetos et al. 2017). Since its first record, *O. patagonica* has been spreading throughout the Mediterranean (e.g., Fine et al. 2001; Sartoretto et al. 2008; Rubio-Portillo et al. 2014a). *Oulastrea crispata* (Lamarck, 1816) (family *incertae sedis*) is an alien zooxanthellate scleractinian first reported in Corsica, where a single colony was found in 2012, which represent the unique current record in the Mediterranean (Hoeksema and Ocaña-Vicente 2014; Fig. 1.6e). The native distribution of *O. crispata* encompass from central Indo-Pacific to Japan, where it forms encrusting colonies up to 10 cm in diameter within illuminated rocky reefs <10 m depth, being rarely found up to 20 m depth (Veron 2000).

There is growing concern for the future of the native zooxanthellate scleractinians in the light of expected seawater warming and other human-related impacts. The performance of native coral species (i.e., skeleton bulk density and porosity, coral photosynthesis, growth and reproduction, and coral population abundance and growth) along a latitudinal gradient is negatively correlated with ST (Goffredo et al. 2007, 2008, 2009, 2015; Caroselli et al. 2011, 2015; Kružić et al. 2012; Airi et al. 2014). Indeed, seawater warming has been related to mass mortality episodes during abnormally high summer STs and appears as a major driver to the decline of native corals (e.g., Cerrano 2000; Garrabou et al. 2009; Kersting et al. 2013; Kružić and Popijać 2015; Kružić et al. 2016), and new mortality events depleting native zooxanthellate scleractinians are expected to occur under projected climate warming scenarios (Marbà et al. 2015). In contrast, the cryptogenic coral *O. patagonica* has been spreading throughout the Mediterranean during the last decades (e.g., Fine et al. 2001; Sartoretto et al. 2008; Rubio-Portillo et al. 2014a), suggesting that increasing STs are less deleterious for this range-expanding species. The alien coral *O. crispata* in the Mediterranean is a cold-tolerant species that natively inhabits within tropical coral reefs and temperate non-reefal conditions, with a high tolerance for low-STs at high latitudes, suggesting that this coral could spread in the future (Yamashiro 2000; Chen et al. 2003; Lien et al. 2013; Hoeksema and Ocaña-Vicente 2014).

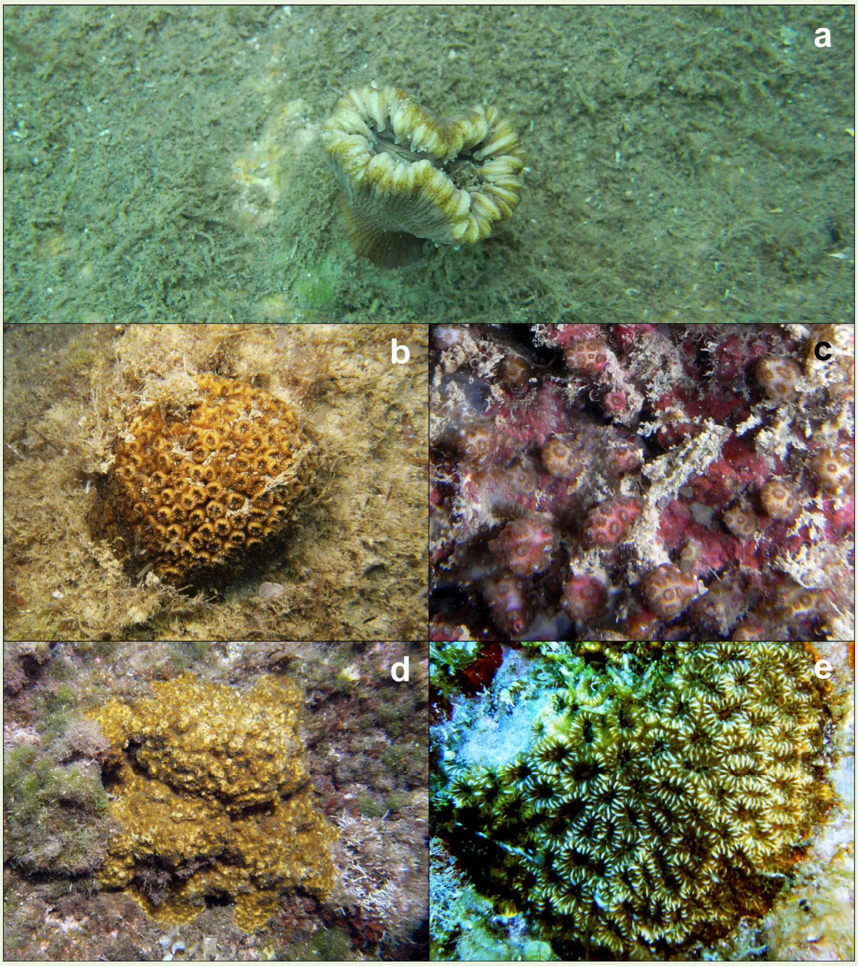


Fig. 1.6 Zooxanthellate scleractinian coral species in the Mediterranean Sea. **a** Solitary polyp of *Balanophyllia europaea*. **b** A globose colony of *Cladocora caespitosa*. **c** Knobby colonies of *Madracis pharensis*. **d** An encrusting colony of *Oculina patagonica*. **e** The encrusting colony of *Oulastrea crispata* at Corsica (photograph by Enric Ballesteros).

1.3. The range-expanding zooxanthellate coral *Oculina patagonica* as a case study

In this **PhD Thesis**, the coral *O. patagonica* (Scleractinia, Oculinidae) was selected as a biological indicator because it is a key structural engineer and long-lived species of which the distribution, abundance and function reflect alterations of ecosystem functioning (Zabala and Ballesteros 1989; Sebens 1991; Jones et al. 1994). *Oculina patagonica* is a colonial coral with a calcium carbonate skeleton that forms encrusting colonies up to ~150 cm in diameter (see Box 1.2). It dwells on rocky substrates from the intertidal zone to ~10 m depth, and it is rarely found below 20 m depth (Fig. 1.8a,b). Within the shallow-waters, it inhabits on a variety of light conditions, from well-lit to dark habitats. In well-lit and shaded rocky surfaces, the colonies appear yellowish-brown in colour due to the presence of zooxanthellae (*Symbiodinium psygmophilum*; Leydet and Hellberg 2016; Grupstra et al. 2017) in the soft coral tissues that grow onto the calcium carbonate exoskeleton (Fig. 1.8a-c). Occasionally, *O. patagonica* can thrive in dark habitats (i.e., overhangs and caves) and colonies appear white in color due to the absence of zooxanthellae (i.e., it is a facultative zooxanthellate species), so the translucent soft coral tissues allow the visualization of the underlying white calcareous skeleton (Fig. 1.8d,e). Besides the natural rocky substrates, *O. patagonica* can settle in a wide range of substrates such as concrete boulders and walls of artificial reefs (e.g., harbor dikes and breakwaters; Fig. 1.8f), and submerged metal objects and trash (e.g., plastic bags, cans, lost nylon fishing lines; Fine et al. 2001).

Box 1.2. Morphological description of *Oculina patagonica*

Oculina patagonica is a colonial scleractinian coral with a calcium carbonate skeleton formed by a group of polyps (i.e., soft tissue) and their individual calices (i.e., skeleton of polyps) that remain attached to each other through a connective coenosarc (soft tissue between polyps) and a cemented coenosteum (i.e., skeleton between calices; Zibrowius 1974; Veron 2000; Fig. 1.7a,b). Calices are round to elliptical in outline with a diameter of ~2-5 mm, and are flat or raised a few mm vertically from the coenosteum. Upon settlement, the primary polyp (i.e., founder of new colony; Fig. 1.7c) grow up asexually by intra-tentacular polyp budding and forms encrusting colonies that can reach up to 150 cm in diameter, generally of circular to ellipsoidal shape, thicker in the center with a thin edge spreading over the rocky substrates (Fig. 1.7d).

The colonies of *O. patagonica* display a wide polymorphism probably due to the variety of substrates on which it grows (horizontal, vertical and overhanging) and the distinct competition with surrounding organisms, together with the hydrodynamic conditions (Zibrowius 1974, 1992; Sartoretto et al. 2008). Two major types of colony shapes are observed (authors' observations). In habitats exposed to low competition for space (i.e., bare rock or sparse turf algae) and/or in horizontal and vertical substrates with high hydrodynamic energy (i.e., low sedimentation), the colonies of *O. patagonica* generally have an encrusting morphology (<1 cm in height) with separated polyps (Fig. 1.7e). Colonies in habitats with relatively high competition for space (i.e., erect algae in photophyllous habitats) and/or in horizontal substrates with low hydrodynamic energy (i.e., high sedimentation) generally have a more massive morphology (up to ~15 cm in height) with small branches (<5 cm in height) and densely crowded polyps (Fig. 1.7f).

Many macroinvertebrate species dwell in either the live or dead portions of the coral skeleton of *O. patagonica*, including sponges, bivalves, cirripeds, vermetid gastropods, crustaceans, polychaetes, nemerteans, sipunculans and nematodes (Bitar and Zibrowius 1997; Templado et al. 2006; Ferrero-Vicente et al. 2016; authors' observations). Some species actively bore into the calcareous coral skeleton (e.g., *Cliona* spp., *Lithophaga lithophaga*), while mobile fauna inhabit the crevices or discarded galleries found inside the calcareous skeletons.

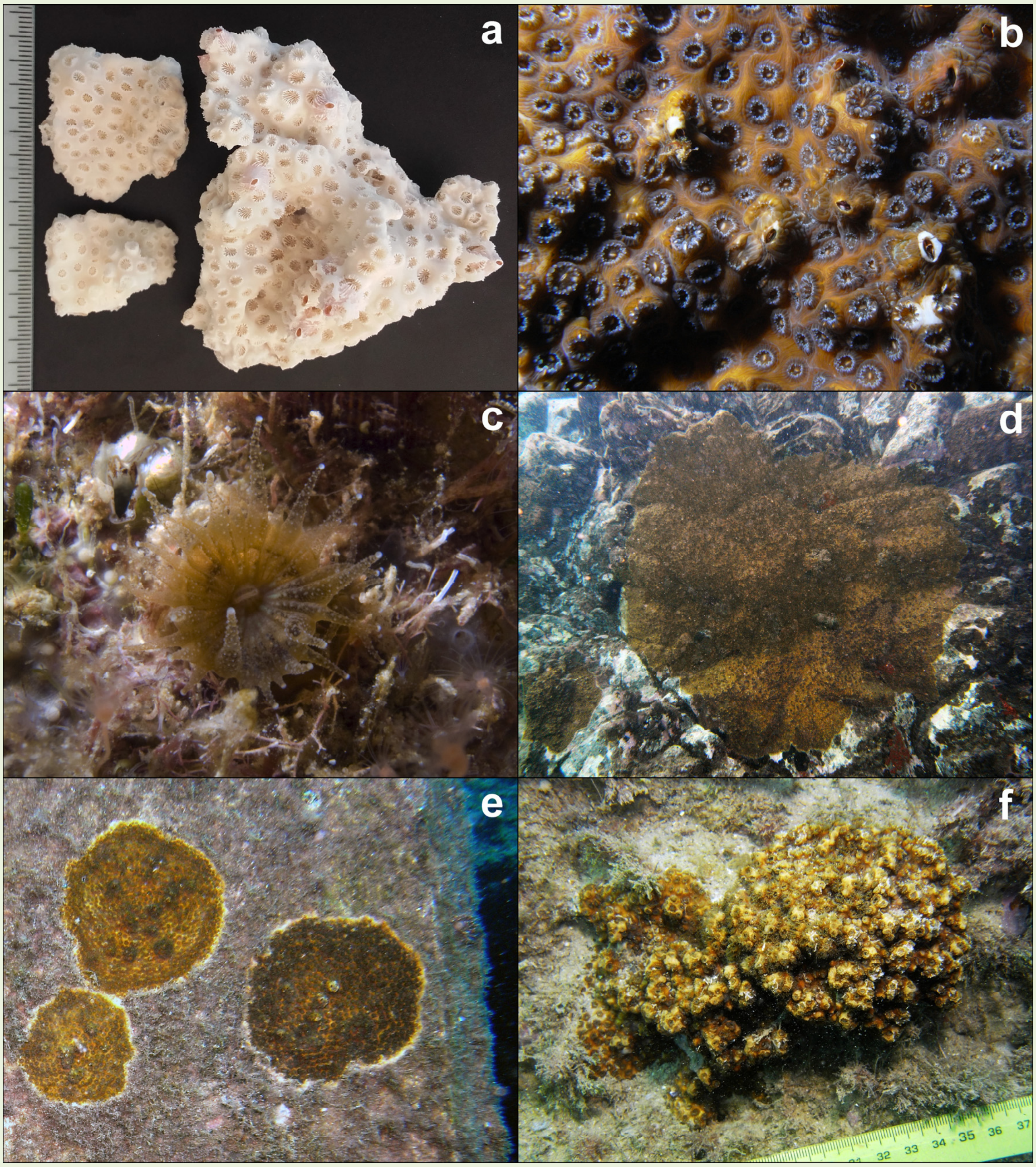


Fig. 1.7 Morphological description of the scleractinian coral *Oculina patagonica*. a Fragments of colony skeletons showing coenosteum between calices. *Scale bars* in mm. **b** Detail of a life colony showing coenosarc between polyps. Note the barnacles attached to the coral skeleton (a,b). **c** Primary polyp founder of a new colony. Note the extended tentacles containing white acrospheres, which are tips containing batteries of nematocysts. **d** A single large colony measuring ~150 cm in mean diameter. **e** Three encrusting colonies of ~1 cm in height dwelling in a smooth vertical substrate of a concrete boulder. **f** A massive colony of ~10 cm in height dwelling in a horizontal substrate with high sedimentation.

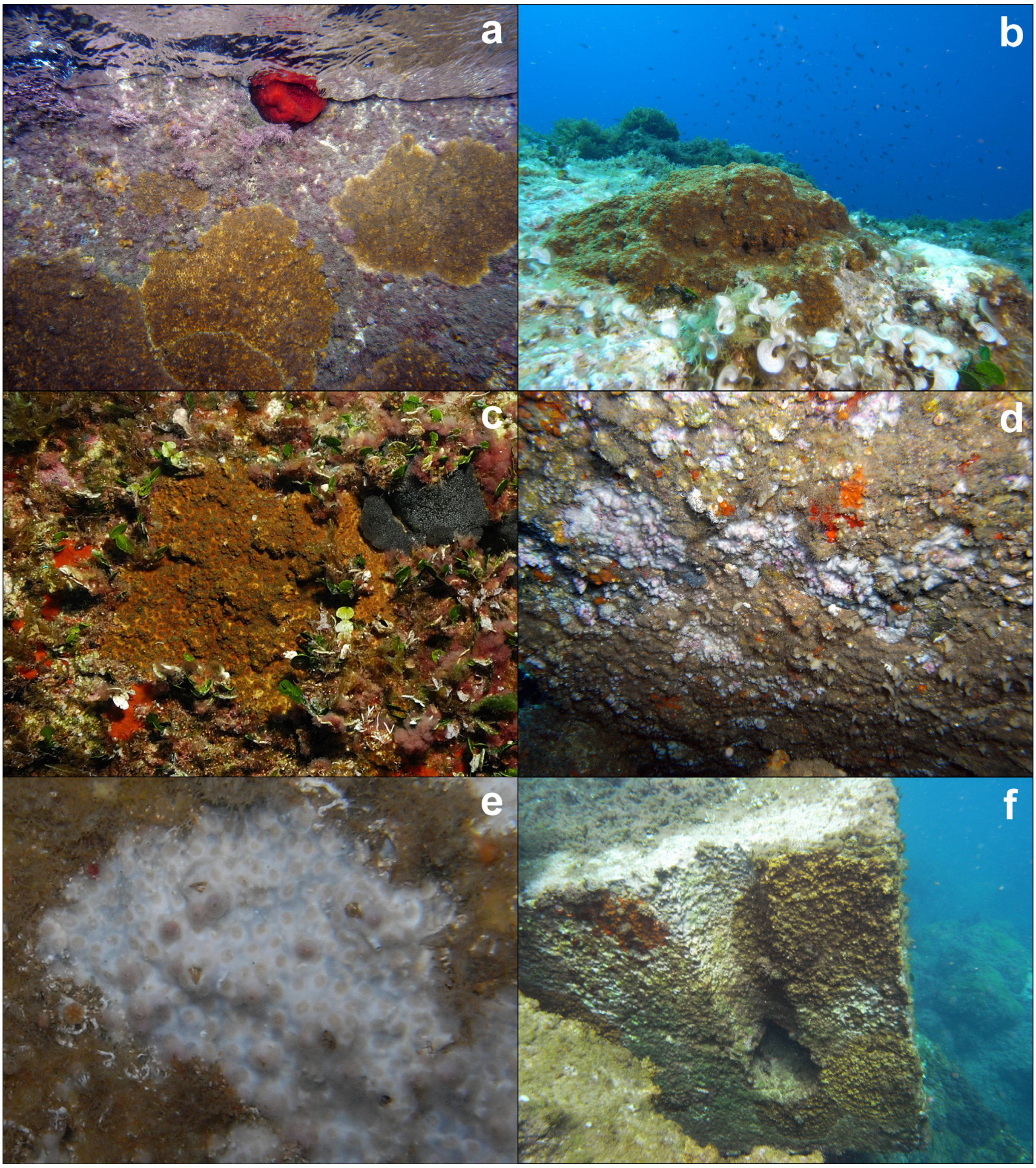


Fig. 1.8 *Oculina patagonica* inhabiting distinct types of shallow-water rocky substrates. Zooxanthellate coral colonies dwelling **a** in a vertical cliff near the sea surface, **b** in a well-lit habitat at ~10 m depth surrounded by photophilic algal assemblages, and **c** in a shaded rocky surface surrounded by sciaphillous assemblages of algae and other sessile invertebrates. **d** Azooxanthellate coral colonies dwelling in an overhanging dark habitat, and **e** colony detail showing translucent soft coral tissues. **f** Coral colonies colonizing the vertical wall of a concrete boulder in an artificial reef.

The first record of the zooxanthellate scleractinian *O. patagonica* in the Mediterranean Sea was a single large colony (i.e., 135 cm in mean diameter) discovered in 1966 in the Ligurian Sea, and this previously unknown species was identified as '*Oculina patagonica* de Angelis, 1908': a ~10,000 years old fossil species from the western Atlantic (Zibrowius 1974). Unfortunately, the origin and taxonomic identification of *O. patagonica* in the Mediterranean is uncertain (i.e., it has not been found alive anywhere else in the world) and it maintain a cryptogenic status (i.e., it cannot be reliably assigned to be either native or alien; Carlton 1966; Zibrowius 1974; Zenetos et al. 2017; see Box 1.3).

Box 1.3. Uncertain taxonomic identification of the coral *Oculina* cf. *patagonica*

The scleractinian coral *O. patagonica* was first recorded in the Mediterranean Sea in 1966, when a single large colony (i.e., 135 cm in mean diameter) was found by an amateur diver in Albissola (~1 km from the Savona harbour, Ligurian Sea; Zibrowius 1974). Previously unknown in museum collections (i.e., coral fauna was well represented, even rare, cryptic and small species) and fossil records from the Mediterranean basin, this 'new' coral species was identified as '*Oculina patagonica* de Angelis, 1908': a ~10,000 years old fossil species from the eastern coast of South America (Brazil-Uruguay-Argentina; de Angelis d'Ossat 1908). It was believed that *O. patagonica* was accidentally introduced in the Mediterranean as a fouling organism during transatlantic commercial shipping from Spain and Portugal between the XVIII-XXth centuries (Zibrowius 1974), such as other macroinvertebrate species introduced in the Mediterranean from the Atlantic and Pacific Oceans (e.g., the sea anemone *Diadumene lineata*; Ramos-Esplá 1991; López-González 1993; Dell'Angelo and Smriglio 2001; Boudouresque and Verlaque 2002).

The original identification of *O. patagonica*, based on fossil remains but not living counterparts (*sensu* Zibrowius 1974), is problematic because morphology is a poor delineation of coral species in general (Fukami et al. 2004) and among *Oculina* species in particular (Eytan et al. 2009). The origin and native range of the Mediterranean *O. patagonica* remain unknown, since living specimens still have not been found in the Atlantic, neither elsewhere in the world (Veron 2000; Schwindt et al. 2014; Veron et al. 2015). Moreover, a recent study showed that known western Atlantic *Oculina* species (namely *O. arbuscula*, *O. diffusa*, *O. varicosa* and *O. robusta*) are genetically distinct from the Mediterranean species *O. patagonica* and diverged >5 million years ago, indicating that *O. patagonica* has not been introduced into the Mediterranean from the western Atlantic in anthropogenic times (Leydet and Hellberg 2015). Thus, the current taxonomic identification of *O. patagonica* remains tentative and the species maintain a 'cryptogenic' status (*Oculina* cf. *patagonica*), as it cannot be reliably assigned to either 'native' or 'alien' in the Mediterranean (Carlton 1996; Zenetos et al. 2017). Professor John Veron and collaborators suggest in a taxonomic note that 'a new name for Mediterranean occurrences of this species is warranted' (www.coralsoftheworld.org; accessed in July 2017). Given the unsolved identification of this species, in this **PhD Thesis** I will refer to the Mediterranean *Oculina* species as *Oculina patagonica*, *sensu* the original and currently valid taxonomic identification by Zibrowius (1974).

Since the first discovery of *O. patagonica*, it has been recorded in several additional locations, and its current distribution includes most biogeographic regions from both western and eastern Mediterranean basins: Balearic Sea, Gulf of Lyons, Ligurian Sea, Adriatic Sea, Aegean Sea, Levant Sea, Algerian and Tunissian waters and Alborán Sea; and adjacent eastern Atlantic coast (Fig. 1.9 and references therein).

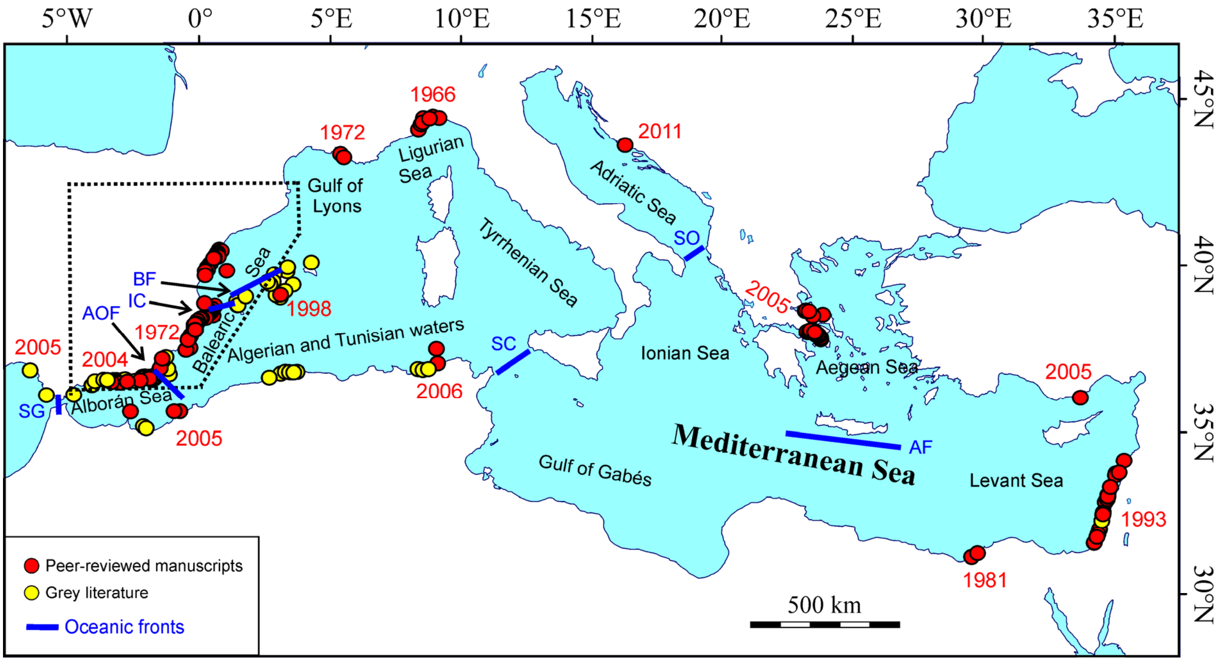


Fig. 1.9 Map of the Mediterranean Sea showing the distribution range of *Oculina patagonica*. The positions of the 279 locations in which the species has been recorded are indicated, distinguishing between records from peer-reviewed manuscripts (*red circles*), and grey literature and authors' unpublished data (*yellow circles*; updated at July 2017). The *dashed blue polygon* indicate the Mediterranean coast of the Iberian Peninsula, the study area in this **PhD Thesis** (note that the locations studied in this **PhD Thesis** are not shown). The year of first record of the species is indicated for each biogeographic region. The positions of the oceanic fronts (*SG*: Strait of Gibraltar, *AOF*: Almeria-Oran front, *IC*: Ibiza Channel *BF*: Balearic front, *SC*: Sicily Channel, *SO*: Strait of Otranto, *AF*: Aegean Front) are indicated (adapted from Millot 2005; Pascual et al. 2017). The references of *O. patagonica* records are indicated below, separated by regions and ordered in an anti-clockwise gyre starting in the Ligurian Sea:

Ligurian Sea: Zibrowius (1974); Zibrowius and Ramos (1983); Fine et al. (2001); Sartoretto et al. (2008); Rodolfo-Metalpa et al. (2006a, 2006b, 2008, 2014); Rodolfo-Metalpa (2007).

Gulf of Lyons: Zibrowius (1974, 1992); Zibrowius and Ramos (1983); Sartoretto et al. (2008).

Balearic Sea: Zibrowius and Ramos (1983); Ramos-Esplá (1985); Ballesteros (1998); Fine et al. (2001); Izquierdo et al. (2007); Junta de Andalucía (2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, personal communication); Casado-Amezúa et al. (2011, 2014); Rodolfo-Metalpa et al. (2014); Rubio-Portillo et al. (2014a, 2014b, 2016); Leydet and Hellberg (2015, 2016); Terrón-Sigler et al. (2015, 2016, personal communication); Ferrero-Vicente et al. (2016); authors' unpublished data.

Alborán Sea and Eastern Atlantic: Templado et al. (2006); Junta de Andalucía (2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, personal communication); Sartoretto et al. (2008); Moreno (2010); Terrón-Sigler et al. (2015, 2016); authors' unpublished data.

Algerian and Tunissian waters: Sartoretto et al. (2008); Lamouti and Bachari (2010, 2011); Lamouti et al. (2011); Rebzani-Zahaf et al. (2013); Bachetarzi et al. (2016).

Levant Sea: Fine and Loya (1995); Bitar and Zibrowius (1997); Kushmaro et al. (1997); Fine et al. (2001); Fine and Loya (2003); Israely et al. (2001); Shenkar et al. (2005, 2006); Çinar et al. (2006); Ainsworth et al. (2008); Sartoretto et al. (2008); Armoza-Zvuloni et al. (2011, 2012); Leydet and Hellberg (2015, 2016).

Aegean Sea: Salomidi et al. (2006, 2013); Leydet and Hellberg (2015, 2016); Dailianis et al. (2016).

*Adriatic Se*a: Cvitković et al. (2013).

The founding definition of an invasive species is restricted to alien species that successfully invade a biogeographic region outside their native distribution range and cause an adverse effect on biological diversity, ecosystem function, socioeconomic values and/or human health in invaded regions (Elton 1958). Thus, the term 'invasive species' is typically paired with adjectives such as ‘non-native, foreign and alien’. However, native species, or long-established cryptogenic species, that experience range-expansion and populations outbreaks can also cause ecological and economic impacts that rival those of well-known alien invasive species (Simberloff 2011; Carey et al. 2012). In this sense, the restriction of invasion biology to non-native species has limited ecological value, both theoretically and practically, and is highly controversial (e.g., Valéry et al. 2013). Given that the coral *O. patagonica* is a cryptogenic species (Box 1.3), it can not strictly be considered an invasive species. Further studies may elucidate if *O. patagonica* is a native species from the Mediterranean (or adjacent eastern Atlantic coasts) or if it is an alien species introduced during the XVIII-XX^th^ centuries in the Mediterranean. However, *O. patagonica* has experienced an invasive behavior in the Mediterranean (see below), and the ‘cryptogenic’ status of *O. patagonica* is not meaningful when assessing the temporal and spatial dynamics of dispersal and the impacts of its invasive behavior on native ecosystems, the main objective of this **PhD Thesis**.

Besides the origin of a species (i.e., native, alien or cryptogenic), the definition of an invasive behavior (i.e., geographical spread and populations outbreaks) generally combines two independent issues, the capacity to harm invaded ecosystems (Elton 1958; Olenin et al. 2010) and to spread geographically (Blackburn et al. 2011; see Box 1.4). The coral *O. patagonica* accomplish both requirements to be considered a species with an invasive behavior in the Mediterranean Sea. First, it has been able to challenge the ecosystem structure and function *via* regime shifting from macroalgae- to coral-dominated communities (Zabala and Ballesteros 1989; Salomidi et al. 2013; Rodolfo-Metalpa et al. 2014; Fig. 1.5f). Second, the species has displayed an invasive behavior during the last decades, experiencing disproportionate increases in distribution range and population abundances over broad geographic scales, spanning ~4,000 km in linear distance, from 6º50’W to 35º04’E in longitude and 44º20’N to 31º01’N in latitude (Fig. 1.9). The wide spread of *O. patagonica* and the persistence of numerous colonies over decades in several regions and habitat types (e.g., natural and artificial rocky reefs) provides compiling evidence of its capacity to disperse and to establish persistent and self-sustaining populations, overcoming multiple establishment events (i.e., survival and reproduction barriers) under a wide range of environmental conditions over broad geographical scales and, thus, it must be considered a species with a fully invasive behavior (Blackburn et al. 2011; Cardeccia et al. 2016; Zenetos et al. 2017). Approximately 99% of alien species are unable to overcome biotic and abiotic barriers and establish self-sustaining populations in the location where introduced (Blackburn et al. 2011; Richardson et al. 2011). Several zooxanthellate scleractinians are gradually shifting their distribution range poleward tracking the migration of STs, and/or increasing abundances in native poleward areas (reviewed in Vergés et al. 2014a; Fig. 1.4), but none has experienced a fully invasive behavior (Blackburn et al. 2011) such as that of *O. patagonica* in the Mediterranean, range shifting its distribution in multiple directions, and establishing abundant populations in several regions separated in space by ~4,000 km (Fig. 1.9). Thus, the successful proliferation of *O. patagonica* is unique and intriguing, and prompts an investigation into what mechanisms explain its invasive behavior that challenges the general dominance of macroalgae in the temperate Mediterranean (Zabala and Ballesteros 1989).

The invasive behavior of a species (i.e., range-expansion process), understood as both geographical distribution range levels and population outbreaks, has been observed to roughly follow the same sequence of stages regardless of the taxonomic identity of the invader: (i) an initial establishment phase with low spread (i.e., lag phase), (ii) an expansion phase marked by increasing spread rates and exponential growth in abundance until space becomes saturated, and (iii) a saturation phase when spread rates reach a plateau (Shigesada and Kawasaki 1997). However, the velocity of the expansion process may vary regionally within the distributional range of a species, depending on acclimatization of species' traits to regionally varying key environmental conditions modulating species' population growth dynamics (Gaston 2003, 2009; Sagarin et al. 2006). The geographical distribution range and the population growth dynamics of range-expanding zooxanthellate coral species such as *O. patagonica* may be determined by the interacting influences of species-specific biological traits, expansion history and dispersal dynamics, and the clines in abiotic factors (i.e., ST, solar radiation and nutrients) and biotic interactions (i.e., competition, facilitation, predation) that modulate species' establishment and success (i.e., survival, growth and reproduction; Brown et al. 1996; Miller and Hay 1996; Miller 1998; Kleypas et al. 1999; Gaston 2009; Guo 2014). The spatial variation in the demographics of zooxanthellate corals may reveal important differences in environmental parameters that affect the establishment, survival, growth and reproduction of corals as individuals, and becomes integrated in the abundance and colony size-frequency distribution of their populations (Bak and Meesters 1998; Meesters et al. 2001; Harriott and Banks 2002; Goffredo et al. 2008; Kružić et al. 2012; Airi et al. 2014). Although previous studies on *O. patagonica* describe its distribution and qualitative abundance at local scales, and provide insights into the underlying factors modulating coral colony growth, there is a lack of large-scale and long-term standardized monitoring which are required to understand the key ecological processes and demographical dynamics involved in the spatial variation in the success of *O. patagonica* populations across the Mediterranean.

Box 1.4. Unified framework in research on biological invasions

Blackburn et al. (2011) proposed an unified framework for research on the geographical spread and population outbreaks of biological invasions, providing a categorization for the different steps during the invasion process (i.e., concepts, terms and definitions; Fig. 1.10). A species that has been transported beyond the limits of its native geographic range (i.e., has overcome the barrier of geography) and is being found in the wild in a location where it was not known to occur previously is considered an introduced alien species. Once a species has been introduced in a new area it must pass through a series of barriers on the pathway to become established (i.e., naturalized) and invasive. An alien species can fail to establish in the new environment because individuals either fail to survive for a significant time period, or survive but fail to reproduce, being incapable of developing self-sustaining populations over a period of time corresponding to multiple generations. Once an alien species has established a self-sustaining population, the alien population can overcome the dispersal and environmental barriers and spread into locations away from the point of introduction, and thus, be considered an invasive species. For an alien species to be considered a fully invasive species, it must overcome multiple establishment (i.e., survival and reproduction) and dispersal events across a broad geographical area and habitat types, facing a wide range of environmental conditions (Fig. 1.10). Note that the successive stages of a range-expanding native species or long-established cryptogenic species (i.e., showing an invasive behavior: geographical spread, population outbreak and persistence) are broadly comparable with the invasion pathway of alien species (Simberloff 2011; Carey et al. 2012; Valéry et al. 2013).

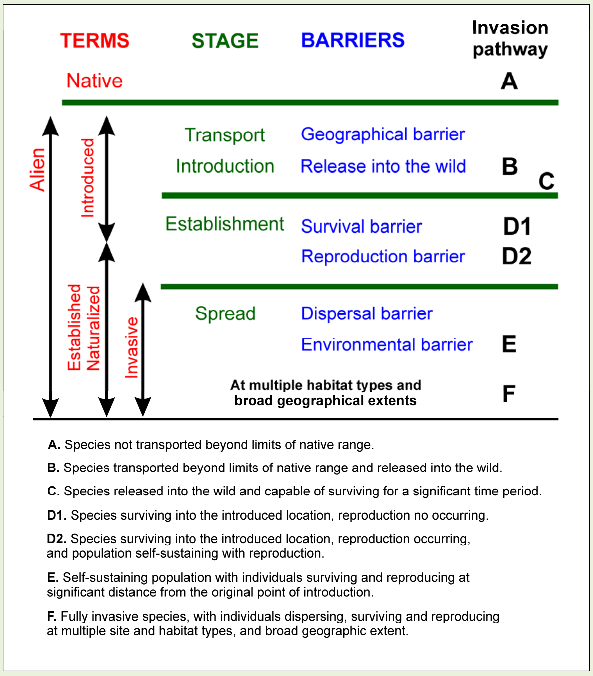


Fig. 1.10 Unified framework for concepts and definitions used in research on biological invasions. Species are referred to by different *terms* depending on where in the invasion process they have reached. The invasion process is divided into a series of *stages*, and in each stage there are *barriers* that need to be overcome for a species or population to pass on to the next stage. The *arrows* describe the movement of a species with respect to the stages and barriers, and the *alphanumeric codes* associated with the arrows relate to the categorization scheme of species with respect to the invasion pathway. Adapted to reflect aquatic ecosystems, from Blackburn et al. (2011).

The review of *O. patagonica* distribution based on previous studies indicate that the Mediterranean coast of the Iberian Peninsula is the most successful region for the species, in terms of both the cumulated coastal length and the number of recorded locations (Fig. 1.9). In this context, the Iberian coast encompass three distinct water masses (Alborán Sea, Balearic Sea and Gulf of Lyons; Millot 2005) separated by oceanographic fronts documented to constitute biogeographical barriers affecting the genetic distribution of marine species (Fernández et al. 2005; Galarza et al. 2009; Pascual et al. 2017; Fig. 1.9) and thus, represents an excellent study system in which to explore the role of environmental conditions in determining the demographics of *O. patagonica* at large spatial scales. In the present **PhD Thesis**, we first document that *O. patagonica* is experiencing an invasive behavior that challenges the present ecosystem framework within the Iberian coast, being able to form encrusting bioconstructions and drive a regime shift from macroalgae- to coral-dominated states in the natural shallow-water rocky ecosystems (**Chapter 4.1**), and to experience an invasive behavior at both population outbreak (**Chapter 4.2**) and geographical distribution range levels (**Chapter 4.3**). Second, we examine the role of abiotic factors in modulating the growth of coral colonies at the range-expanding area in the northeastern Iberian coast (**Chapter 4.4**). Third, to test the hypothesis that the growth of *O. patagonica*, which spatially competes with macroalgae, could be enhanced by the availability of open space (i.e., depauparate algal communities and barren grounds), we evaluate the effects of sand scouring (**Chapter 4.1**), sea urchins herbivory (**Chapter 4.2**) and the general availability of open space in natural benthic communities (**Chapter 4.5**) in the population growth of *O. patagonica*. Fourth, we provide a baseline quantitative assessment of its current occurrence and demographics along the whole Mediterranean Iberian coast, including natural and artificial locations (**Chapters 4.1**, **4.2**, **4.3**, **4.5**). Finally, we layered our broad spatial scale observations of *O. patagonica* occurrence, demographics and colony size-structure, together with our and previous empirical and experimental studies on the interaction between biological traits and key environmental factors modulating coral performance, to identify the causes of the geographic range structure and invasive behavior of the species along the Mediterranean Iberian coast. This knowledge is fundamental to understand the drivers modulating *O. patagonica* expansion under past and present environmental scenarios, and to predict whether its invasive behavior would substantially impact shallow-water, macroalgae-dominated rocky ecosystems in the temperate Mediterranean Sea under current global change.

2. OBJECTIVES

Photograph by Juan Carlos Calvín

Chapter 2

2. OBJECTIVES

The general objective of this **PhD Thesis** is to study the demographics and population ecology of the zooxanthellate coral *Oculina patagonica* in the Mediterranean Sea, to contribute understanding the interaction among the main intrinsic and extrinsic factors in modulating the establishment and population growth dynamics of this range-expanding species under current global change. To achieve this aim, five field studies were performed along the coast of the Iberian Penisula in the western Mediterranean, using descriptive and long-term experimental approaches. The main objectives of each study are described below:

- **Chapter 4.1. A phase shift from macroalgal to coral dominance in the Mediterranean.** The objective of this chapter was to document the first record of a shallow-water natural rocky community dominated by the zooxanthellate coral *O. patagonica*, showing that this range-expanding species is able to drive a phase shift from macroalgal- to coral-dominated ecosystems in the South-Balearic Sea.

- **Chapter 4.2. Sea urchins predation facilitates coral invasion in a marine reserve.** In this chapter the objectives were 2-fold: i) to examine the pattern of variation over a 9-yr period (2002–2010) in the abundance and colony size-frequency distributions of *O. patagonica* at a marine reserve in the South-Balearic Sea, and ii) to contribute understanding of the mechanisms that have driven the temporal pattern of variation in demographics of this species.

- **Chapter 4.3. Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean.** The objectives of this chapter were 2-fold: i) to characterize the dynamics of an ongoing northward shift in the distribution range of *O. patagonica* along ~400 km coast of the North-Balearic Sea and Gulf of Lyons over a 19-yr period (1992–2010), and ii) to contribute understanding of the main factors modulating the geographical spread of this species at high-latitudes.

- **Chapter 4.4. Recurrent partial mortality events in winter shape the dynamics of the zooxanthellate coral *Oculina patagonica* at high latitude in the Mediterranean.** The objectives of this chapter were 2-fold: i) to examine the effects of the seasonal variation in seawater temperature and light on the growth and mortality of *O. patagonica* colonies at the range-expanding area in the North-Balearic Sea over a 4-yr period (2008–2012), and ii) to contribute understanding of the main abiotic factors modulating the spread of this species at high-latitudes.

- **Chapter 4.5. Variation in demographics of the zooxanthellate coral *Oculina patagonica* along the Mediterranean Iberian coast in relation to environmental parameters.** The objectives of this chapter were 2-fold: i) to examine spatial variation in the demographics of *O. patagonica* (occurrence, density, coverage, colony partial mortality and size-structure) along ~1,300 km coast of the Mediterranean Iberian Peninsula (Alborán Sea, Balearic Sea and Gulf of Lyons) and provide a rigid quantitative baseline of its current performance (2009–2011), and ii) to contribute understanding of the role of abiotic and biotic factors in modulating the demographics of this species at large spatial scales.

Despite this PhD Thesis has been conceived as a whole, each study has been submitted as separated manuscripts for publications in scientific journals and, therefore, each manuscript was written as a standalone unit to allow independent reading. This is the reason why some points have to be repeated along the introduction and discussion of some manuscripts, somewhat that can produce an annoying sense of redundancy. Note that the coral *O. patagonica* was first described as an alien species in the Mediterranean, introduced from the western Atlantic (Zibrowius 1974), but recent genetic studies question this statement (Leydet and Hellberg 2015) and thus, its current origin status is cryptogenic. This is the reason why, in sentences from **Chapters 4.2** and **4.3**, the subject '*O. patagonica*' is sometimes accompanied by the adjective 'invasive', despite it refer strictly to species with an alien origin status (i.e., manuscripts were published in 2011 and 2013, before the evidences challenging its origin status in 2015). We sincerely apologize for these inconveniences. **Chapters 4.1**, **4.2**, **4.3** and **4.4** have already been published. Original text, figures and tables that appear in the published manuscripts have been reproduced in this **PhD Thesis**, but format has been unified in order to keep it consistent throughout the document. References have been unified in a single reference list at the end of the document.

3. ADVISERS' REPORT

Chapter 3

3. ADVISERS' REPORT

Dr. **Rafel Coma i Bau** and Dra. **Marta Ribes I Llordés**, co-advisers of this PhD Thesis entitled **'Demographics and population ecology of the range-expanding zooxanthellate coral *Oculina patagonica* in the Mediterranean Sea'**, certify that the dissertation presented here has been carried out by **Eduard Serrano i Gras** in its totality and participating in all the tasks. As advisers, we have participated in designing, guiding and correcting the chapters written by the PhD candidate.

Publication status and authors' contributions of the manuscripts of this PhD Thesis

- **Chapter 4.1. A phase shift from macroalgal to coral dominance in the Mediterranean**

Eduard Serrano, Rafel Coma, Marta Ribes

Published in Coral Reefs 31:1199 (2012). Impact Factor year 2016: 2.93

Authors' contributions: Conceived and designed the experiments: ES RC MR. Performed the experiments: ES. Analyzed the data: ES. Contributed reagents/materials/analysis tools: RC MR. Wrote the paper: ES RC MR

- **Chapter 4.2. Sea urchins predation facilitates coral invasion in a marine reserve**

Rafel Coma, Eduard Serrano, Cristina Linares, Marta Ribes, David Díaz, Enric Ballesteros

Published in PLoS ONE 6(7):e22017 (2011). Impact Factor year 2016: 3.54

Authors' contributions: Conceived and designed the experiments: RC ES CL. Performed the experiments: RC CL ES DD EB. Analyzed the data: RC ES MR. Contributed reagents/materials/analysis tools: RC EB MR. Wrote the paper: RC ES EB MR

- **Chapter 4.3. Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean**

Eduard Serrano, Rafel Coma, Marta Ribes, Boris Weitzmann, Maria García and Enric Ballesteros

Published in PLoS ONE 8(1):e52739 (2013). Impact Factor year 2016: 3.54

Authors' contributions: Conceived and designed the experiments: ES RC MR BW MG EB. Performed the experiments: ES BW MG RC EB. Analyzed the data: ES RC MR EB. Wrote the paper: ES RC MR EB

- **Chapter 4.4. Recurrent partial mortality events in winter shape the dynamics of the zooxanthellate coral *Oculina patagonica* at high latitude in the Mediterranean**

Eduard Serrano, Marta Ribes, Rafel Coma

Published in Coral Reefs 36:27-38 (2017). Impact Factor year 2016: 2.93

Authors' contributions: Conceived and designed the experiments: ES MR RC. Performed the experiments: ES RC. Analyzed the data: ES MR RC. Contributed reagents/materials/analysis tools: MR RC. Wrote the paper: ES MR RC

- **Chapter 4.5. Variation in demographics of the zooxanthellate coral *Oculina patagonica* along the Mediterranean Iberian coast in relation to environmental parameters**

Eduard Serrano, Marta Ribes, Rafel Coma

Submitted to the journal 'Science of the Total Environment'. Impact Factor year 2016: 4.90

Authors' contributions: Conceived and designed the experiments: ES MR RC. Performed the experiments: ES RC. Analyzed the data: ES RC MR. Contributed reagents/materials/analysis tools: MR RC. Wrote the paper: ES MR RC

Regarding to the authors of the different chapters, BW and MG are the only that have not been awarded a PhD degree. We hereafter guarantee that none of the information contained in the corresponding Chapter (4.3) will be used to elaborate part of a PhD Thesis.

For all the above, we consider that the contribution of the PhD candidate grants him the right to defend his PhD Thesis in front of a scientific committee.

Barcelona, January 2018

Dr. **Rafel Coma i Bau**[1]　　　　Dra. **Marta Ribes i Llordés**[2]

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4. RESULTS

Chapter 4

4.1. A phase shift from macroalgal to coral dominance in the Mediterranean

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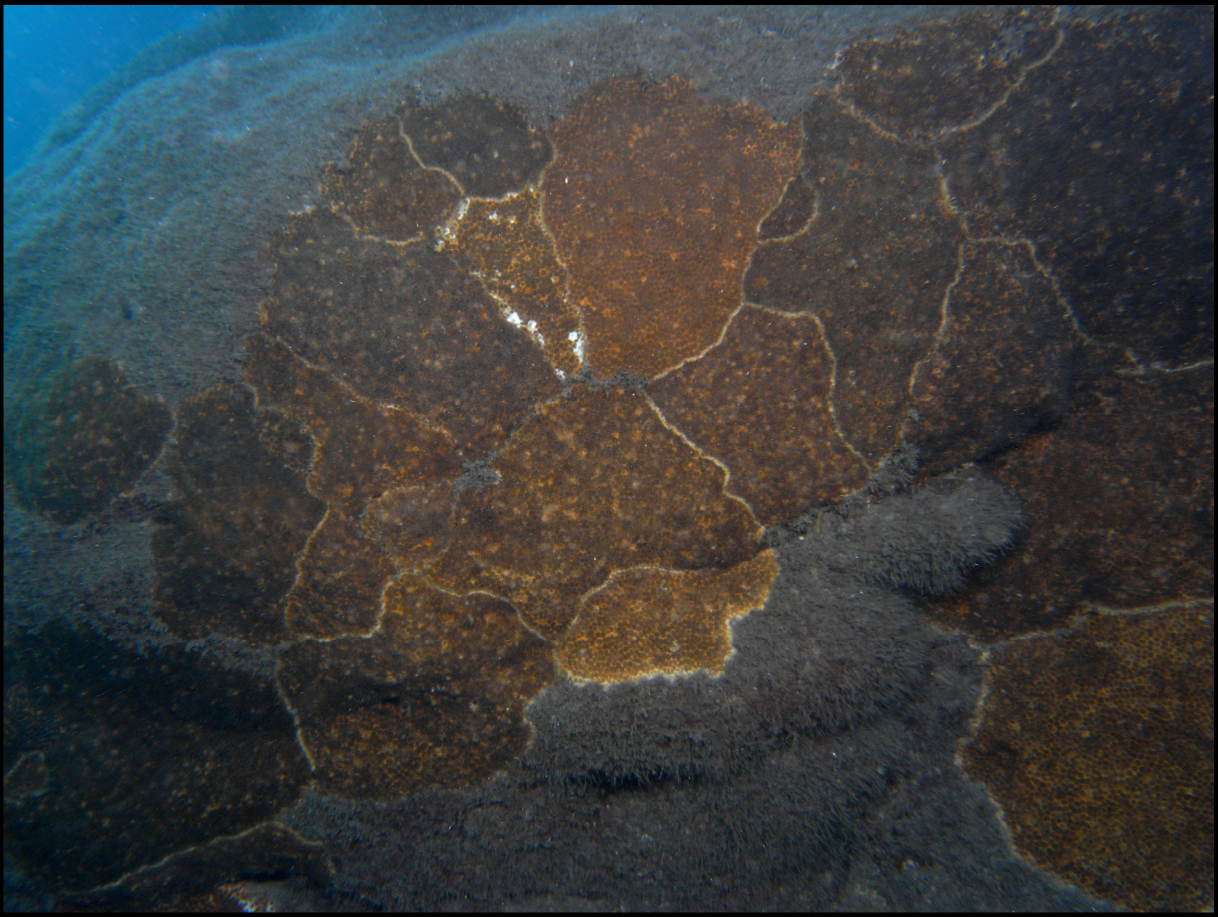
Published in: *Coral Reefs 31:1199 (2012)*

DOI: 10.1007/s00338-012-0939-3



Chapter 4.1

Reef sites

Macroalgae dominate Mediterranean shallow water assemblages, whilst corals are extremely rare. *Oculina patagonica* is a zooxanthellate coral that was first recorded in the Mediterranean in 1966 and is thought to originate in the SW Atlantic. Although it is spreading in the Mediterranean, it has never been observed as main component of a natural community. In 2009, *O. patagonica* was found to be abundant in shallow water (0–3 m depth) at Torre Pirulico in SE Spain (37º4'70"N–1º50'59"W). Based on 25 random 1-m^2 plots, the mean density was 24 (±2 SE) colonies m^{-2}, covering 55 ± 5% of the 750 m^2 study area (Fig. 1a,b). Coral colonies ranged from 0.07 to 3578 cm^2 (mean = 229 ± 11 cm^2, n = 603) and their size distribution was positively skewed with 37.5% colonies <100 cm^2, indicating that strong recruitment was the main cause of the species' high abundance. Other components of the benthic community included turf algae (36.6%), erect algae (7.3%), sponges (0.9%), calcareous-encrusting macroalgae and bare rock (0.2%) (n = 30 random 0.25-m^2 quadrats). Sea urchins were absent and physical disturbance from sand scouring (Fig. 1c) was the main source of open space for *O. patagonica* to colonize.

Whilst high cover of *O. patagonica* has been recorded on artificial habitats, cover on natural substrata is generally sparse (<15%; Fine et al. 2001; Sartoretto et al. 2008; Chapter 4.2). It is unclear how *O. patagonica* outcompetes algae and other invertebrates. Densities at Torre Pirulico are the highest ever reported. This is a coral community dominated by *O. patagonica*.

Our finding of a persistent phase shift from macroalgal to coral dominance in the Mediterranean contrasts with the reported trend in many coral reef ecosystems. Macroalgae are important primary producers in temperate coastal ecosystems and this change in the dominant trophic group may affect ecosystem function.

Acknowledgments

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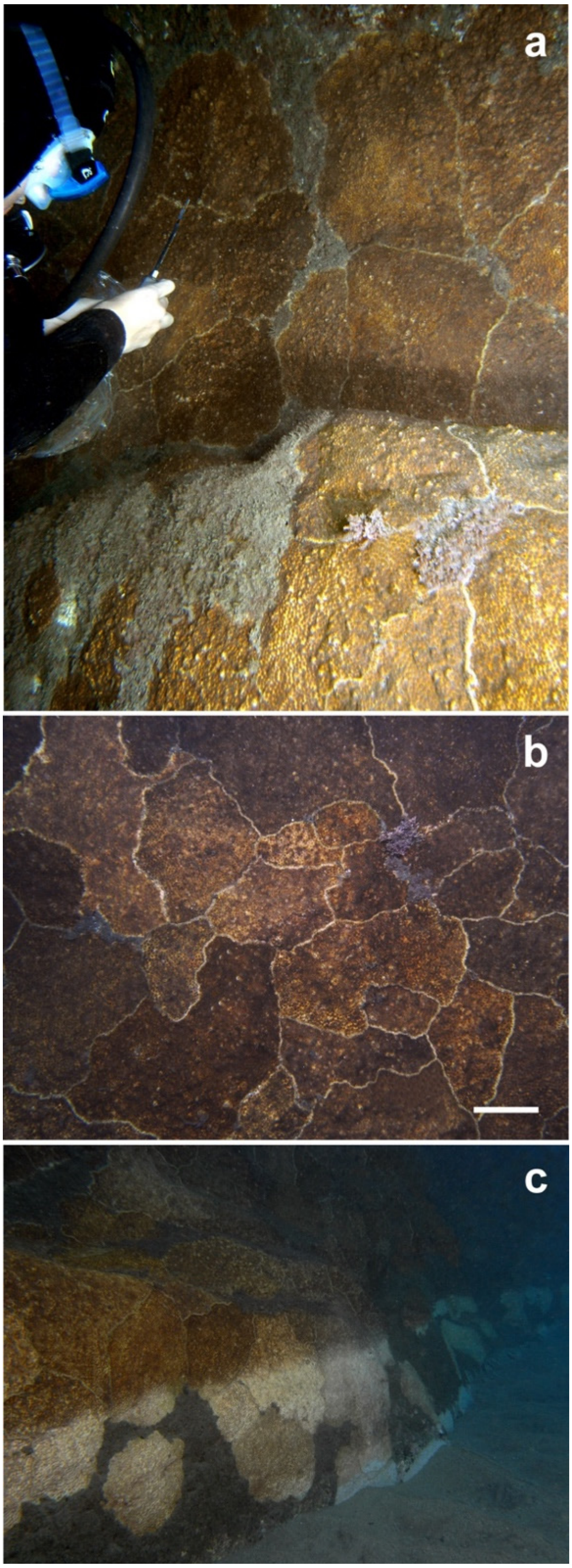

Fig. 4.1.1 a,b Community dominated by *Oculina patagonica* in the western Mediterranean. *Scale bar* 20 cm. **c** The shallow water community was severely affected by sand scouring.

4.2. Sea urchins predation facilitates coral invasion in a marine reserve

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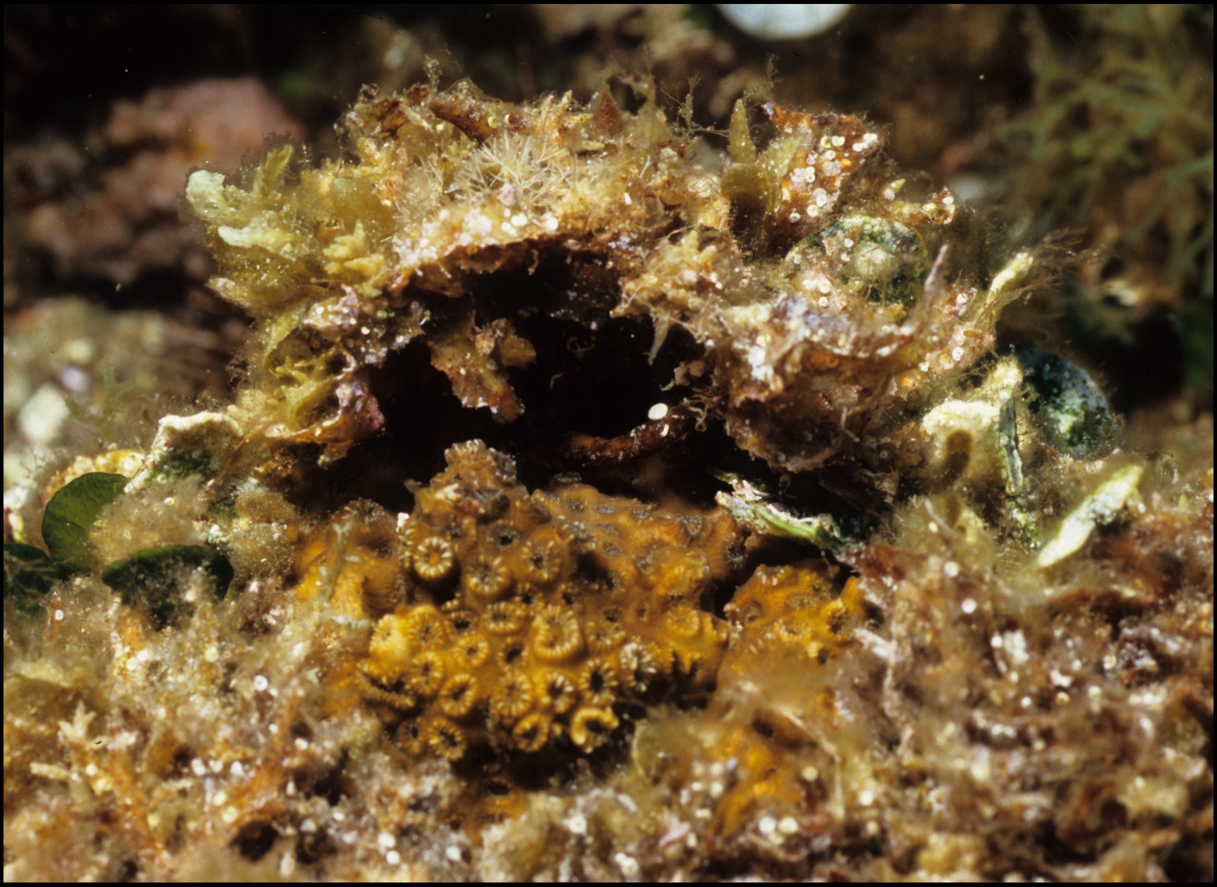

Photograph by Enric Ballesteros

Abstract

Macroalgae is the dominant trophic group on Mediterranean infralittoral rocky bottoms, whereas zooxanthellate corals are extremely rare. However, in recent years, the invasive coral *Oculina patagonica* appears to be increasing its abundance through unknown means. Here we examine the pattern of variation of this species at a marine reserve between 2002 and 2010 and contribute to the understanding of the mechanisms that allow its current increase. Because indirect interactions between species can play a relevant role in the establishment of species, a parallel assessment of the sea urchin *Paracentrotus lividus*, the main herbivorous invertebrate in this habitat and thus a key species, was conducted. *O. patagonica* has shown a 3-fold increase in abundance over the last 8 years and has become the most abundant invertebrate in the shallow waters of the marine reserve, matching some dominant erect macroalgae in abundance. High recruitment played an important role in this increasing coral abundance. The results from this study provide compelling evidence that the increase in sea urchin abundance may be one of the main drivers of the observed increase in coral abundance. Sea urchins overgraze macroalgae and create barren patches in the space-limited macroalgal community that subsequently facilitate coral recruitment. This study indicates that trophic interactions contributed to the success of an invasive coral in the Mediterranean because sea urchins grazing activity indirectly facilitated expansion of the coral. Current coral abundance at the marine reserve has ended the monopolization of algae in rocky infralittoral assemblages, an event that could greatly modify both the underwater seascape and the sources of primary production in the ecosystem.

Introduction

Natural and human-caused disturbances can trigger the fall of a dominant trophic group of organisms and the rise of another (Petraitis and Dudgeon 2004). The relevance of this change to the ecosystem varies. But, if the affected group has an important impact on elemental cycles, the change in composition can affect the flows of energy and materials (Sousa 1984; Eviner and Chapin 2003). In the marine realm, the decline of coral reefs and the shift from coral to macroalgae-dominated communities are the clearest examples of the widespread implications and consequences of these changes (Hoegh-Guldberg 1999; Bruno et al. 2009; Hughes et al. 2010). In contrast, the dominance of macroalgae in the rocky shallow infralittoral zone is a common pattern in temperate marine environments (Witman and Dayton 2001) where they represent the primary source of energy and organic matter (Ballesteros 1989). Macroalgae usually represent the dominant trophic group on Mediterranean infralittoral rocky bottoms (Zabala and Ballesteros 1989), although suspension feeders (e.g., mussels, some polychaetes) can occasionally outcompete algae in enriched (eutrophic) waters (Bellan-Santini 1968; Di Geronimo et al. 1984; Pinedo et al. 2007). Native zooxanthellate corals (e.g., *Cladocora caespitosa*) can also constitute the dominant trophic group (Kružić and Požar-Domac 2003; Kružić and Benković 2008). However, the exotic coral *Oculina patagonica* De Angelis D'Ossat 1908 has become widespread in the Mediterranean (Fine et al. 2001; Rodolfo-Metalpa 2007; Sartoretto et al. 2008) since its discovery in 1966 in the Gulf of Genova (Italy; Zibrowius 1974), which challenges present conceptual framework (Zabala and Ballesteros 1989).

Populations of *O. patagonica* were first described in 1973 as isolated colonies at some locations in the western Mediterranean. Abundant populations were observed only in areas highly affected by humans (Zibrowius and Ramos 1983). Later reports have discovered populations in natural habitats (Ramos-Esplá 1985; García-Raso et al. 1992; Fine et al. 2001; Ballesteros et al. 2008). Therefore, in addition to its geographical spread in the Mediterranean, the species appears to be increasing in abundance in some areas. This population increase may affect the stability of algae as the dominant trophic group in shallow Mediterranean rocky communities and prompts an investigation into what mechanisms are likely to be involved in the increase of *O. patagonica*.

Short- and long-term changes in shallow Mediterranean communities from natural habitats are known to be regulated by bottom-up mechanisms (nutrient availability, irradiance, catastrophic events) as well as top-down controls (mainly herbivory; Ballesteros 1989, 1991; Sala et al. 1998a; Hereu et al. 2008). But the Mediterranean is being affected by the main global change threats (i.e., overfishing, habitat degradation, pollution, species introduction and global warming; Coll et al. 2010; Simó et al. 2010). Then, anthropogenic impacts (i.e., nutrient uploads, climate change, overfishing and their associated cascading effects) interact with natural mechanisms to ultimately shape the underwater seascape on most Mediterranean shores. In this context, our understanding of the synergistic effects of global change threats on the dynamics of invasion of exotic species is still scarce. To avoid some of the anthropogenic impacts, mainly overfishing, the study was conducted at a Marine Protected Area (MPA), where management plans permit underwater assemblages to attain and maintain their natural population status (Agardy 1997).

The effects of global change threats on the population dynamics of species are unlikely to be additive but mediated by their biotic interactions (Montoya and Raffaelli 2010). Then, occurrence and determination of the effects of key species is especially relevant. Key species are species that are important to ecosystem structure and function by driving ecosystem processes or energy flow (Piraino et al. 2002). Although invasion of exotic species is a widespread threat to the integrity and functioning of native ecosystems, the role that key species play in invaded communities is still poorly known. Therefore, a major challenge to our understanding of ecosystem functioning is determining whether a few species have a preponderant role in shaping community composition (Paine 1966; Lawton 1992; Power et al. 1996).

The pattern of dominance of macroalgae in shallow habitats from temperate ecosystems is especially evident in the rocky shallow infralittoral zone from oligotrophic seas such as the Mediterranean (Ballesteros 1991), where erect algae dominate (Zabala and Ballesteros 1989). The only exception to this pattern occurs under extreme physical disturbance and/or high sea urchin densities wherein encrusting coralline algae predominate (Verlaque 1987a; Hereu 2004).

In the Mediterranean, the reduction of fish abundance is one of the main factors causing changes in the structure of rocky infralittoral assemblages (Sala 2004; Micheli et al. 2005; Guidetti 2006). However, the grazing activity of fishes, mostly *Sarpa salpa* do not create open spaces and/or coralline barrens (Verlaque 1987a). The most important biological perturbation that generates open space in Mediterranean shallow rocky habitats is herbivory by sea urchins (Benedetti-Cecchi and Cinelli 1995; Verlaque 1987b; Sala et al. 1998a; Bulleri et al. 1999). Grazing activity by sea urchins can remove algal canopies and/or prevent their recovery, providing and maintaining cleared patches in the substratum on which other organisms can settle and survive (Palacín et al. 1998a; Hereu et al. 2008). Mediterranean herbivorous fishes play a secondary role in shaping infralittoral assemblages (but see Vergés et al. 2009; Sala et al. 2011), and some predators (e.g., *Diplodus* spp.) even benefit algae by altering the behavior and abundance of sea urchins (Hereu 2006).

Studies of trophic cascades in which sea urchins play a pivotal role have contributed to an understanding of benthic community structure (Sala et al. 1998a; Pinnegar et al. 2000; Micheli et al. 2005; Guidetti 2006). Therefore, sea urchins, considered a key species in Mediterranean shallow infralittoral ecosystems because they control the growth of seaweed populations (Verlaque and

Nédelec 1983; Verlaque 1984), may contribute to an understanding of the cause of coral increase. Sea urchin densities seem to be controlled mainly by the abundance of predators, the presence of refuges and resource availability (Sala et al. 1998b; Cardona et al. 2007; Guidetti and Sala 2007; Hereu et al. 2008). Thus, the hypothesis is that an increase in the abundance of a zooxanthellate coral that spatially competes with macroalgae could be mediated by sea urchins through the creation of barren areas that enhance coral settlement or survival.

Other factors that can affect the structure and dynamics of benthic communities such as predation, competition, facilitation, diseases and environmental conditions (Hughes 1989; Knowlton and Jackson 2001; Bruno et al. 2003) should not be disregarded to contribute to the understanding of the coral pattern of variation. They were examined on the basis of our observations as well as from those of other studies in the area (see SM 4.2.1 in supplementary material, SM).

In order to understand the dynamics of *O. patagonica*, in 2002 we started an assessment of the coral population in the shallow infralittoral environments of Islas Hormigas (Murcia, SE Spain), a well-conserved Marine Protected Area (MPA) excluded of major human impacts where *O. patagonica* was already present (Fig. 4.2.1). The aims of the study were twofold: (1) to examine abundance and the pattern of variation of the coral *O. patagonica* over time in the MPA Cabo de Palos-Islas Hormigas, and (2) to contribute to the understanding of the main mechanisms that may have allowed the coral's abundance and its variation to occur.

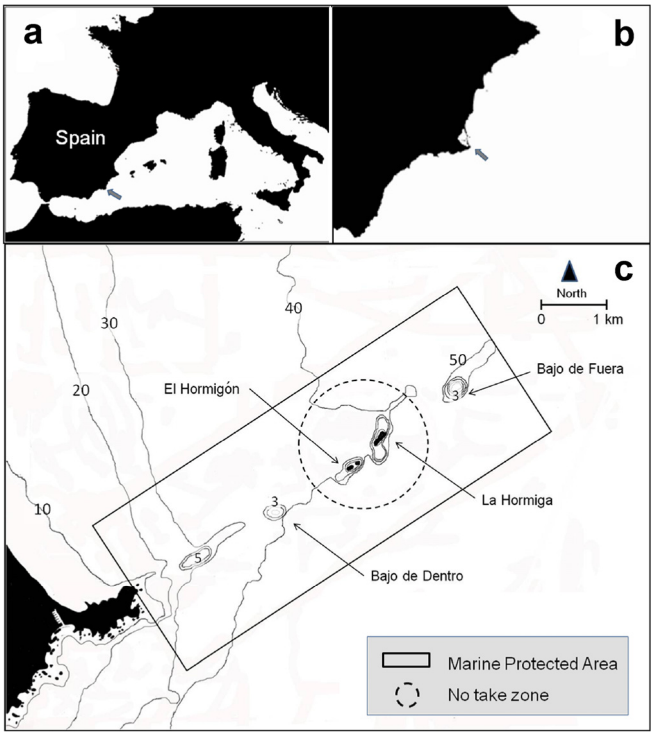

Fig. 4.2.1 Study sites. a Location of Cape of Palos (south-east Spain) in the NW Mediterranean. **b** Location of the Marine Reserve of Cape of Palos-Islas Hormigas. **c** Location of 4 study sites at the Cape of Palos-Islas Hormigas Marine Reserve: Bajo de Dentro, Bajo de Fuera, La Hormiga and El Hormigón.

Results

Density and coverage of *Oculina patagonica* over time

The density of coral colonies of *O. patagonica* increased at La Hormiga and El Hormigón (Fig. 4.2.1) over the study period (2002–2010; Fig. 4.2.2a,b). Mean density varied from 0.60 to 1.37 colonies m^{-2} at La Hormiga and from 0.75 to 1.97 colonies m^{-2} at El Hormigón. These measurements represent an average density increase of 0.091 ± 0.021 (slope ± SE) and 0.176 ± 0.027 colonies m^{-2} yr^{-1} (Fig. 4.2.2a,b), respectively, resulting in total increases of 128% and 163% for each respective location over the 8-yr time period (Fig. 4.2.2a,b).

The proportion of surface bottom occupied by *O. patagonica* varied from 2.75 to 10.34% at La Hormiga and from 5.55 to 15.09% at El Hormigón. These variations represent an average increase in cover of 0.923 ± 0.267% yr^{-1} (slope ± SE) and 1.350 ± 0.281% yr^{-1} (Fig. 4.2.2c,d), respectively, resulting in total increases of 276% and 172% for each respective location over the 7-yr time period (2003–2010; Fig. 4.2.2c,d).

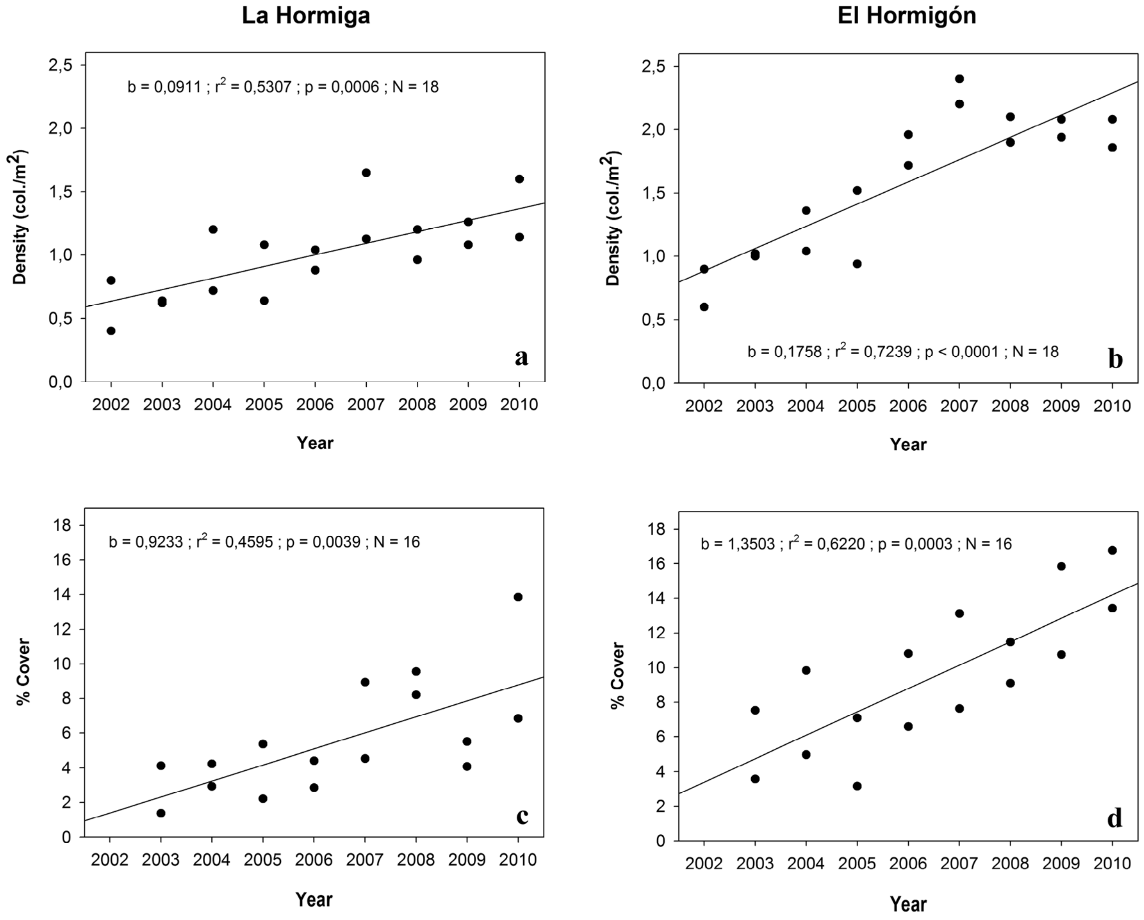

Fig. 4.2.2 Trends exhibited by the density and the coverage of *Oculina patagonica* over time at La Hormiga and El Hormigón. Pearson product moment correlations between coral density and time and between coral coverage and time are indicated.

Size structure of *O. patagonica* over time

The increase in mean colony size between 2003 and 2010 was not statistically significant (El Hormigón: $p = 0.0704$, $n = 8$; La Hormiga: $p = 0.1063$, $n = 8$; Table 4.2.1). The coefficient of variation (SD/mean) did not vary over time (El Hormigón: 1.52 ± 0.23, mean ± SD, $p = 0.3453$, $n = 8$; La Hormiga: 1.71 ± 0.39, $p = 0.9315$, $n = 8$).

The proportion of the smallest size class (0–100 cm^2) over the study period ranged from 17 to 28% at El Hormigón and from 17 to 36% at La Hormiga, indicating the prevalence of small size classes at both locations (SM 4.2.2, SM 4.2.3, Table 4.2.1; skewness provided similar information and, therefore, it is not shown). The proportion of the smallest size class exhibited its highest values from 2006 to 2007 at both locations (Table 4.2.1). These results indicate that recruitment success of the coral contributed to the density increase observed in both populations during these years. The kurtosis coefficient of the size structure of colonies at both locations showed results that were more peaked than normal distributions (Table 4.2.1) which indicates that the change in demographic parameters was recent.

Table 4.2.1. *Oculina patagonica*. Descriptive statistics regarding the size distribution of the populations at study sites. *Area*: sampled area at each site and year; *N*: number of colonies examined at each site; *sig. (>2)*: kurtosis is significant if absolute value of coefficient SE >2.

Location	Year	Area (m^2)	N	Colony size (cm^2)				kurtosis (g_2)			%Ni colonies
				Mean	SE	Min.	Max.	g_2	SE	sig. (>2)	<100 cm^2
El Hormigón	2003	100	98	417.2	63.9	4.9	4128.3	18.05	0.48	37.36	27.55
	2004	50	60	617.0	99.1	15.9	3848.5	5.23	0.61	8.60	21.67
	2005	100	123	416.7	43.5	19.6	3068.0	8.05	0.43	18.59	17.89
	2006	100	184	473.1	63.8	9.6	7854.0	40.11	0.36	112.53	28.26
	2007	100	230	451.1	50.0	7.1	7854.0	45.23	0.32	141.50	26.96
	2008	80	160	514.4	63.7	12.6	5345.6	15.63	0.38	40.99	18.75
	2009	100	201	661.6	80.2	7.1	8576.8	24.16	0.34	70.78	17.91
	2010	100	197	766.2	79.7	0.8	6013.2	7.24	0.34	21.01	17.26
La Hormiga	2003	100	63	436.7	117.6	15.9	7088.2	42.95	0.59	72.20	19.05
	2004	50	48	372.8	63.0	19.6	2164.8	8.50	0.67	12.61	16.67
	2005	100	86	434.5	79.3	19.6	6361.7	50.37	0.51	98.01	25.58
	2006	100	95	382.3	49.0	4.9	2375.8	4.85	0.49	9.90	35.79
	2007	80	111	485.3	101.6	4.9	8251.6	32.81	0.46	72.10	29.73
	2008	100	108	822.3	158.4	7.1	11309.8	19.18	0.46	41.59	16.67
	2009	100	117	409.6	57.1	7.1	5674.5	45.62	0.44	102.81	22.22
	2010	100	137	754.6	109.3	0.8	9940.2	29.94	0.41	72.80	18.25
Bajo de Fuera	2002	100	100	392.7	72.8	7.1	6361.7	46.15	0.48	96.49	34.00
	2010	50	148	402.3	44.1	0.8	2827.4	6.34	0.40	16.00	30.41
Bajo de Dentro	2002	100	55	262.1	62.9	8.3	2375.8	12.23	0.63	19.30	49.09
	2010	100	231	257.8	24.9	0.2	3318.3	30.91	0.32	96.91	35.50

Sea urchins population over time

Density of urchins increased over time (Time effect; Fig. 4.2.3; Table 4.2.2). However, the pattern of variation over time differed between both species (Time-Species interaction; Table 4.2.2). The density of both species was constant and low from 2003 to 2005 (*P. lividus* mean density: 1.73 and 2.05 individuals per m^2 (ind m^{-2}) at La Hormiga and El Hormigón, respectively; *A. lixula* density: 0.14 and 0.21 ind m^{-2} at La Hormiga and El Hormigón, respectively). Density of *P. lividus* increased and then remained constant and high from 2007 to 2010 (mean density: 4.36 and 5.51 ind m^{-2} at El Hormigón and La Hormiga, respectively). This density increase was mainly caused by the high recruitment observed in 2006 and 2007 (Fig. 4.2.3a). In contrast, the density of *A. lixula* increased steadily from 2006 to 2010 (Fig. 4.2.3b).

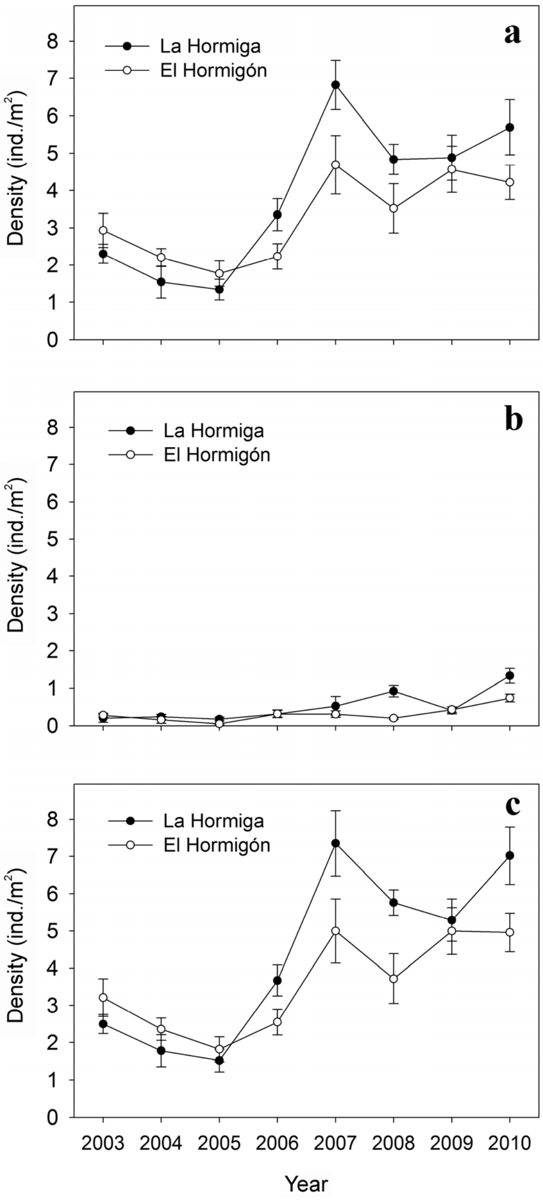

Fig. 4.2.3 Density of sea urchins (ind m^{-2}; mean ± SE) over time. Only sea urchins with >2 cm in test diameter were counted. **a** *Paracentrotus lividus*. **b** *Arbacia lixula*. **c** both sea urchins species together.

Table 4.2.2. Summary of a three-way ANOVA comparing sea urchins density among locations (La Hormiga, El Hormigón), time (2003 to 2010) and species (*Paracentrotus lividus*, *Arbacia lixula*). The species and time factors were considered as fixed in the analyses and location was randomized.

Effect	df	MS	F	p
Location	1	0.3080	13.17	0.1644
Time	7	0.7637	14.52	0.0011
Species	1	23.9064	20937.67	0.0044
Location x Time	7	0.0526	1.73	0.2427
Location x Species	1	0.0011	0.04	0.8517
Time x Species	7	0.1609	5.30	0.0214
Location x Time x Species	7	0.0304	0.68	0.6856
Error	32	0.0445		
Cochran's test			No significant	
Transform			Nil	

The abundance of *P. lividus* was about 8 times greater than the abundance of *A. lixula* (mean density 3.52 ind m^{-2} *versus* 0.41 ind m^{-2}, respectively, Species effect; Table 4.2.2). Therefore, the pattern of variation in abundance of both sea urchins over time was mainly driven by *P. lividus*. Density varied from 1.46 to 7.02 ind m^{-2} at La Hormiga and from 1.62 to 4.96 ind m^{-2} at El Hormigón, which represent an increase of 381 and 206%, respectively over the 7-yr time period, although mainly due to the increase during the 2006–2007 time-period (Fig. 4.2.3c).

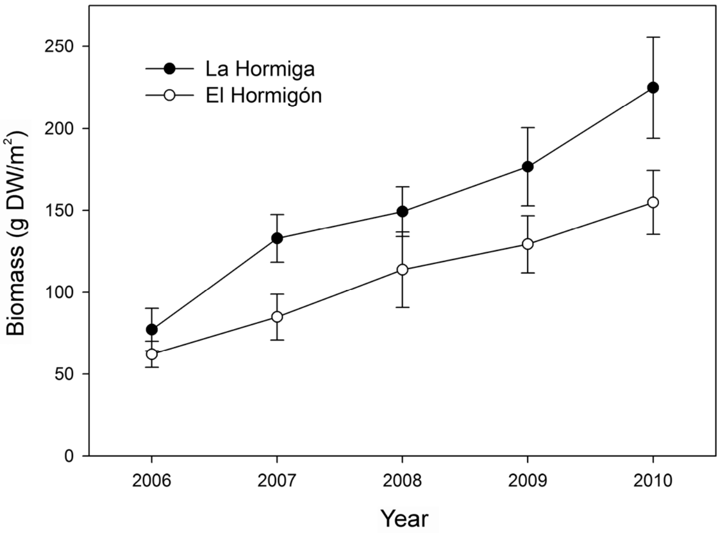

Fig. 4.2.4 Biomass (g dry weight m^{-2}; mean ± SE) of the sea urchin *Paracentrotus lividus* at La Hormiga and El Hormigón between 2006 and 2010.

We studied size structure of *P. lividus* between 2006 and 2010. The highest frequencies of small sea urchins (size class 2, 2–3 cm MTD) were found in 2006 and 2007, suggesting a high level of recruitment in the preceding years (SM 4.2.4). This recruitment appears to form the basis of the overall urchin density increase observed during this time period. However, although density stopped increasing after 2007 (Fig. 4.2.3c), the biomass of *P. lividus* demonstrated a similar increase over time at La Hormiga and El Hormigón (Fig. 4.2.4; two-way ANOVA comparing *P. lividus* biomass among locations and time, Time effect, $F_{4,10} = 18.90$, $p = 0.0073$), mainly due to the increase in mean size of the individuals (SM 4.2.4). This effect was similar in both locations (Location-Time interaction, $F_{4,10} = 0.40$, $p = 0.80$).

Sea urchins and coral abundance

The abundance of *O. patagonica* (density and coverage) at the scale of 50 m^2 was strongly related to sea urchin densities at La Hormiga and El Hormigón over the study period 2003–2010 (Fig. 4.2.5).

In 2002 and 2010, an examination of coral density at two other locations (Bajo de Dentro and Bajo de Fuera; Fig. 4.2.1) allowed us to determine whether the increase in abundance observed at La Hormiga and El Hormigón was also present at other locations. Density of coral colonies increased over time at all four locations (2-way ANOVA comparing coral colonies density among locations and time, $F_{1,-} = 48.06$, $p = 0.0056$; Fig. 4.2.6). However, the increase in coral colony density did not differ among locations ($F_{3,3} = 1.68$, $p = 0.34$; Fig. 4.2.6).

Levels of sea urchin density at Bajo de Dentro (8.6 ± 0.8 ind m^{-2}, mean ± SE) and Bajo de Fuera (9.6 ± 0.7 ind m^{-2}) were similar to those observed at La Hormiga (7.0 ± 0.8 ind m^{-2}), and higher than those observed at El Hormigón (5.0 ± 0.5 ind m^{-2}) (one-way ANOVA comparing sea urchins density among locations in 2010, $F_{3,36} = 4.93$, $p = 0.0057$; Scheffe's contrast test).

These results reveal a local-scale pattern of increase in the abundance of both coral colonies and sea urchins. The pattern has occurred in four places that are nearby to each other (within 4 km distance) but separated by 50–80 m deep channel (two of the locations are small islands, La Hormiga and El Hormigón, and the other two, Bajo de Dentro and Bajo de Fuera, are rocky bommies).

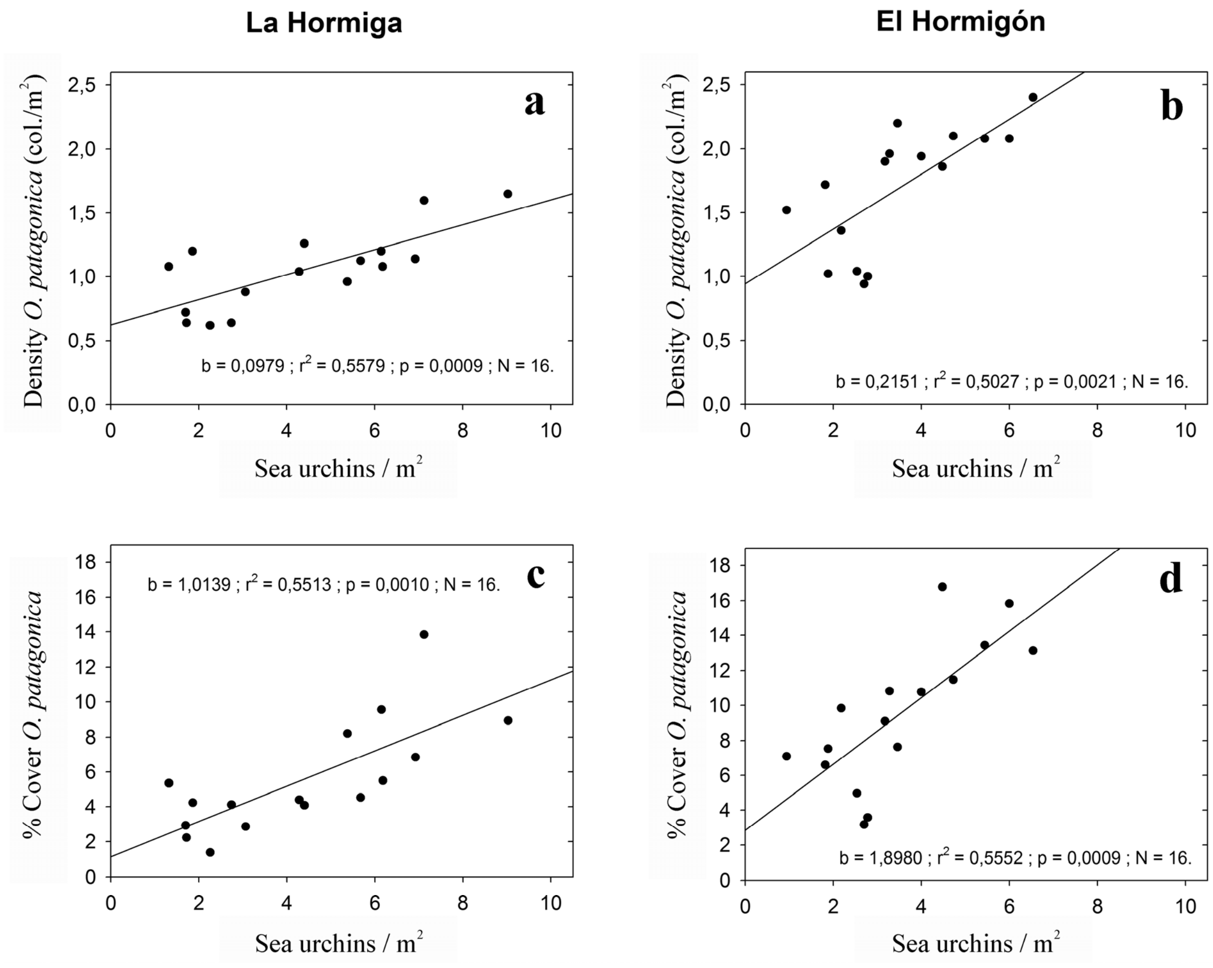

Fig. 4.2.5 Pearson product moment correlation between the density of both sea urchin species (*Paracentrotus lividus* and *Arbacia lixula*) and abundance of the coral *Oculina patagonica* at both studied locations: La Hormiga, **a** density and **c** cover; El Hormigón, **b** density and **d** cover.

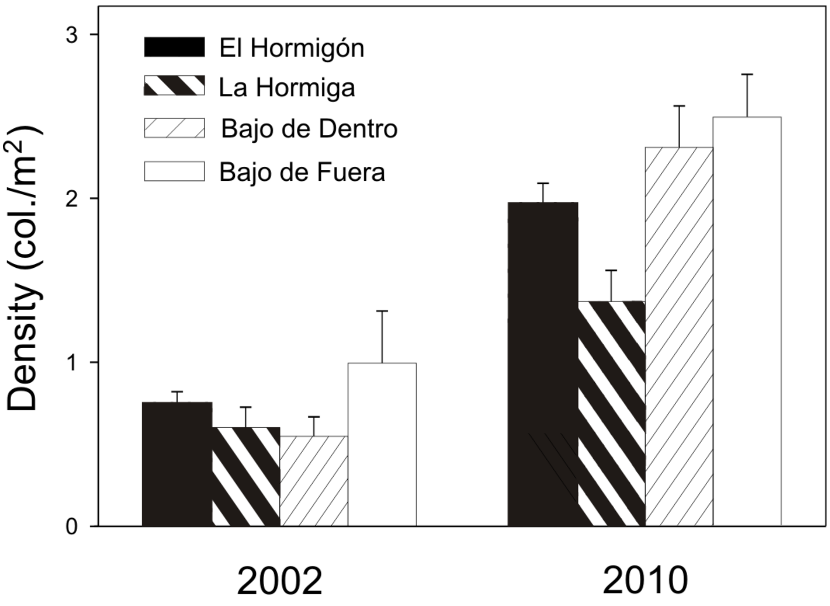

Fig. 4.2.6 Density of *Oculina patagonica* colonies in 2002 and 2010 at the four studied sites.

Colony size and presence in open spaces

Open spaces on the substrata were common at La Hormiga and El Hormigón and were covered by encrusting corallines or bare rock. The number of open spaces associated with *O. patagonica* did not differ between the two locations (La Hormiga and El Hormigón; two-way ANOVA comparing abundance of open spaces associated to coral colonies among locations, main effect location: $F_{1,3,1501}$ = 0.02, p = 0.91) or over time, despite showing an increasing trend (2005, 2006, 2007, 2010; main effect Time, $F_{3,-}$ = 1.43, p = 0.3886). On average, the mean number of open spaces associated with coral colonies over the entire study period was 3.68 ± 0.23 (SE) per 10 m^2. The mean size of these open spaces was 0.81 ± 0.34 (SE) m^2 in 2010. The proportion of space occupied by open spaces (16.0% ± 1.9; mean ± SE) did not differ between both locations (One-way ANOVA comparing proportion surface bottom occupied by open spaces among both locations, $F_{1,38}$ = 2.47, p =0.12).

The contrast between the expected proportion of small colonies (up to 100 cm^2) associated with open spaces and the observed proportion (see methods) is shown in Fig. 4.2.7. The observed number of small colonies associated with open spaces was larger than that expected on the four sampled occasions (2005, 2006, 2007 and 2010; Chi-square, χ^2 = 25.79, df = 3, p <0.0001). Thus, small colonies were found to be present on open spaces about 68% more frequently than expected according to random distribution.

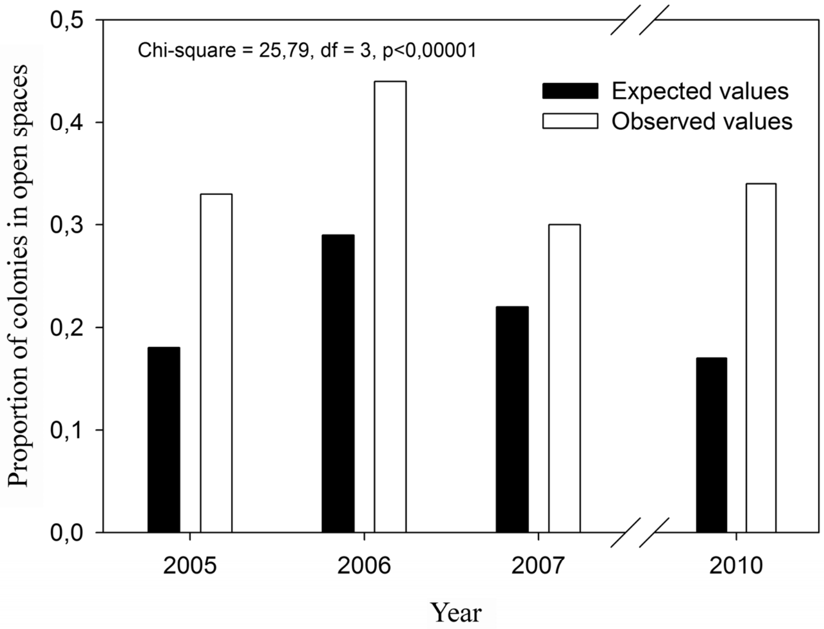

Fig. 4.2.7 Contrast between the observed proportion of small colonies (up to 100 cm^2) on open spaces and that expected from the consideration of the abundance of the different colony size classes and their random distribution on open spaces in 2005, 2006, 2007 and 2010.

Discussion

Causes of variation in coral abundance

The increasing abundance of coral colonies of *Oculina patagonica* at the studied MPA from 2002 to 2010 is likely driven by environmental conditions that favor coral's growth. Two main requirements must be met for *O. patagonica* to be able to increase its abundance in a space-limited habitat such as the one in this study: 1) an increase in space availability driven by physical disturbances (i.e., storms) and/or biological interactions (i.e., overgrazing); and 2) the capacity of the species to recruit, grow and survive.

Physical perturbations, such as large storms, can create open spaces (Witman 1987) such as those observed at the study sites. However, over the study period, open spaces have regularly been observed at the study sites despite a lack of large storms over the study period (authors' observations; García-Charton et al. 2008b).

Abundance of the main herbivorous fish species (*Sarpa salpa*) did not vary over the study period (García-Charton et al. 2008b), nor can they create open spaces (Verlaque 1987b). In fact, the most important biological perturbation that generates open space in Mediterranean shallow rocky habitats is herbivory by sea urchins (Verlaque 1987a; Sala et al. 1998a). A threshold of 7–9 adult sea urchins m^{-2} may cause an ecological shift from macroalgae assemblages to coralline barrens (Verlaque 1987b; Hereu 2004). Current sea urchin abundance in the study area (5–9 ind m^{-2}) is similar to densities known to cause barrens, and is therefore great enough to be considered a feasible explanation for the open spaces regularly present at our study sites.

The second requirement necessary for coral colonies to increase in abundance is the capacity of the coral species to recruit, grow and survive. Statistical results concerning the size structure of the coral colonies identifies high recruitment as a main factor causing this increase in coral abundance. This result is consistent with evidence that recruitment can also be a critical cause of changes in coral-macroalgae abundance (Hughes 1996; Hughes and Tanner 2000; Elmhirst et al. 2009). However, in this study, recruitment did not result in a decrease in mean colony size (Table 4.2.1), which indicates that the species is indeed meeting its requirements for growth and survival.

The polychaete *Hermodyce carunculata* appears to be the main predator of *O. patagonica* in the Mediterranean (Fine et al. 2002). The presence and the effects of this worm were observed on very rare occasions during the study (see SM 4.2.1). Therefore, predation does not seem to be an important factor affecting the coral populations at our study sites.

Sea surface temperature in the NW Mediterranean is exhibiting a pattern of increase (Vargas-Yáñez et al. 2010) and current evidence indicates that the coral species may benefit from the lengthening of the growing season due to the warming pattern (Rodolfo-Metalpa et al. 2008; Coma et al. 2009). However, analysis of the SST data showed that lengthening of the growing season did not vary over the study period nor did mean annual temperature (see SM 4.2.1). These results are most probably related to the short-term oscillatory pattern that sea water temperature exhibits in the NW Mediterranean (Vargas-Yáñez et al. 2010). Therefore, the observed pattern in coral abundance can not be attributed to a variation in sea water temperature.

At the study area, an increase in sea urchin population density would increase the availability and persistence of cleared patches, the first crucial step for the establishment of coral colonies. This observation is in agreement with the observed relationship between sea urchins abundance and that of *O. patagonica* (Fig. 4.2.6). Furthermore, the presence of small coral colonies that have settled preferentially on areas cleared by sea urchins (Fig. 4.2.7) and the size of the cleared spaces provide compelling evidence about the positive relationship between sea urchin density and coral abundance. This result, together with the observed pattern of coral recruitment, implies that the increase in sea urchins abundance is one of the main causes of the increase in density and coverage of coral colonies (Fig. 4.2.8).

Although a causal relationship cannot be inferred from the statistical correlation observed between the abundance of coral and sea urchins, the existence of the correlation is a proof of concept of the basic idea underlying the hypothesis. It is apparent that sea urchin grazing promotes the recruitment of *O. patagonica* colonies, in accordance with results obtained in coral reef ecosystems (Sammarco 1980; Edmunds and Carpenter 2001; Carpenter and Edmunds 2006). Thus, interspecific facilitation appears to be one of the main mechanisms involved in the observed increase in abundance of coral colonies (Fig. 4.2.8). These results highlight the crucial role that herbivory by sea urchins appears to play in increasing the abundance of coral colonies.

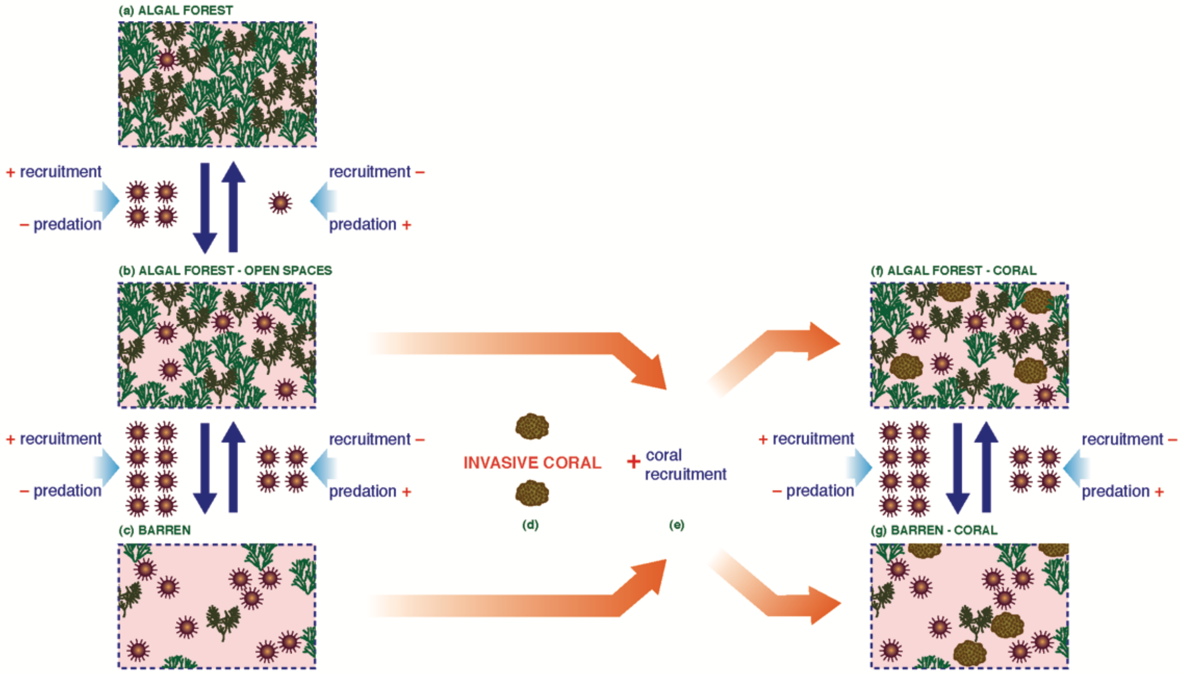

Fig. 4.2.8 Schematic representation of the observed interactions. The two major assemblages in Mediterranean rocky infralittoral ecosystems are represented at the left side: **a** erect algal forest and **c** coralline barrens. Variations in sea urchins density and their grazing impact is the main driver of the shift from algal forests to coralline barrens and *vice versa*. **b** Intermediate densities of sea urchins create and maintain open spaces in the space-limited algal forest. These open spaces are usually filled up again by erect algae in a dynamic process of creation and removal of open spaces. However, under the presence of the invasive coral *Oculina patagonica* **(d)**, these open spaces facilitate coral recuitment **(e)** and increase the abundance of the coral to the extent of matching that of some dominant erect macroalgal species. Therefore, under the presence of *O. patagonica* and high to medium sea urchin grazing, two new assemblages flourish: **f** an algal forest-coral assemblage and **g** a coral-coralline barren assemblage, depending on the abundance and grazing impact of sea urchins.

The main fish species identified as successful sea urchin predators are the Sparidae *Diplodus sargus*, *Diplodus vulgaris* and *Sparus aurata*, and the Labridae *Coris julis*, *Labrus merula*, *Labrus viridis*, *Symphodus roissali* and *Symphodus tinca* (Quignard 1966; Khoury 1987; Sala 1996, 1997). Populations from all these fish species have not varied significantly over the study period (García-Charton et al. 2008b). Nutrient levels and the presence of sea urchins refuges did also not vary over the study period (García-Charton et al. 2008b). Therefore, recruitment appears to be the primary factor contributing to the increase in sea urchins abundance. Although the factors responsible for large fluctuations in sea urchin abundance remain poorly understood, there is evidence that high level of recruitment can outweigh fish predation (Sala et al. 1998a; Boudouresque and Verlaque 2007). Our study provides evidence that a change in the demography of a sea urchin species can drive a relevant change in community structure. Under unchanged fish predation, nutrients and refuge conditions, the increase of *P. lividus* biomass resulted from both a high recruitment and a good period of growth for sea urchins. Two non-exclusive causes may have contributed to the success of *P. lividus*: i) favourable climatic conditions, and ii) low predation on reproductive populations and on planktonic larvae. However, this study can not distinguish between both causes and, most probably, it may have been a combination of them.

Relevance of the current coral abundance

The percent cover observed for *O. patagonica* at our study sites (10–15%) was only slightly lower than those reported for total coral cover in coral reef ecosystems (e.g., Great Barrier Reef: 27%, Indo-Pacific: 22%, Caribbean: 7%, Florida Keys: 16%; Bruno and Selig 2007; Bruno et al. 2009; Hughes et al. 2010), emphasizing the importance of this species within the benthic community of this temperate ecosystem.

Macroalgae species composition exhibits regional, bathymetric and seasonal changes in the biomass of the dominant species (Ballesteros 1991). Interannual changes have also been documented in relation to species substitution, sea urchin activity and overfishing (Boudouresque et al. 1990; Sala et al. 1998a; Thibaut et al. 2005). However, none of these spatial and temporal variations imply a change in the dominant trophic group (i.e., all changes involve algal species). Even in the case of successfully introduced species, changes in dominant species generally involve the replacement of the dominant algal species by an exotic algae species (Boudouresque and Verlaque 2002).

Algal assemblages at the study sites were dominated by different species of macroalgae as it is the case in other well-conserved areas in the central western Mediterranean (Calvín 2004; Martí et al. 2005). No relevant changes on relative abundance of the main dominant macroalgae species was observed over the study period but a decrease in abundance of *H. scoparia* (see SM 4.2.1).

Detailed data using photo-quadrats (Martí et al. 2005) in similar shallow infralittoral habitats illustrate that erect macroalgae account for roughly 69.9–91.0% of surface cover, calcareous encrusting macroalgae account for 28.6–7.5% cover and invertebrates (mainly sponges) account for the remaining 1.5%. Therefore, the current coverage of *O. patagonica* at the study sites is unusual for Mediterranean shallow water assemblages, matching the abundance of several species of dominant erect macroalgae. Thus, *O. patagonica* is able to initiate an important change in community structure and end the monopolization of algae in shallow assemblages, an event that could greatly modify both the underwater seascape and the sources of primary production in the ecosystem.

Despite the differences between the temperate Mediterranean and coral reef environments, the observed processes may be similar to those observed in the Caribbean, where the recovery of *Diadema antillarum* populations is known to have enhanced coral recruitment (Edmunds and Carpenter 2001;

Carpenter and Edmunds 2006). However, in Caribbean coral reef communities, as in those in other areas, the positive effects of urchins on coral may be diminished or even negated by increases in coral diseases, temperature-related mortality, and coastal habitat degradation (Hoegh-Guldberg 1999; Jackson et al. 2001; Harvell et al. 2004). Like the Caribbean, the Mediterranean is also affected by coastal habitat degradation, rising temperatures and diseases (Vargas-Yáñez et al. 2010; Coma et al. 2009; Ivanov et al. 2009; Lejeusne et al. 2010). However, in the western Mediterranean these disturbances appear to be affecting *O. patagonica* less than other suspension-feeders thriving in similar habitats, such as *Cladocora caespitos*a and different species of sponges, which have been severely affected by recent mass mortality events (Pérez et al. 2000; Garrabou et al. 2009; Cebrian et al. 2011).

Our study describes the processes causing the increase of *O. patagonica* inside a single MPA. However, the increasing number of areas that this coral has been reported in the western Mediterranean (Sartoretto et al. 2008) suggests that the processes described here could also be underway in other areas. In addition, this growth and expansion could be linked to an increase in sea urchin populations related to changes in the food web directly or indirectly enhanced by overfishing or pollution (Verlaque 1984; Sala et al. 1998a; Pinnegar et al. 2000; Thibaut et al. 2005; Eklöf et al. 2008).

Shallow infralittoral rocky bottoms in the Mediterranean are undergoing profound changes that result in the disappearance of important habitat engineering species (Thibaut et al. 2005; Hereu et al. 2008). These changes are often linked to overfishing (Sala et al. 1998a), habitat destruction (Thibaut et al. 2005), invasive species (Boudouresque and Verlaque 2002), mass mortality events (Rodolfo-Metalpa et al. 2005; Maldonado et al. 2010; Cebrian et al. 2011) or pollution (Arévalo et al. 2007). In this work, we document that the selective predation by sea urchins on the dominant species (macroalgae) created open spaces that enhanced coral settlement and survival. Therefore, within the conditions of the study, trophic interactions contributed to the success of an invasive coral in the Mediterranean because sea urchins grazing activity indirectly facilitated expansion of the coral (Fig. 4.2.8). We have also presented evidence that the invasive zooxanthellate coral is growing in abundance to levels completely unexpected in the Mediterranean, an event that challenges the current conceptual framework (Zabala and Ballesteros 1989), offering an excellent opportunity to study the mechanisms that sustain present benthic communities in this habitat. Furthermore, we discovered new evidence regarding the crucial role of sea urchins in Mediterranean infralittoral communities by demonstrating that sea urchin grazing activity not only causes changes in algal composition, but also facilitates the expansion of an invasive coral.

Materials and Methods

Study area

The study was conducted at the Cabo de Palos-Islas Hormigas Marine Reserve which is located in the southeastern part of the Iberian Peninsula (Cape of Palos: 37º38'01"N–0º41'04"W).

Sampling

The density and size of coral colonies of *Oculina patagonica* was assessed at 4 locations (Fig. 4.2.1) in 2002 and 2010. Yearly assessments of the coral populations were conducted in spring at two locations (La Hormiga and El Hormigón) within the marine sanctuary of the Marine Reserve (where no activities other than scientific research can be conducted since 1995) from 2003 to 2010. Although the species is abundant at depths from the surface to 9 m, the greatest abundance was observed around 6 m (Serrano 2008). At this depth, two randomly located transects (50 m x 1 m) were performed by SCUBA divers. Only colonies with at least 50% of their surface area lying within the belt-transect were counted to avoid boundary effect biases to the spatial sampling method (Nugues and Roberts 2003).

Within the study area, the colonies of *O. patagonica* displayed a predominantly encrusting growth form with a circular-ellipsoidal shape. The surface area of the colonies was estimated by means of *in situ* measuring of the longest dimension of the colony (length, L) and its perpendicular axis (width, W) with a ruler to the nearest millimeter. The surface area was calculated (S, cm^2) using the formula $S = \pi[(L+W)/4]^2$ according to Fine et al. (2001).

The abundance of sea urchins (*Paracentrotus lividus and Arbacia lixula*) along the same 50 m^2 transects was also recorded every year from 2003 to 2010. Sea urchin abundance was recorded in plots measuring 10 m^2. Between 2006 and 2010 size-structure of sea urchins was also estimated by measuring maximum test diameter without spines (MTD). All individuals larger than 2 cm in test diameter were counted and measured with calipers along the whole transect.

To determine whether coral recruitment was facilitated by the presence of open spaces we examined small coral colonies (up to 100 cm^2) associated with open spaces (a discrete area deprived of, but bordered by, erect macroalgae). A colony was considered to be associated with an open space if a minimum of 50% of the perimeter of the coral colony was in contact with the open space. We examined whether or not each coral colony within the random transects was associated to an open space on a minimum of a 100 m^2 in 2005, 2006, 2007 and 2010. The observed number of small colonies associated with open spaces was contrasted to that expected. Expected values were estimated by multiplying the total of colonies associated with open spaces by the proportion that the small colonies size class represents from the overall coral population. Observed and expected values from the four different year assessments was tested using Chi-square.

The size of the open spaces within the transects in contact with *O. patagonica* was estimated in 2010. Percent cover of open spaces was assessed within randomly located 1 m^2 squares ($n = 20$) by estimating abundance of open spaces in 20 randomly distributed square meters at La Hormiga and El Hormigón. Each square meter estimate was conducted by adding the estimates of 4 adjacent 0.50 x 0.50 m quadrats. Quadrats were subdivided into 25 squares (each representing 4% of the quadrat), and the open spaces in each subdivision were recorded.

Statistical analysis

Variation of coral density over time at La Hormiga and El Hormigón was examined using a Pearson product moment correlation. Variation of coral cover (proportion of surface occupied by coral colonies in each 50 m^2 transect) over time was examined with the same method. A two-way ANOVA was conducted comparing coral density among 4 locations (La Hormiga, El Hormigón, Bajo de Fuera and Bajo de Dentro) and time (2002 and 2010) to examine whether the abundance of the species varied over the study period at the four locations. Prior to analysis, normality was checked using a Kolmogorov test. Homogeneity of variance was tested using Cochran's test, and whenever necessary, data were transformed (Underwood 1997). Statistics were performed using STATISTICA 6 software package.

Coral size distribution was analyzed by estimating mean colony size, the coefficient of variation (i.e., standard deviation as percentage of the mean), skewness and kurtosis. Variation of the mean colony size over time (2003 to 2010) was examined using a Pearson product moment correlation. Variation of the coefficient of variation over time was examined with the same method. Skewness and kurtosis coefficients were considered significant if g_1 per SES (standard error of skewness) or g_2 per SEK (standard error of kurtosis) was greater than 2 (Sokal and Rohlf 1995).

A two-way ANOVA was used to determine whether the number of open spaces varied between locations (La Hormiga and El Hormigón) and over time. Time was considered to be fixed in the analyses, and location was randomized. A one-way ANOVA was used to determine whether the amount of space occupied by open spaces varied between both locations.

A three-way ANOVA was used to compare sea urchin densities among species (*Paracentrotus lividus* and *Arbacia lixula*), locations (La Hormiga and El Hormigón) and time (2003–2010). The factors of species and time were considered to be fixed in the analyses, and location was random. A one-way ANOVA was used to examine variation in the density of both sea urchin species among the four locations in 2010. Pearson product moment correlation was used to examine the relationship between the abundance of both sea urchin species and the abundance (density and coverage) of *O. patagonica*.

The following equation was used to transform *P. lividus* density and size structure into *P. lividus* biomass: $DW = 0.0013 \times D^{2.571}$; where DW is dry weight in grams and D is the test diameter without spines (Hereu 2004). A two-way ANOVA was conducted to compare *P. lividus* biomass among locations (La Hormiga and El Hormigón) and time (2006–2010) to examine whether the species exhibited a similar pattern over the study period at both locations. Time was considered to be fixed and location was randomized in the analyses.

Acknowledgments

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Supplementary Material (SM)

SM 4.2.1 Assessment of other factors that may affect the dynamics of the coral and sea urchin populations.

Here we provide the detailed information on the assessment of other factors that may have affected the dynamics of the coral and sea urchin populations. A summary of each factor assessment is provided in the main body of the study.

Other factors such as physical disturbance, abundance of herbivorous fishes, abundance of sea urchin predators, predation, changes in the main components of the benthic community, and sea water temperature that could have affected the dynamics of the coral and sea urchins populations were examined on parallel studies (Calvín 2004; García-Charton et al. 2008a, 2008b) and over the numerous dives conducted at the study area.

Physical disturbance

Whether physical disturbance (large storms) caused open spaces in the substrata were recorded on our dives and on the data from the annual monitoring of the MPA. Open spaces have regularly been observed at the study site despite the lack of large storms over the study period (authors' observations; García-Charton et al. 2008b).

Abundance of fish species

Fish population studies have documented an important increase in abundance of piscivorous fish species at the marine reserve between the establishment of the protection measures in 1995 and 2006 (García-Charton et al. 2008a). However, over the study period, the monitoring of fish populations at the study zone have shown that abundance of the main herbivorous fish species (*Sarpa salpa*) and, that of the main fish species identified as successful sea urchin predators (the Sparidae *Diplodus sargus, Diplodus vulgaris* and *Sparus aurata*, and the Labridae *Coris julis, Labrus merula, Labrus viridis, Symphodus roissali* and *Symphodus tinca*; Quignard 1966; Khoury 1987; Sala 1996, 1997) did not vary (García-Charton et al. 2008b).

Predation

The polychaete worm *Hermodice carunculata* is the main described predator of the coral *O. patagonica*. The presence and effects (a clear dotted pattern, see Fine et al. 2002) of the polychaeta on the coral was recorded on our dives. The presence and the effect of this worm were observed on very rare occasions during the study.

Changes in dominant benthic species

We estimated the relative abundance of the dominant benthic species of the community using a semiquantitative method at La Hormiga and El Hormigón at about 6 m depth in 2010. This method involves identifying the main species of the community in specific replicated quadrats, and assigning to each species an abundance code based on its contribution to the total coverage. The used codes were 0: species not present; 1: species <5% of total; 2: species <10% of total; 3: species = 10-35% of total; 4: species = 35-70% of total; 5: species >70% of total. Relative abundances were contrasted with those previously obtained in 2004 during the characterization of this benthic community at La Hormiga and El Hormigón using the same method (Calvín 2004) to determine whether any outstanding change in dominant species composition occurred over the study period.

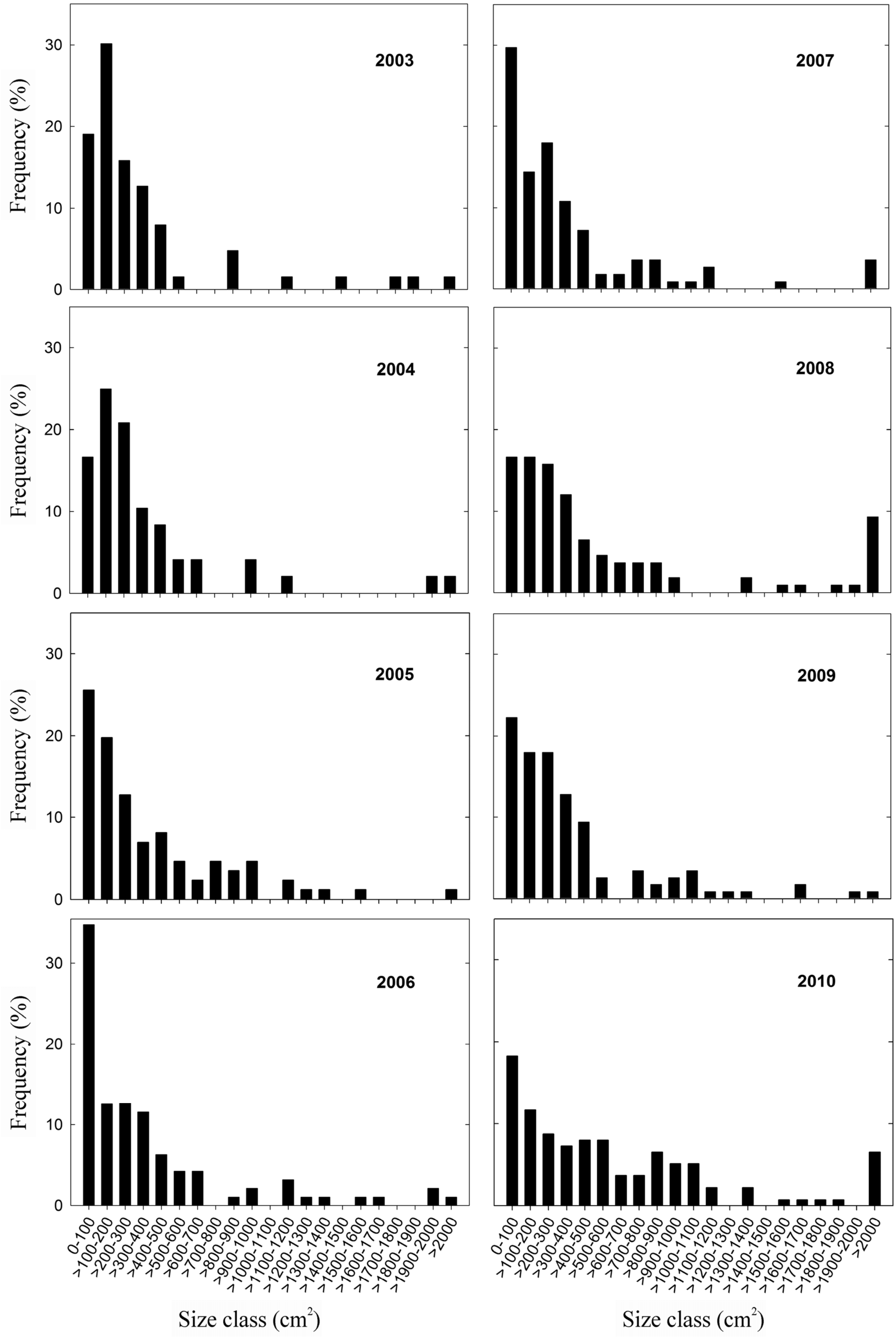
Characterization of the benthic community of the MPA conducted in 2004 (Calvín 2004) showed that assemblages at the study sites were dominated by different species of macroalgae (*Dictyopteris polypodioides, Sargassum vulgare, Neogoniolithon brassicaflorida*, *Padina pavonica* and *Halopteris scoparia*). Assessment of the benthic community in 2010 showed the same dominant macroalgae species except for a decrease in abundance of *Halopteris scoparia*.

Sea surface temperature

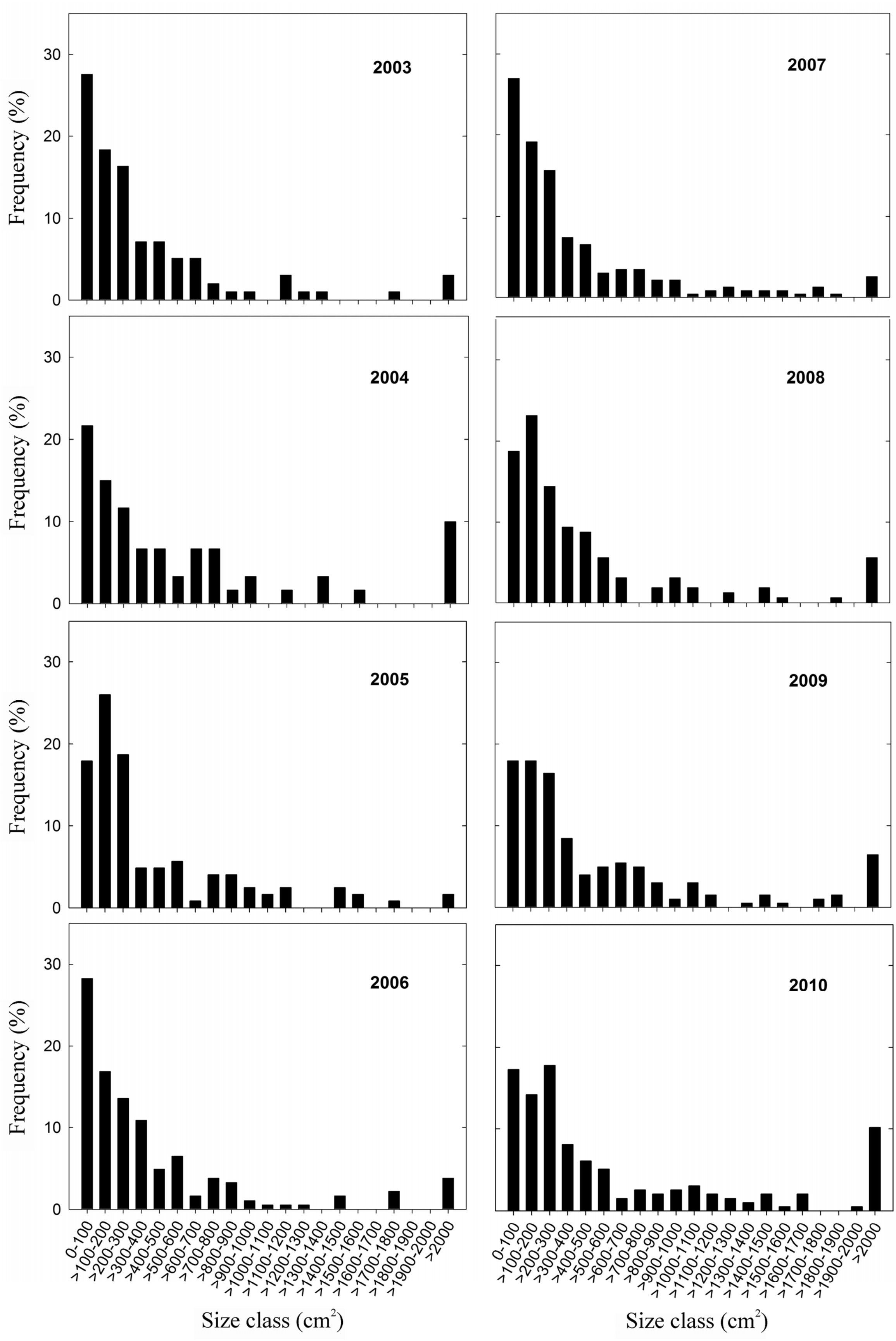
Sea surface temperature (SST) in the NW Mediterranean is exhibiting a pattern of increase (Vargas-Yáñez et al. 2010). Therefore, sea warming should be considered as a factor that may affect the dynamics of the coral because current evidence indicate that the species may benefit from a lengthening of the growing season of the coral due to temperature increase (Rodolfo-Metalpa et al. 2008; Coma et al. 2009).

Daily mean sea surface temperature (SST) from the MPA from January 2003 to December 2010 was examined using satellite measurements by the MODIS (aqua) sensor system, made available as ‘Ocean Level-2’ HDF data by the NASA Goddard Space Flight Center. HDF files were read and processed using Mathlab R2009a software. In the analysis, we only considered high-quality sensor readings of temperature (flag values of 0 or 1), discarding less-reliable readings (flag values of 2 or 3). Suitable SSTs readings (n = 1536) used in our analyses corresponded to daily means in a 9-km^2 area centered at the following coordinates: 37º39'7.09"N–0º39'15.72"W (El Hormigón). Achievement of sea surface temperature of 18ºC has been determined to be a good indicator of summer conditions (Coma et al. 2009) that favor *O. patagonica* growth. Then, we calculated the number of days that temperature was >18ºC to examine whether lengthening of the summer period has occurred over the time period of the study and may have affected the coral species. We estimated the date in spring that SST was ≥18ºC and the date in fall that it dropped below it on the basis of daily mean values. To avoid bias introduced by short term temperature oscillations, the criteria used to determine these dates was that after the date in spring that SST reached ≥18ºC, daily mean SST values had to remain ≥18ºC at least 80% of the days during the following two weeks. Accordingly, after the date in fall that SST dropped <18ºC, daily mean SST values had to remain <18ºC at least 80% of the days during the following two weeks. Mean annual temperature was also determined. The number of days that SST was ≥18ºC (used as an indicator of summer conditions that favor growth of the species) was 198 ± 13 d yr^{-1} and did not vary over the study period ($r^2 = 0.02$, $p = 0.74$, $n = 8$). Mean annual temperature was 19.31 ± 0.24ºC and did also not show a significant change over the study period ($r^2 = 0.15$, $p = 0.34$, $n = 8$).

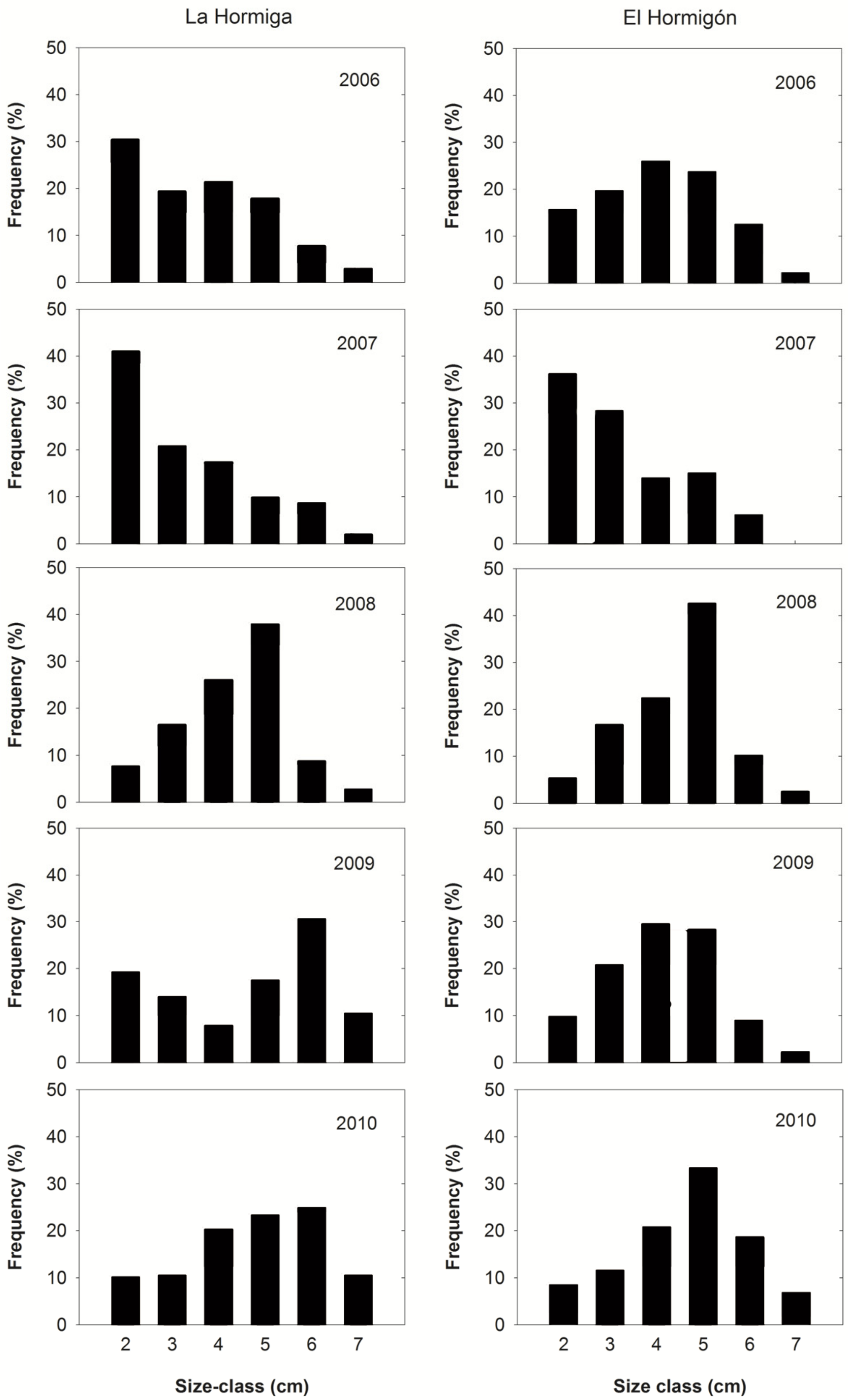
SM 4.2.2 Size-frequency distribution of *Oculina patagonica* populations between 2003 and 2010 at La Hormiga.



SM 4.2.3 Size-frequency distribution of *Oculina patagonica* populations between 2003 and 2010 at El Hormigón.



SM 4.2.4 Size-frequency distribution of the populations of the sea urchin *Paracentrotus lividus* between 2006 and 2010 from La Hormiga and El Hormigón.



4.3. Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean

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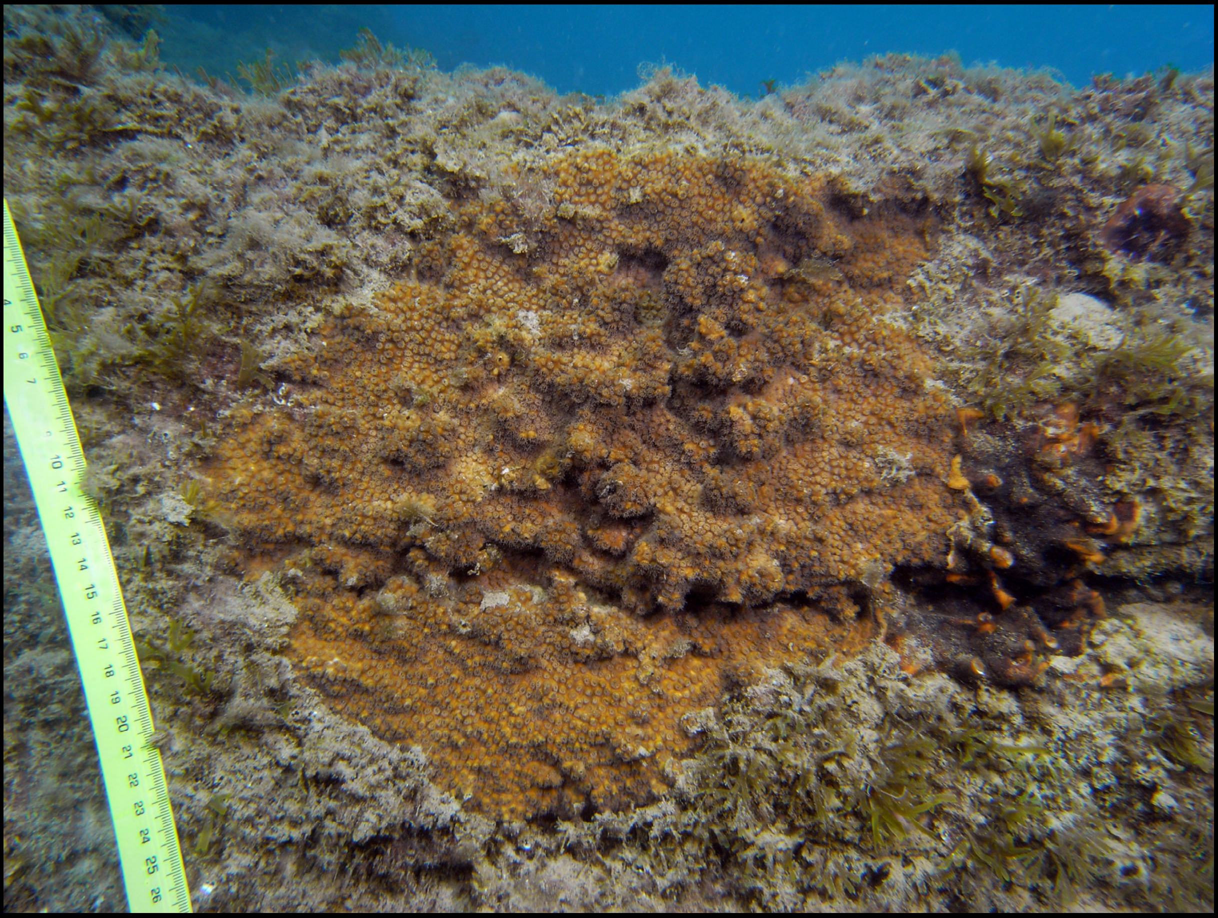

Chapter 4.3

Abstract

The hermatypic coral *Oculina patagonica* can drive a compositional shift in shallow water benthic marine communities in the northwestern Mediterranean. Here, we analyze a long-term, large-scale observational dataset to characterize the dynamics of the species' recent northward range shift along the coast of Catalonia and examine the main factors that could have influenced this spread. The variation in the distributional range of *O. patagonica* was examined by monitoring 223 locations including natural and artificial habitats along >400 km of coastline over the last 19 years (1992–2010). Abundance of the species increased from being present in one location in 1992 to occur on 19% of the locations in 2010, and exhibited an acceleration of its spreading over time driven by the join action of neighborhood and long-distance dispersal. However, the pattern of spread diverged between artificial and natural habitats. A short lag phase and a high slope on the exponential phase characterized the temporal pattern of spread on artificial habitats in contrast to that observed on natural ones. Northward expansion has occurred at the fastest rate (22 km yr^{-1}) reported for a coral species thus far, which is sufficiently fast to cope with certain climate warming predictions. The pattern of spread suggests that this process is mediated by the interplay of (i) the availability of open space provided by artificial habitats, (ii) the seawater temperature increase with the subsequent extension of the growth period, and (iii) the particular biological features of *O. patagonica* (current high growth rates, early reproduction, and survival to low temperature and in polluted areas). These results are indicative of an ongoing fundamental modification of temperate shallow water assemblages, which is consistent with the predictions indicating that the Mediterranean Sea is one of the most sensitive regions to global change.

Introduction

Human activities (e.g., overfishing, trawling, coastal development, deployment of man-made infrastructures, transportation, use of fossil fuels and pollution) are currently affecting marine ecosystems worldwide (EEA 2006; Airoldi and Beck 2007; Hoegh-Guldberg and Bruno 2010). Two main phenomena – climate change and the introduction of alien species – appear to be increasing the rate of change in species distribution boundaries, making it possible to examine such changes on a decade time-scale (Barry et al. 1995; Kinlan and Hastings 2005; Hawkins et al. 2009; Raitsos et al. 2010). The distributions of a wide range of taxa are expanding poleward (Poloczanska et al. 2007; Hawkins et al. 2009), and at the same time, coral reefs are undergoing rapid degradation due to increasing anthropogenic impacts, particularly climate change (Hughes 1994; Hoegh-Guldberg 1999; Sutherland et al. 2004; Hoegh-Guldberg et al. 2008). The poleward expansion of corals favored by increasing temperatures could compensate for the degradation of corals in their normal distribution range because of warming. However, it has been argued that coral species appear to be unable to disperse or adapt rapidly enough to cope with the current rate of change (Pounds et al. 1999; Hilbert et al. 2001; Hoegh-Guldberg et al. 2007, 2008), but see (Maynard et al. 2008; Yamano et al. 2011).

The Mediterranean Sea is an optimal study site for early detection and characterization of the effects of global change on marine species ranges for several reasons. First, it is a semi-enclosed sea that is being affected by climate change at a faster rate than many other marine areas (Calvo et al. 2011), and second, it is a hot spot for alien species, some of which are of tropical origin and have entered the Mediterranean via the Suez Canal (Galil 2009; Occhipinti-Ambrogi and Galil 2010; Zenetos et al. 2010). An understanding of the spread dynamics of alien species and the main processes determining this spread are crucial for predicting future changes in their distributions in the context of global environmental change (Barry et al. 1995; Glasby and Connell 1999). Accurate predictions of the future distribution ranges of alien species that are able to change the structure and functioning of native ecosystems (Sala et al. 2011; Chapters 4.1, 4.2) are essential for determining their effects and for supporting management actions.

The most accurate records regarding the rate and the spatial pattern of the spread of alien species come from annual field surveys (Hastings et al. 2005). However, surveys repeated with high frequency in areas ranging from tens to hundreds of kilometers are rare, mainly due to the cost of monitoring large areas in detail. Thus, distributional data for most introduced species have low accuracy given that they comprise a relatively limited number of observations (Arim et al. 2006; Lyons and Scheibling 2009).

Oculina patagonica De Angelis D'Ossat 1908 is an alien, non-lessepsian scleractinian zooxanthellate coral that presumably originated from the southwest Atlantic and was first recorded in the

Mediterranean Sea in 1966 (when a single colony was found in the Gulf of Genoa; Zibrowius 1974). The unsolved problem is that the original description of *O. patagonica* is based on fossil material from Holocene deposits on the temperate coast of South America, and living specimens have not been found in this area. In the late 1970s, *O. patagonica* was abundant along ~300 km of the southeast coastline of the Iberian Peninsula, indicating that this species had been present in this area for a long time when it was first recorded (Zibrowius and Ramos 1983; Fine et al. 2001; Sartoretto et al. 2008). This species is also currently abundant on the coast of Israel where it was first recorded in 1993 (Fine et al. 2001). During the last decade, *O. patagonica* has exhibited a 3-fold increase in certain littoral locations in southeastern Iberia (Chapter 4.2), and isolated colonies have been found in several new areas throughout the Mediterranean (see Sartoretto et al. 2008 for a review), suggesting that *O. patagonica* is spreading geographically. The species presumably spread from the western basin to the levant basin via the intense intra-Mediterranean maritime traffic (Fine et al. 2001). Both asexual dispersal in the form of polyp expulsion (Kramarsky-Winter et al. 1997) and the release of gonads from colonies attached to ship hulls (Zibrowius 1974), which is favored because the species is capable of reproducing sexually when colonies are small (Fine et al. 2001), have been proposed as the primary vectors of invasive transport. Moreover, the species' ability to thrive and reproduce despite wide variations in temperature, salinity, UV radiation, turbidity and hydrodynamic conditions (Fine et al. 2001; Armoza-Zvuloni et al. 2011) may have favored the species' spread throughout the Mediterranean.

In this study, the spread of *O. patagonica* was examined by monitoring >400 km of coastline over the last 19 years on the Catalan coast (northwestern Mediterranean). Whereas *O. patagonica* is abundant ~30 km south of the Catalan coast (Casado-Amezúa et al. 2011; authors' unpublished data), it was not recorded in the adjacent area to the north prior to 1992 (Sartoretto et al. 2008). Here, we analyze a long-term, large-scale observational dataset in order to characterize the dynamics of the species' recent northward range shift along the Catalonian coast and examine the main processes that could have influenced this spread.

Materials and Methods

Distribution surveys

The study was performed along the Catalan coast in the northeastern region of the Iberian Peninsula (northwestern Mediterranean). The study area encompassed more than 400 km of coastline from Les Cases d'Alcanar in the south (40º31'N–0º30'E) to Portbou in the north (42º26'N–3º10'E; Fig. 4.3.1). A total of 223 locations were examined for the presence of the scleractinian coral *O. patagonica* over a period of 19 years (1992–2010) at intervals ranging between 1 and 2 years as part of a monitoring protocol designed to determine the arrival and occurrence of alien species in the shallow infralittoral zone. We surveyed both natural (n = 169) and artificial (n = 54) habitats. The natural habitats were rocky reefs, while the artificial habitats included man-made structures, primarily dikes, breakwaters and harbor walls. The mean linear distance between the examined locations was ~2 km. At each location and sampling date, the presence or absence of the coral was determined through close examination of at least 1500 m^2 of the sea floor using SCUBA.

The results of the systematic monitoring of *O. patagonica* were translated into absence/presence records over time at each location. The cumulative numbers of locations where the species was present were used to reconstruct the pattern of its spread (Pyšek and Prach 1993; Mihulka and Pyšek 2001). The initial detection of the coral was unequivocal for colonies larger than 5–10 cm in diameter; however, smaller colonies could be overlooked. It was noteworthy that over the study period, the species did not disappear from any location after its initial detection there. Thus, although the initial detection underestimates spread rate of *O. patagonica*, this species persistence in all locations where it was found over the study period indicates that the detection of small colonies provides a fair estimation of when this species became established. This pattern is most likely related to the size-dependent nature of coral mortality (Connell 1973; Sakai 1998). To reduce the bias introduced by the fact that not all locations were examined every year, gaps in the data obtained at a particular location after the coral was first detected were marked as the species being present based on species persistence. Then, to examine the pattern of *O. patagonica* spread over the study period, we calculated the cumulative number of locations where the species was present and expressed this as a percentage of the total number of locations.

Regression models were fitted to the standardized cumulative number of locations where the species was present over time (termed standardized spread curves; Pyšek 1991; Mihulka and Pyšek 2001), and the slope of the linear regression of the log-transformed cumulative number of locations was used as a measure of spreading success (Pyšek and Prach 1995; Mihulka and Pyšek 2001). A standardized spread curve was calculated separately for each of the two habitat types (i.e., natural and artificial).

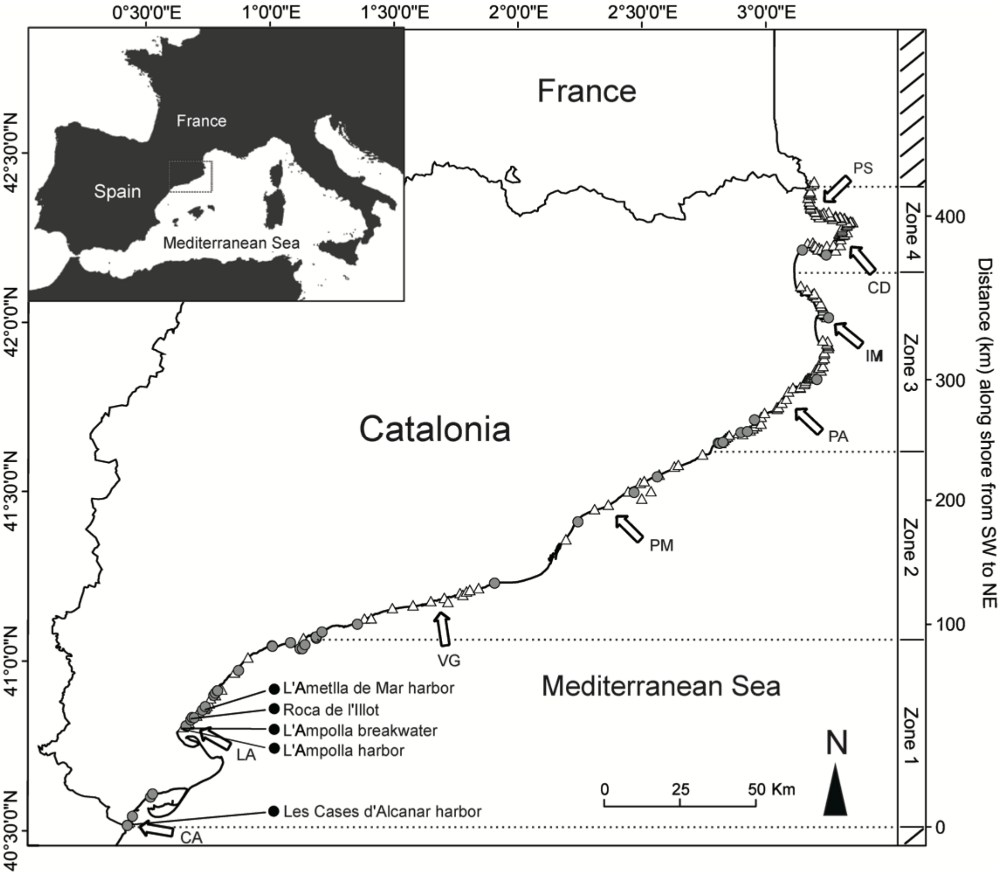

Fig. 4.3.1 Map of the Catalan coast in the northeastern region of the Iberian Peninsula (northwest Mediterranean Sea). The positions of the 223 surveyed locations are indicated. *Blank triangles* (n = 180) represent surveyed locations in which *Oculina patagonica* was not found. Locations in which *O. patagonica* was found are represented by *grey circles* (n = 38; density <0.05 colonies m^{-2}) and *black circles* (n = 5; density >0.05 colonies m^{-2}). The linear coastal length from the southernmost location (in km) is represented on the right-hand y-axis. Four zones of ~100 km in length have been distinguished from the south (zone 1) to the north (zone 4) to examine the patterns in coral abundance. Sea surface temperature data have been obtained from two locations in each zone (indicated by *white arrows*): Les Cases d'Alcanar (CA), L'Ampolla (LA), Vilanova i la Geltrú (VG), Premià de Mar (PM), Port d'Aro (PA), Illes Medes (IM), Cadaqués (CD) and Port de la Selva (PS).

The different phases of the spreading process (lag, exponential and saturation; Shigesada and Kawasaki 1997) were examined in the standardized spread curves. The beginning of the exponential phase was defined as the year in which the parameters of the standardized spread curve changed. This phase was detected using a maximum likelihood estimation of classic regression parameters for partitioned models (Quandt 1958, 1960). The shift was set at the F-value of maximum significance ($p < 0.0001$). The coefficient of the linear regression of the cumulative number of locations after the lag phase over time was used as a measure of the rate of the exponential phase. Differences in the slopes of the overall standardized spread curves and in the slopes of the exponential phase were tested using the homogeneity of slopes test (Zar 1999).

We examined whether the northern limit of the distribution of *O. patagonica* varied over time. The linear correlation coefficient of the northern distribution limit of the species over time was used to estimate the expansion rate (km yr^{-1}).

Current distribution and abundance (2008–2010)

Between 2008 and 2010, field surveys also included measurements of all coral colonies and an annotation of the depth of each colony. Within the study area, the *O. patagonica* colonies displayed a predominantly encrusting growth form with a circular-ellipsoidal shape. A colony was defined as any distinct, single coral skeleton with living tissue. A specimen divided by partial mortality into separate patches of living tissue that was morphologically still one entity was considered as a single colony. Neighboring colonies in close proximity, which were found on several occasions, were measured as distinct. The surface area of the colonies was estimated by means of *in situ* measurements of the longest dimension of the colony (length, L) and its perpendicular axis (width, W) to the nearest millimeter using a ruler. The surface area (S, cm^2) was calculated using the formula $S = \pi[(L + W)/4]^2$ according to Fine et al. (2001).

Two methods were used to estimate coral abundance on hard substrata between 0 and 10 m in depth (or until the maximum depth when the depth was <10 m), which is the depth range within which *O. patagonica* has been reported to be the most abundant (Fine et al. 2001; Sartoretto et al. 2008; authors' observations). When the species was scarce (hereafter, present), we assessed its abundance by counting and measuring all colonies present on 1500 m^2 of the seabed using SCUBA. When the species was abundant (hereafter, populations), we conducted three replicates of randomly localized 40 m^2 transects (40 x 1 m, see SM 4.3.1 in supplementary material, SM). Only colonies with at least 50% of their surface area lying within the belt transect were counted and measured to avoid boundary effect biases in the spatial sampling method (Nugues and Roberts 2003). Coral abundance data were standardized based on the area surveyed, and the species density and percent cover values were calculated for each location.

We utilized the standard error (SE) sample size function to determine the minimal sampling area needed to assess the density and percent cover of the coral populations (Coma et al. 2006; Linares et al. 2008). Preliminary sampling to obtain coral abundance estimates was conducted at one of the study locations (Les Cases d'Alcanar) by examining an area of 200 m^2 using 5 m^2 belt transects (5 x 1 m) set randomly on the substrate between depths of 2 and 4 m.

We partitioned the entire coast into four similar zones (each ~100 km of coastal length; Fig. 4.3.1) to identify the mechanisms that contribute to the variation in the abundance of *O. patagonica* colonies across the study area. The number of locations where the species occurred was calculated separately for each zone to examine whether the coral exhibited an identifiable pattern along the coast. The proportion of locations where the coral occurred in each of the four zones was calculated separately for the two habitat types (i.e., natural and artificial).

Temperature

Temperature has long been considered to be one of the main environmental factors controlling coral species distributions (e.g., Veron 1995; McManus and Vergara 1998). We obtained a sea surface temperature (SST) time series from 8 locations distributed along the ~400 km Catalan coast (Fig. 4.3.1). The cumulative distances between the locations at which temperature was examined, ordered from south to north, are indicated in SM 4.3.2.

Daily mean SSTs were obtained from January 2003 to December 2010 from satellite measurements performed by the MODIS (aqua) sensor system (http://oceancolor.gsfc.nasa.gov/), which were made available as ‘Ocean Level-2’ HDF data by NASA's Goddard Space Flight Center. HDF files were read and processed using Matlab R2009a (MathWorks Inc., Natick, MA, USA). In the analysis, we considered only high-quality temperature readings (flag values of 0 or 1), and we discarded less reliable readings (flag values of 2 or 3). The suitable SST readings used in our analyses corresponded to the daily means in a 9-km^2 area centered on the geographic coordinates indicated in SM 4.3.2.

Over the SST study period, the mean annual temperature and mean annual 95th and 5th percentiles were determined for each location along the Catalan coastline. On the basis of the SST data recorded daily, we also calculated the number of days that the temperature was above or below different thresholds specifically chosen because of their biological consequences (i.e., relying on previous field observations and/or thermo-tolerance experiments performed on *O. patagonica*; Kushmaro et al. 1997; Rodolfo-Metalpa et al. 2008). To examine whether exposure to summer conditions (>18ºC; Coma et al. 2009) and to upper sublethal temperatures (24 and 26ºC) could affect the target species, we determined the day in spring/summer on which the SST reached ≥18ºC, ≥24ºC and ≥26ºC; and the day in late summer/fall on which it dropped below each temperature. To avoid any bias introduced by short-term temperature oscillations, we determined that after the date on which the SST reached ≥XºC, the daily mean SST values had to remain ≥XºC on at least 80% of the days throughout the following two weeks (i.e., 11 of 14 d). These temperature thresholds were used to assess the temperature regimes among 8 locations distributed along the 400 km of the Catalan coastline.

Due to the assumptions made by the Pearson's correlation analyses, we estimated the confidence intervals when the *n* value was <12. The 95% confidence intervals were calculated using bias-corrected bootstrapping with 1,000 resamples, which were considered significant when the confidence limits did not include zero (Efron 1981). All analyses were computed using STATISTICA 7.0, except for the bootstrapping analyses, which were implemented with R (R Development Core Team 2012).

Results

Current distribution along the Catalan coast

We found that *O. patagonica* was present in wide areas along the study coast at a depth range of 0–10 m. The species was rarely observed below this depth, although a few colonies were found down to 28 m depth.

O. patagonica abundance decreased from south to north, and significant populations (defined as those with a density of >0.05 colonies m^{-2}) were found in 5 locations, all of which were situated in the southernmost zone of the studied region (Fig. 4.3.2a). At all other locations where this species was observed, it occurred at a density of <0.05 colonies m^{-2}. Occurrence of the species at densities of <0.05 colonies m^{-2} was defined as presence. Four of these populations were located in artificial habitats, and one was located in a natural habitat. The density of *O. patagonica* populations in the artificial habitats ranged from 0.24 to 1.07 colonies m^{-2} (0.46 ± 0.20 colonies m^{-2}, mean ± SE), which was approximately three-fold higher than the density observed in the single natural habitat (0.17 ± 0.02 colonies m^{-2}, mean ± SE). The percentage of the sea floor occupied by the species (percent cover) in artificial habitats ranged from 0.51 to 5.51% (2.48 ± 1.13%, mean ± SE), which was approximately two-fold higher than that of the population in the single natural habitat (1.35 ± 0.48%, mean ± SE). The species density at the 38 locations where it was present was also two-fold higher in artificial habitats than in natural habitats (0.0042 ± 0.0009 *versus* 0.0020 ± 0.0004 colonies m^{-2}, respectively, mean ± SE; One-way ANOVA, $F_{1,36} = 4.66$, $p = 0.0377$). Of the total number of *O. patagonica* colonies measured (n = 670), 80% were found in artificial habitats, and 20% were located in natural habitats.

In accordance with the species abundance, the maximum colony size decreased from south to north. The locations with the largest colony sizes (>1,000 cm^2) were mainly found in the southernmost zone of the region (Fig. 4.3.2b). The maximum colony size was less than 1,000 cm^2 at all other locations, with the exception of the location where a discrete long-distance dispersal event occurred in the year 2000 (see below). The maximum colony size did not vary between the artificial and natural habitats (1156 ± 363 *versus* 925 ± 255 cm^2, mean ± SE, respectively; One-way ANOVA, $F_{1,38} = 0.26$, $p = 0.61$).

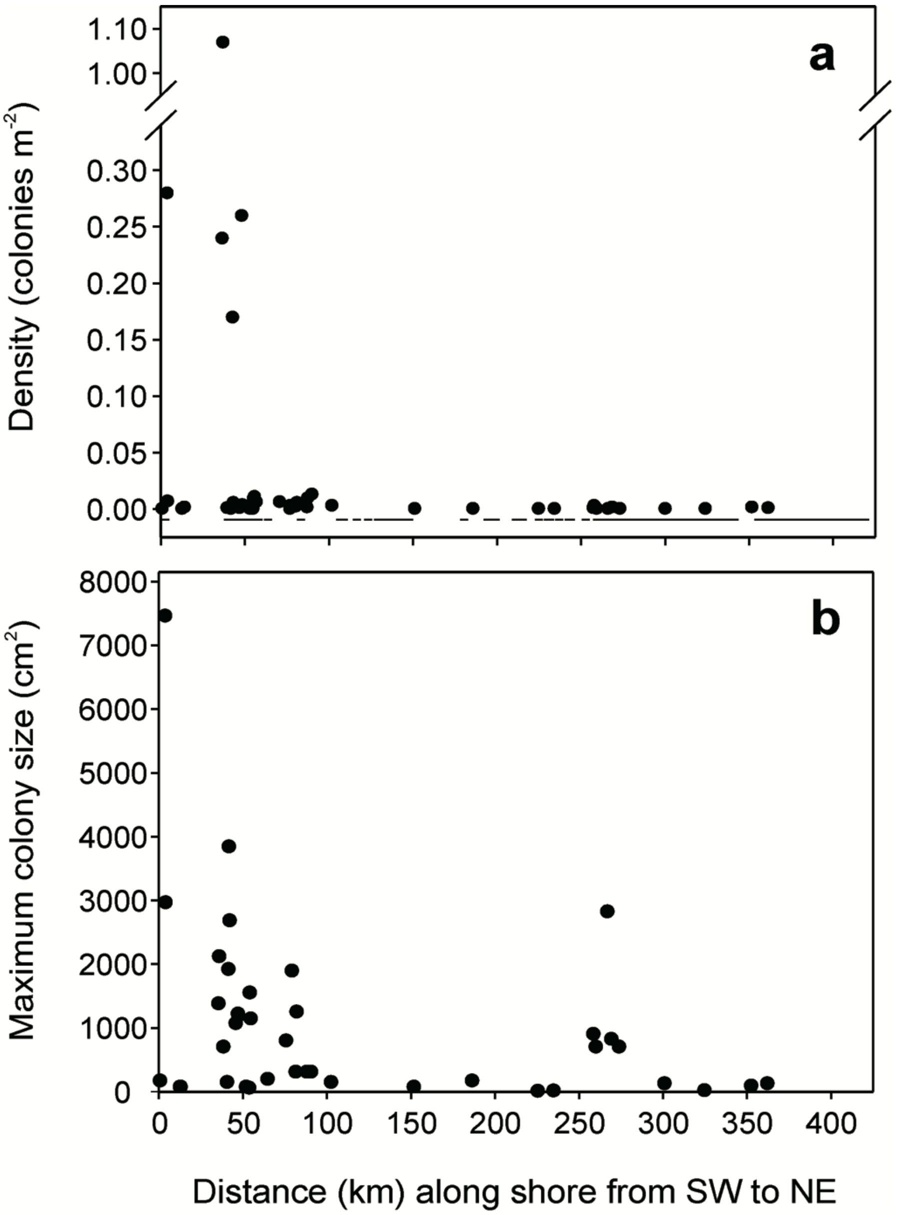

Fig. 4.3.2 Density and maximum colony size of *Oculina patagonica* along the Catalan coast. a Current coral density (colonies m^{-2}) in the locations at which the species was observed along the linear length of the Catalan coast (km). *Horizontal lines* below the zero line indicate locations at which *O. patagonica* was not encountered. **b** Maximum colony size (cm^2) in the locations at which the species was observed in 2010.

The proportion of locations where the species occurred decreased steadily from 61% in the southernmost zone to 3% in the northernmost zone (Fig. 4.3.3), although this pattern differed depending on habitat type (i.e., natural and artificial). In artificial habitats, the proportion of locations where the species occurred decreased steadily from 94% in the southernmost zone to 11% in the northernmost zone (Fig. 4.3.3), while in natural habitats, the proportion of locations where the species occurred decreased steadily from 38% in the southernmost zone to 2% in the northernmost zone (Fig. 4.3.3).

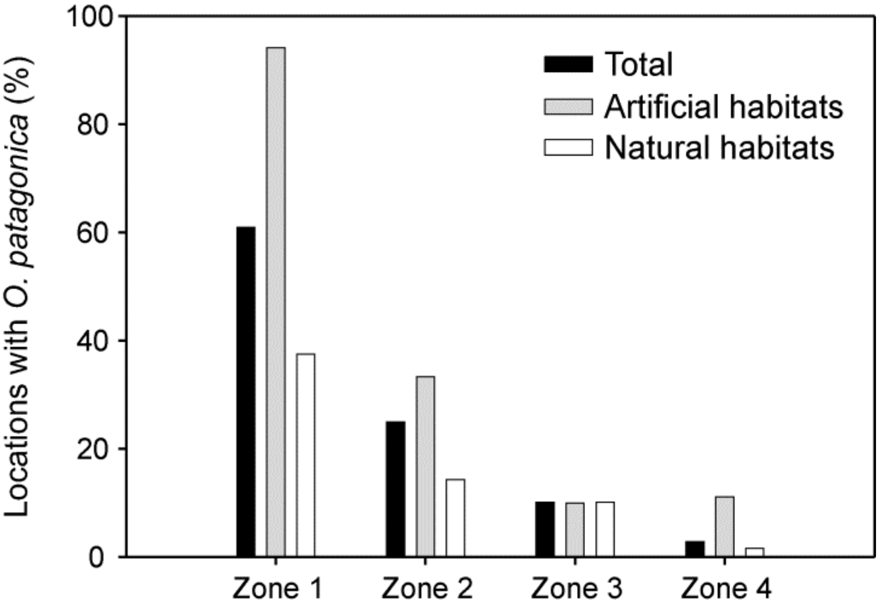

Fig. 4.3.3 Proportion of locations where *Oculina patagonica* was observed in four zones along the Catalan coast. See Fig. 4.3.1 for a description of the four zones. The proportion of locations at which the species was encountered in 2010 is given based on the total number of locations and the distinguishing habitat type (i.e., natural and artificial).

Temporal variation of species distribution

A solitary colony of *O. patagonica* was discovered for the first time in a natural habitat located in the southernmost area of the Catalan coast (Les Cases d'Alcanar) in 1992. A year later, an *O. patagonica* colony was recorded for the first time in an artificial habitat. From 1993 until 2010, the number of locations at which the species was present along the Catalan coast increased exponentially (Fig. 4.3.4a). In 2010, the species was present in 19% of all explored locations (43 of the 223 explored locations; Fig. 4.3.4a). However, this pattern diverged markedly between the two distinct habitat types; the species was observed in 44% of the artificial habitats and only in 11% of the natural habitats (Fig. 4.3.4b).

Exponential regression models provided the best fit to the increase in the cumulative number of locations over time. The cumulative number of locations where *O. patagonica* has been found over the 19-yr study period increased ~1% every year (Fig. 4.3.4a) and showed a pattern of geographic spreading (Fig. 4.3.5). The overall pattern of geographic spreading was characterized by a lag phase of 9 years and a steady increase since 2001 (Fig. 4.3.4a; Table 4.3.1). However, this pattern diverged between natural and artificial habitats (Fig. 4.3.4b); the duration of the lag phase for the natural habitats was approximately twice that of the lag phase associated with artificial habitats (Table 4.3.1). The number of locations at which the species was present at the end of the lag phase was low for both habitat types (2–9% of the examined locations), indicating that the exponential phase began immediately after *O. patagonica* established foci in a particular region (Table 4.3.1). Throughout the entire study period, the slope associated with the artificial substrata was slightly higher than that associated with the natural substrata. This effect was accentuated in the exponential phase, during which the slope for the artificial substrata was significantly higher than that for the natural substrata (F = 29.18, $p < 0.05$; Table 4.3.2). Between 2001 and 2006, the overall slope of the exponential phase was reduced because the natural habitats were still in the lag phase. After 2006, the slope exhibited an increasing trend because both habitats were in the exponential phase (Fig. 4.3.4; Table 4.3.2). Therefore, the species is spreading faster among artificial habitats than natural habitats.

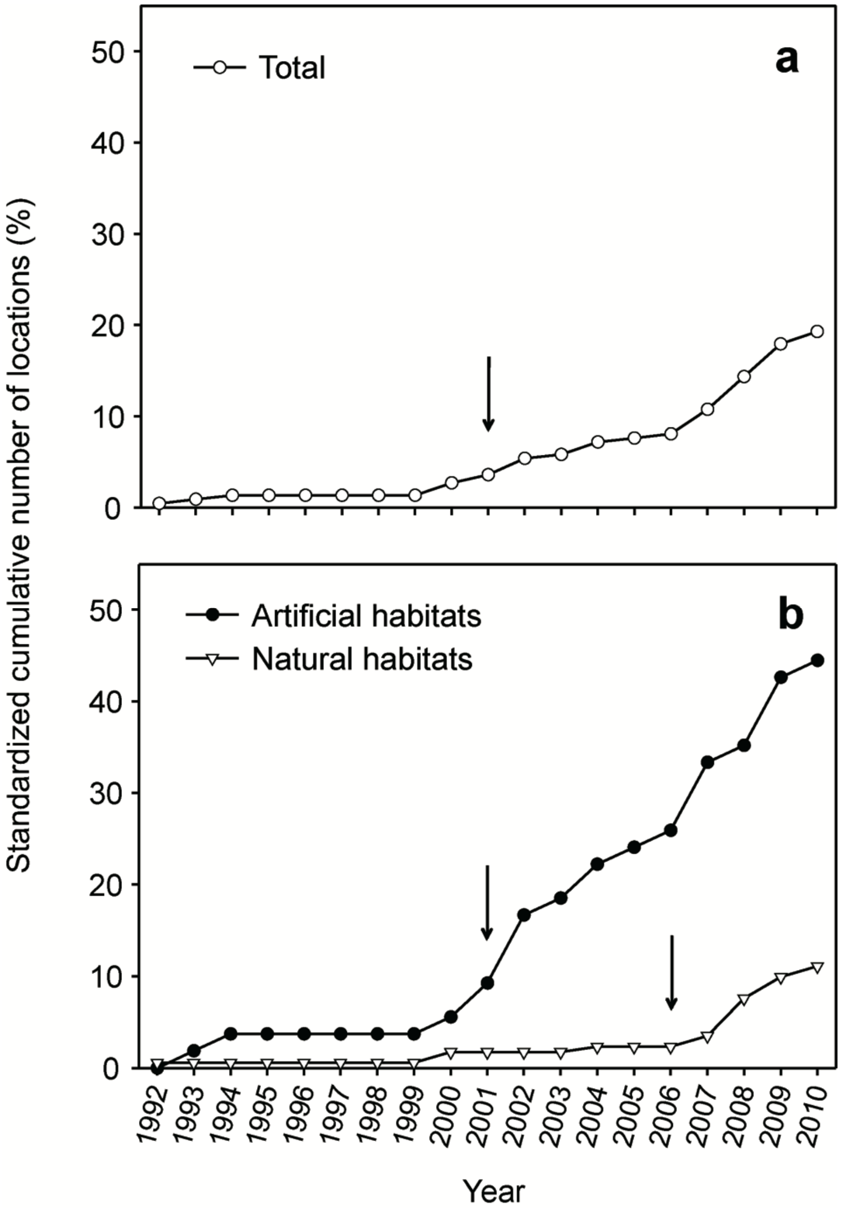

Fig. 4.3.4 Standardized spread curves of *Oculina patagonica* from 1992 to 2010 along the Catalan coast. The standardized cumulative number of locations where the species occurred is given for **a** the total data and **b** the distinguishing habitat type (i.e., natural and artificial). The beginning of the exponential phase is indicated by an *arrow* (see Methods).

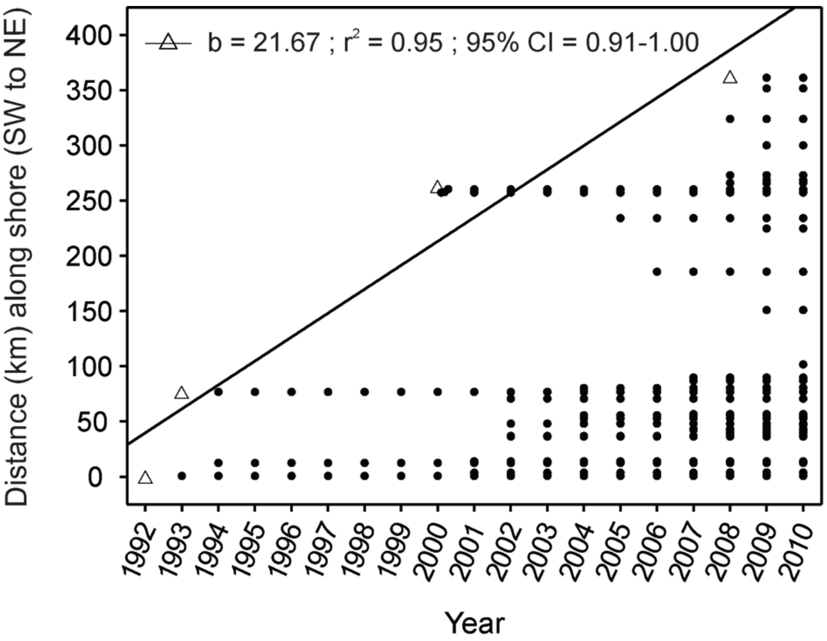

Fig. 4.3.5 *Oculina patagonica* records obtained on the Catalan coast throughout the study period (1992–2010). Records of the coral occurrence (*full circles*) throughout the Catalan coastal length (km) from 1992–2010 illustrate the spreading of the species over time. *Blank triangles* indicate the change in the northern latitudinal limit over time. The expansion rate (km yr^{-1}) was calculated as the slope of the Pearson product-moment correlation between the change in the northern latitudinal limit of the coral species and time (n = 4). *95% CI*: 95% confidence interval calculated with bootstrapping.

Table 4.3.1 Characteristics of the standardized spread curves of *Oculina patagonica* along the Catalan coast. A standardized spread curve is given for the total data and the distinguishing habitat type (i.e., artificial and natural). *N*: number of studied locations; *L*: lag phase; *E*: exponential phase; *Loc. no.*: number of locations; *%N*: percentage of the cumulative number of locations at which the species was observed at the beginning of the exponential phase.

		First detection	Duration of L	Beginning of E		
Data	N	in Catalan waters	(years)	Year	Loc. no.	% N
Total	223	1992	9	2001	8	3.59
Artificial	54	1993	8	2001	5	9.26
Natural	169	1992	14	2006	4	2.34

Table 4.3.2 Spread rate of *Oculina patagonica* along the Catalan coast. Coral spread rate for the 19-yr study period (left side of the Table), is expressed as the slope of the linear regression of the log-transformed standardized cumulative number of locations where the species was present *versus* time. For the exponential phase (right side of the Table), the spread rate is expressed as the slope (b) of the linear regression of the standardized cumulative number of locations where the species was present *versus* time. In each case, estimates were calculated separately for the total data and the distinguishing habitat type (i.e., natural and artificial). *SE*: Standard error. *N*: number of years. *95% CI*: 95% confidence interval calculated with bootstrapping.

	Entire study period					Exponential phase				
Data	Slope (b)	SE of b	r^2	p-value	N	Slope (b)	SE of b	r^2	95% CI	N
Total	0.08	0.00	0.96	<0.0001	19	1.71	0.19	0.91	(0.83–0.98)	10
Artificial	0.08	0.01	0.94	<0.0001	18	3.74	0.20	0.98	(0.94–1.00)	10
Natural	0.07	0.01	0.88	<0.0001	19	2.40	0.28	0.96	(0.90–1.00)	5

Latitudinal distribution limit and spreading patterns

The northern limit of the distribution of *O. patagonica* varied over time, exhibiting a northward geographic spread (Fig. 4.3.5). Over the 19-yr study period, this limit spread 361 km northward at a mean rate of 21.67 ± 3.70 km yr^{-1} (mean ± SE). The presence of *O. patagonica* in the littoral zone underwent lag phases over time (see above), and some long-distance dispersal events ranging between 76 and 182 km (120 ± 32 km; mean ± SE; Fig. 4.3.5) created new invasion foci. After the lag phase, the mean square displacement (MSD) between the locations at which the species was present over time showed a scaling exponent of α ~2 (MSD is proportional to t^{α}, where t is time and α is the scaling exponent; Fig. 4.3.6), which indicates an acceleration of spreading over time (Méndez et al. 2010). This accelerating pattern is strongly driven by a few intermittent long-distance dispersal events. To distinguish local dispersal from long-range dispersal, we estimated the MSD in the southern region of the coral's distribution (first ~100 km of coastline; Fig. 4.3.5), which is separated from the northern region by ~50 km of coastline where the species is not present (Fig. 4.3.2a). After the lag phase (in 2001), the MSD of the southern region (0–150 km) showed a scaling exponent of $\alpha = 0.43$, indicating a decline of spreading over time (Fig. 4.3.6).

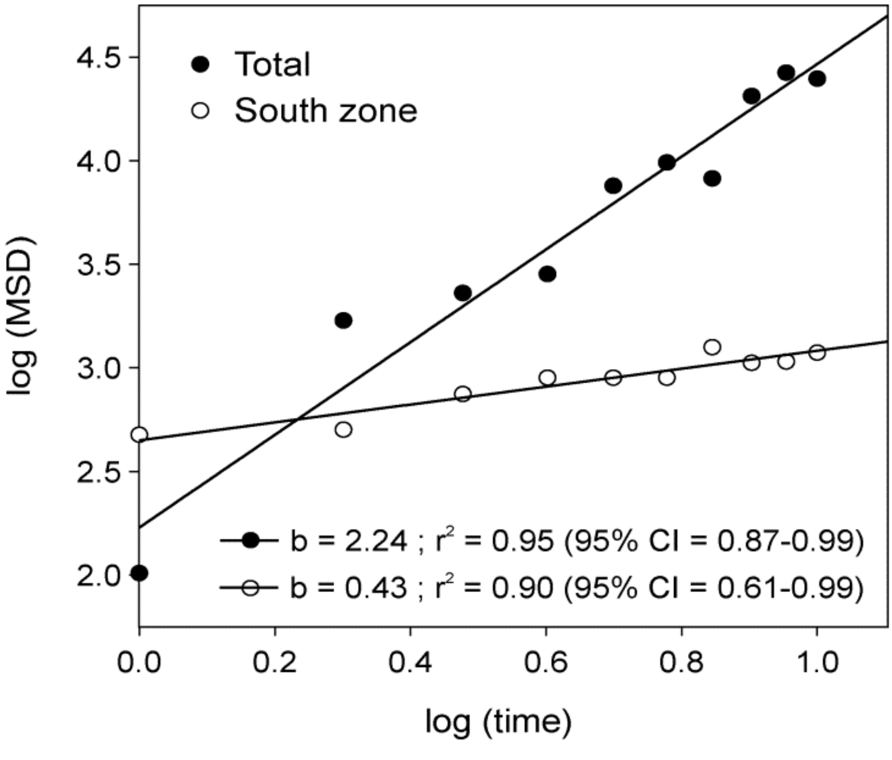

Fig. 4.3.6 Patterns of *Oculina patagonica* dispersal. Mean square displacement (MSD) between the locations at which the coral species was found after the lag phase. The dispersal of the species during the exponential phase of spreading is provided separately for the overall distribution (Total) and for the southern zone (0 to 100 km coastal length). MSD is proportional to t^{α} where t is time and α is the scaling exponent. *95% CI*: 95% confidence interval calculated with bootstrapping.

Latitudinal temperature analysis

The SST along the studied coastline displayed a northward latitudinal decrease in the mean annual temperature of 0.55 ± 0.05ºC/100 km, ranging from 18.72 ± 0.13ºC (mean ± SE) in the south (CA) to 16.68 ± 0.13ºC in the north (PS; Fig. 4.3.7a). The mean annual temperature did not vary over 8 years according to the available satellite data (2003–2010) at any of the 8 examined locations (data not shown). This is most likely related to the short-term oscillatory pattern in northwest Mediterranean temperatures (Vargas-Yáñez et al. 2010). The mean annual 95th percentile (p95) decreased by 0.91 ± 0.09ºC/100 km with increasing latitude, ranging from 26.84 ± 0.35ºC (mean ± SE) in the south (CA) to 23.24 ± 0.44ºC in the north (PS; Fig. 4.3.7b). The mean annual 5th percentile (p5) did not vary significantly due to the local temperature conditions of the southernmost location (CA), which is subjected to discharge from the Ebro River (Fig. 4.3.7c). However, when this local effect was not considered, p5 exhibited a similar significant pattern of a northward decrease [0.26 ± 0.09ºC/100 km, $r^2 = 0.62$, 95% confidence interval = 0.41–1.00 (bootstrap analysis), n = 7]. We are aware that the *n* value was inappropriate for the Pearson's correlation method, but bootstrapped confidence intervals provided an estimate of the probability that the true correlation coefficient do not include zero.

We calculated the number of days on which the SST was ≥18ºC as a temperature indicator of warm conditions that favor *O. patagonica* growth (Rodolfo-Metalpa et al. 2008) as long as the upper sublethal threshold is not reached (Kushmaro et al. 1997). The mean annual number of days on which the SST was ≥18ºC exhibited a decreasing latitudinal pattern from south to north, ranging from 188 ± 4 d yr^{-1} in the south (CA; mean ± SE) to 143 ± 5 d yr^{-1} in the north (PS) (Table 4.3.3). Additionally, the mean annual number of days on which the SST was ≥18ºC was 24% lower in the north (PS-CD) than in the south (CA) and exhibited an average decrease of 12.35 ± 1.13 d yr^{-1} (slope ± SE) for each 100 km northward (Table 4.3.3). We calculated two indicators of elevated temperature conditions that have been documented to cause colony damage and decrease the growth of *O. patagonica* after a certain period of exposure: (1) the annual number of days on which the SST was ≥24ºC (Rodolfo-Metalpa et al. 2008) and (2) the annual number of days on which the SST was ≥26ºC (Kushmaro et al. 1997). The mean annual number of days on which the SST was ≥24ºC exhibited a northward decrease, ranging from 90 ± 4 d (mean ± SE) in the south (CA) to 8 ± 5 d in the north (PS). The mean annual number of days on which the SST was ≥24ºC was 91% lower in the north (PS) than in the south (CA) and exhibited an average decrease of 22.41 ± 2.05 d yr^{-1} (slope ± SE) for each 100 km northward (Table 4.3.3). The mean annual number of days on which the SST was ≥26ºC exhibited a northward decrease of 7.21 ± 1.15 d/100 km (Table 4.3.3), ranging between 31 ± 7 d in the south (CA) and 0 d in the north (PA and upper northern locations). Colony damage related to high temperature was not observed during exposure to summer temperature conditions from 2008–2010 at the southern location (LA), where the SST was ≥24ºC for 61–82 d yr^{-1} and was ≥26ºC for 0–28 d yr^{-1} (colonies monitored seasonally over the period 2008 and 2010, authors' unpublished data). In contrast, colony damage that was apparently related to exposure to low temperature during the winter was observed every year (authors' unpublished data).

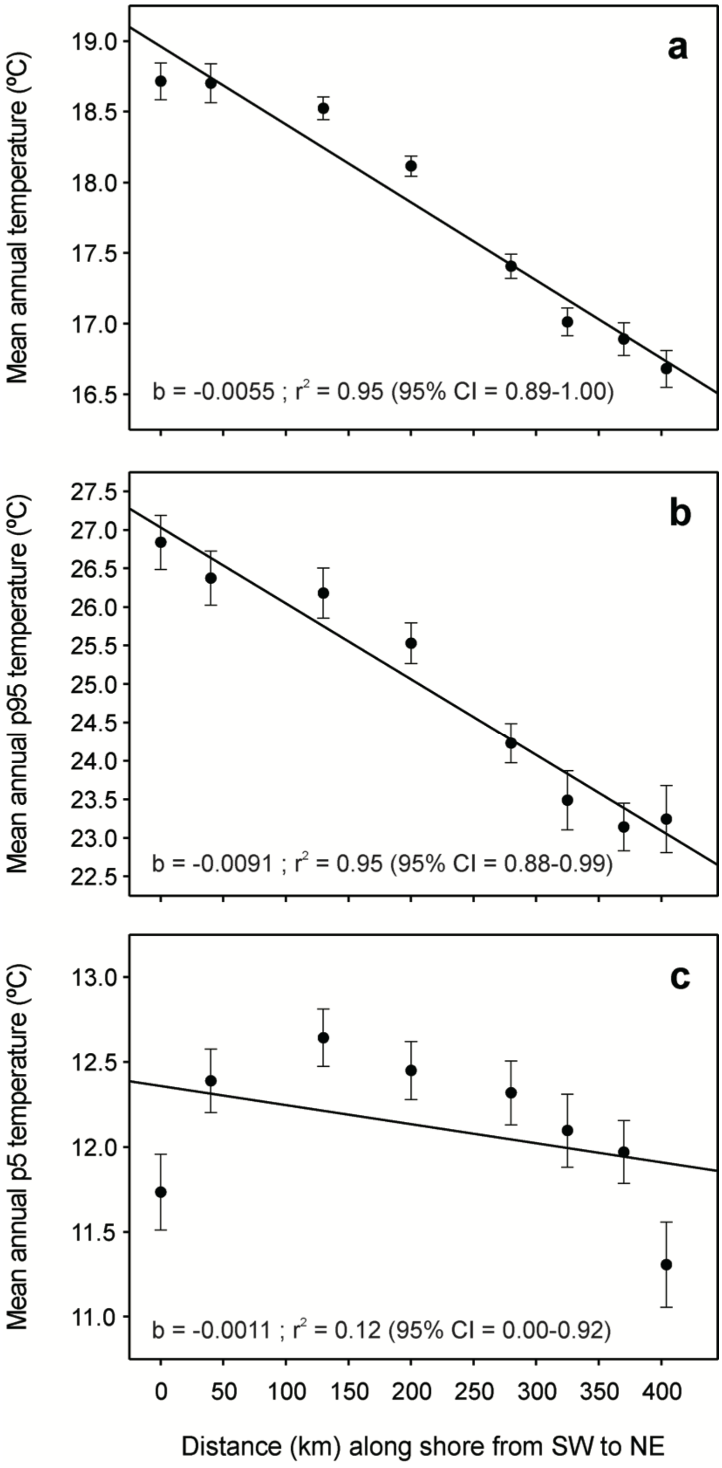

Fig. 4.3.7 Sea surface temperature (SST) obtained from NASA satellite measurements over the last 8 years (2003–2010). See Fig. 4.3.1 and SM 4.3.2 for a description of the studied locations (n = 8). **a** Mean annual temperature; **b** mean annual temperature 95th percentile (p95); **c** mean annual temperature 5th percentile (p5). Pearson product-moment correlation between the distance (km) along the shore from SW to NE (see Fig. 4.3.1) and the temperature along the Catalan coast. *95% CI*: 95% confidence interval calculated with bootstrapping.

Table 4.3.3 Sea surface temperature thresholds along the Catalan coast. Pearson product-moment correlation between coastal length (km from south to north, see Fig. 4.3.1) and sea surface temperature (SST) indicators (mean annual number of days on which the temperature was above 18ºC, 24ºC and 26ºC per year from 2003 to 2010) along the Catalan coast. *SE*: standard error. *N*: number of locations where SST was measured along the Catalan coast. Temperature values were obtained from satellite data, see Methods. *95% CI*: 95% confidence interval calculated with bootstrapping.

SST indicator	slope (b)	SE of b	r^2	95% CI	N
no. of days ≥18ºC	-0.12	0.01	0.95	(0.86–1.00)	8
no. of days ≥24ºC	-0.22	0.02	0.95	(0.89–0.99)	8
no. of days ≥26ºC	-0.07	0.01	0.87	(0.71–0.98)	8

Discussion

Small cryptic alien species may be present at low numbers for years before they are detected (Crooks and Soulé 1999). However, this is most probably not the case for the alien coral *O. patagonica* in Catalonia because (1) it occurs mainly in the shallow infralittoral zone, which has been well studied in previous taxonomic surveys during the 1970s and early 1980s (Camp and Ros 1980; Gili 1986; Zabala 1986; Uriz 1987; Ballesteros 1992); (2) it achieves a large colony size (>50 cm in diameter); (3) it is easy to identify and has previously been detected in other Mediterranean areas (Zibrowius 1974; Zibrowius and Ramos 1983); and (4) the Catalan coast was regularly explored (every 1–2 years) at a high resolution (mean distance between locations of 2 km) throughout the entire study period (1992–2010) with the specific objective of detecting alien species in this habitat. We therefore conclude that *O. patagonica* should be a recent addition to the studied coast.

Although the regular monitoring of *O. patagonica* has allowed us to characterize the dynamics of its spreading, the initial detection of the species at a sampling station did not necessarily correspond to the date of its arrival because we were not able to detect very small colonies with one polyp or a very low number of polyps. In fact, according to Lodge (1993), the proportion of species introduced outside of their original range that become established is generally low for a wide variety of reasons, and the time of establishment is ecologically more relevant than the time of first arrival. The fact that *O. patagonica* did not disappear from any of the locations where it had been detected over the 19-yr monitoring period indicates that our time of initial detection is a conservative estimate of the time of establishment.

Spreading dynamics

The use of a standardized spread curve has allowed us to characterize a 9-yr lag period, during which the spreading rate was much lower than that in the exponential phase. After the establishment of the species at a particular location, its colonies begin to grow and reproduce. Thus, the observed lag phase could be related to the fact that broadcast spawning corals, such as *O. patagonica* (Fine et al. 2001), rely on an external fertilization process (in which gametes are released into the water column for dispersal) that requires a critical density of adults to ensure successful fertilization (Levitan et al. 1992; Lewis and Kareiva 1993; Veit and Lewis 1996; Taylor and Hastings 2005). Additionally, the species is a gonochoric coral, and a skewed sex ratio has been documented at certain locations with low coral abundance (Fine et al. 2001). Therefore, Allee effects could be contributing to the observed lag phase in this species' spreading dynamics. Surprisingly, the lag phase of this coral species is within the range documented for most invasive benthic macroalgae (5–10 years; Lyons and Scheibling 2009), which is likely attributable to the particular biological characteristics of *O. patagonica* (see below). The beginning of the exponential phase occurred when *O. patagonica* was present at 3.6% of the total number of investigated locations, indicating that the exponential phase began shortly after the species established foci in the region.

The observed northward spread of *O. patagonica* across the study area coupled with the northward decrease in coral abundance and maximum colony size, providing strong evidence of a recent and ongoing poleward expansion. The MSD estimate for the southern region of *O. patagonica* distribution, which is indicative of the pattern of dispersal to nearby locations, showed a decrease in spreading over time (Méndez et al. 2010). This finding is consistent with the fact that the species faces less favorable conditions while spreading northward (Miller 1998; Woodroffe 2011). However, the MSD estimate for the overall distribution indicated a pattern of spreading acceleration over time. The differences in the patterns emerging from the two estimates are based on the occurrence of a few intermittent long-distance dispersal events (i.e., punctuated dispersal; Davis et al. 2000). The occurrence of intermittent long-distance dispersal events exerted a large effect on the overall pattern of spreading of the species by promoting a regime shift from a decreased to an accelerated pattern of spreading over time. Thus, the rapid spreading of *O. patagonica* appears to have been accomplished through the interplay of two spatial scales of dispersal: neighborhood dispersal and long-distance dispersal interspersed with lag periods. This rapid spreading is consistent with a large increase in the spreading rate that may be caused by a small number of long-distance dispersal events, as documented in other observed and modeled populations (Neubert and Caswell 2000; Clark et al. 2003; Underwood et al. 2007).

Various tropical corals appear to be shifting their distributions to higher latitudes in the western Atlantic (6–10 km yr^{-1}; Vargas-Ángel et al. 2003, *sensu* Sorte et al. 2010), the Indo-Pacific (Marsh

1993) and the western Pacific (2–14 km yr^{-1}; Yamano et al. 2011). The northward spreading rate of *O. patagonica* observed in this study (22 km yr^{-1}) is the highest reported for a native or alien scleractinian coral to date and is consistent with the recently documented presence of isolated colonies of this species in distant zones throughout the Mediterranean (Sartoretto et al. 2008).

Gametogenesis has been observed in colonies from the study area (authors' unpublished data). Dispersal to nearby areas can be achieved through the dispersion of planula larvae and via the polyp expulsion mechanism (Kramarsky-Winter et al. 1997). Long-distance dispersal can also be achieved through planula dispersion mediated either by currents or ballast waters as previously suggested (Zibrowius 1974; Sartoretto et al. 2008). However, the capacity of this species to settle on floating objects (Fine et al. 2001, authors' observations) and to thrive in harbors and polluted areas (Zibrowius 1992) suggests that drifting on artificial substrata may be another vector favoring dispersal. Long-distance dispersal mediated by floating objects has been shown to contribute to the spreading of rapid colonizer species of coral (Bertelsen and Ussing 1936; Jokiel 1984; Sammarco et al. 2004; Hoeksema et al. 2012). Although sea surface circulation along Catalonia typically occurs in a southwestward direction (Millot 1999), strong southern winds also occur regularly (Sammari et al. 1995), which may help to explain the observed northward spreading of *O. patagonica* (SM 4.3.4). This spreading, *via* the above-mentioned dispersal mechanisms, indicates the high capacity of this species for dispersal, recruitment, growth and survival, which is consistent with its biological characteristics (see below).

Causes of northward expansion

Successful establishment in a new area is dependent on the physical environment and the life-history traits of the species together with biological interactions (Connell 1961; Wethey 2002). However, the response of a species to environmental change could affect the outcome of biotic interactions such as competition and predation (Byers 2002; Kennedy et al. 2002; Stachowicz et al. 2002; Meiners et al. 2004). For example, when *O. patagonica* comes into contact with a bryozoan species, the competitive outcomes vary depending on whether the coral is affected by bleaching (Fine and Loya 2003). Competition between macroalgae and corals plays a significant role in determining the composition of benthic communities (Hoegh-Guldberg 1999; Bruno et al. 2009; Hughes et al. 2010). Macroalgae are dominant in shallow habitats in temperate ecosystems (Miller and Hay 1996; Miller 1998; Witman and Dayton 2001), and this dominance is especially evident in the Mediterranean (Zabala and Ballesteros 1989; Ballesteros 1989, 1991). Although macroalgae have been strongly affected during the last century due to habitat alteration along the Catalan coast, the shallow infralittoral zone in which the species dwells is still spatially limited (Thibaut et al. 2005; Pinedo et al. 2007). In the northwest Mediterranean Sea, extreme physical disturbances and/or the high sea urchin abundance are the main mechanisms that create significant open spaces in an otherwise spatially limited macroalgal community (Palacín et al. 1998a; Navarro et al. 2011). Although the Catalan coast was affected by several large storms (defined as storms with waves ≥3 m) during the study period, only the storm of December 2008 was sufficiently large to cause relevant changes in the availability of open spaces (Sanchez-Vidal et al. 2012). Thus, the observed pattern of northward spreading cannot be attributed to a variation in the occurrence of physical disturbances. With regard to herbivory pressure, an increase in sea urchin abundance has been shown to increase the availability of open spaces and facilitate an increase in the abundance of coral species by reducing the competitive dominance of algae (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006; Chapter 4.2). However, sea urchin abundance did not increase over the course of the study, and in some areas, it decreased due to legal and illegal fishing (Palacín et al. 1998b; Corbacho 2010). Hence, the northward spread also cannot be attributed to a change in sea urchin abundance. Therefore, we conclude that physical and biotic disturbances have not varied much over the last twenty years, and although some changes in the composition of macroalgal communities have been detected, no major structural changes have occurred.

Although the main reasons for the northward expansion of *O. patagonica* are difficult to identify, the observed pattern of spread suggests some factors that must have played a relevant role in promoting the spread of this species. The high proportion of *O. patagonica* in artificial habitats in contrast to natural habitats (see Results) indicates that artificial habitats represent important places that foster the abundance and dispersal of this species. Space availability is the main initial difference between natural and artificial habitats. Assemblages flourishing in artificial habitats become similar to those of adjacent rocky bottoms over time; however, even after many decades, the assemblages do not usually resemble each other because artificial habitats are characterized by a higher space availability and a lower species richness, both of which are factors that increase habitat invasibility by primary space occupiers such as *O. patagonica* (Glasby and Connell 1999; Stachowicz et al. 1999; Davis et al. 2000; Chapman 2003; Gacia et al. 2007). Thus, space availability plays a crucial role in explaining the differential spreading observed between the two types of habitats, which is consistent with previous results showing that open spaces created by the grazing activity of sea urchins enhances the settlement and survival of *O. patagonica* (Chapter 4.2).

The deployment of coastal infrastructure causes ecological impacts by altering water flow, light penetration and sedimentation rates in shallow coastal waters (Bulleri and Chapman 2010), which negatively affects the growth of scleractinian corals (Fabricius 2005). However, field studies and laboratory experiments have revealed that *O. patagonica* has an exceptional capacity to grow under a wide range of environmental conditions (Fine et al. 2001); as such, it is less affected than many native species by the above-mentioned side effects of artificial habitats. Therefore, the increased space availability on artificial substrata and the increasing deployment of artificial marine habitats in

Catalonia (SM 4.3.3) appear to be the main causes of the observed differences in the spreading dynamics of the species between the two habitat types. Artificial habitats may be acting as corridors that facilitate the expansion of this species. Thus, although *O. patagonica* has been known to occur south of Catalonia since the 1970s (Zibrowius and Ramos 1983; Fine et al. 2001), the fact that the species did not reach the study area until the early 1990s, despite the presence of significant amounts of artificial substrata prior to that time and several large populations within <30 km of the first discovery site on the Catalan coast (some with >20% cover; Casado-Amezúa et al. 2011; authors' unpublished data), is indicative of a change in the spreading dynamics at the end of the 1990s and throughout the 2000s, which may be related to temperature.

Water temperature is among the main factors affecting the distribution of corals (Gaston 2000; Walther et al. 2002; Clark et al. 2003) and has been increasing over the last decades in the northwest Mediterranean (Calvo et al. 2011). Temperature has been hypothesized to limit coral reef growth directly by reducing the capacity of corals to achieve successful reproduction and recruitment (Harriott 1999; Hughes et al. 1999; Hughes and Tanner 2000), reducing coral growth (Lough and Barnes 2000) and causing coral mortality as a result of cold temperature episodes (Lirman et al. 2011). Damage to *O. patagonica* colonies in winter (partial mortality) occurs in the southern locations of the study area (authors' unpublished data) and is likely to be related to cold temperatures as previously documented (Rodolfo-Metalpa et al. 2008). Despite this damaging effect, *O. patagonica* is especially abundant in these southern areas; therefore, current winter temperature (11.7ºC, the lowest 5th percentile except for the km 400) is not preventing the northward expansion of the species. The results raise the questions of: a) whether extreme cold temperature events may have prevented the northward establishment of this coral in the past, and b) whether the current 5th temperature percentile at km 400 (11.3ºC) may prevent further northward spread of the species.

A long-term data series (1974–2010) obtained *in situ* at 0.5 m depth was used to estimate the rate of the mean annual temperature increase on the Catalan coast (0.032ºC yr^{-1}; Calvo et al. 2011). Based on this estimation, the mean annual temperature has increased ~0.6ºC over the 19-yr study period. Additionally, the growing season (number of days with SST ≥18ºC) has been lengthened by 0.76 d yr^{-1} due to the warming pattern; therefore, it has increased by ~14 d over the study period (1992–2010; authors' unpublished data). This corresponds to a 10% increase of the period in which the species' growth is 2-folds higher than that at lower temperature (Rodolfo-Metalpa et al. 2008). However, the warming pattern also increases the occurrence of extreme high temperature episodes (Coma et al. 2009; Bensoussan et al. 2010), and previous experiments have shown that high temperatures affect *O. patagonica* (Kushmaro et al. 1997; Rodolfo-Metalpa et al. 2006a, 2008). Interestingly, we have not observed coral bleaching and/or partial mortality in relation to high temperatures in the region; thus, the current high summer temperatures have not caused conspicuous harm to the species in the study area. This finding is consistent with the fact that the upper sea temperature thresholds that were documented to cause damage to this coral in Israel (i.e., >36–44 d above 26ºC; Kushmaro et al. 1997) have not been reached in the study area. Thus, the current pattern of seawater temperature increase favors coral growth by extending the growing period of the species, as has been documented in other species from terrestrial ecosystems (Peñuelas and Filella 2001). The lack of apparent damage to the colonies submitted to the highest 95th temperature percentile (26.8ºC) indicates that, if the current pattern of sea warming is maintained, lengthening of the species' fast growing period will continue to favor the species growth during the following decades because most of the study area is far below the value of this percentil. *O. patagonica* exhibited a rapid increase after 1999. The cause of this timing can not be addressed, however, it coincided with the time period in which warming accelerated in the Eastern Mediterranean Sea causing an amplification of the entry of alien species (Raitsos et al. 2010).

Although successful establishment is affected by environmental conditions and interspecific interactions, the expansion of a population mainly depends on growth and dispersal and, consequently, on the life-history characteristics of each species (Shigesada et al. 1995; Crooks and Soulé 1999). Therefore, biological traits that are characteristic of an opportunistic colonizer may have contributed to the observed pattern of *O. patagonica* expansion; these traits include (a) the ability to function as a facultative zooxanthellate species, (b) the capacity to reproduce both sexually and asexually and to be fertile at an early age (1–2 years; Kramarsky-Winter et al. 1997; Fine et al. 2001), (c) the ability to survive extreme environmental conditions (i.e., in tide pools, at temperatures of 10–40ºC and at salinities of 28–50‰ (Fine et al. 2001), and (d) the capacity to survive and grow in harbors, polluted areas, and areas affected by severe sand scouring as well as on undisturbed natural rocky bottoms (Zibrowius 1992).

Although environmental conditions are among the major determinants that shape species distribution ranges (Gaston 2000; Walther et al. 2002) and represent the main factors controlling coral species (McManus and Vergara 1998), the abundance of artificial habitats and the biological characteristics of *O. patagonica* have played a significant role in the ongoing expansion of this species. In short, the rapid spread process appears to be a response to global change mainly mediated by the interplay of (i) the availability of open space provided by artificial habitats, (ii) seawater temperature increase (mainly by extending the growth period), and (iii) the particular biological features of *O. patagonica* (high current growth rates, early reproduction, and survival to low temperature and in polluted areas).

Despite the evidence that some coral species appear to be responding to climatic warming by expanding their distributions toward the poles (Wooddroffe 2011, see above), it has been argued that latitudinal migration is unlikely to occur rapidly enough to respond to the current projected temperature change (3–6ºC over the next 100 years; IPCC 2007) due to the significant distance involved (i.e., the latitudinal temperature gradient is ~1.5ºC/1000 km), the effects of temperature on reproduction and the decrease in carbonate ion concentrations at high latitudes (Guinotte et al. 2003; Hoegh-Guldberg et al. 2007; Hoegh-Guldberg 2009). The present study has characterized the rapid northward expansion of a coral species at high latitudes (40–42ºN), a process that has been enhanced by artificial reef structures ahead of the migrating coral. Furthermore, *O. patagonica* is able to reproduce under the environmental conditions at these high latitudes (authors' unpublished data) and even adapt to the effects of repeated bleaching events (Armoza-Zvuloni et al. 2011). Thus, a coral species with particular biological characteristics that allow it to withstand the temperature challenge that accompanies northward migration as well as the natural and anthropogenic side effects that this type of migration involves (i.e., competition with macroalgae, high sediment loads, turbidity, water chemistry) has accomplished a successful northward expansion and may be able to keep pace with the global warming prediction of ~3ºC over the next 100 years.

It is crucial to develop an understanding of the characteristics and the spread rate of a coral that is able to profoundly alter the habitat within which it thrives. In the southeast region of the Iberian littoral zone in the Mediterranean Sea, *O. patagonica* has exhibited a large increase in cover over the last decade (from 3–5% to 10–15%; Chapter 4.2). Furhermore, this species has been able to induce a persistent phase shift from macroalgal to coral dominance at a particular location (Chapter 4.1), which challenges the current conceptual framework (Zabala and Ballesteros 1989). In this evolving context, the rapid northward spread of the species over the last two decades is indicative of an ongoing fundamental modification of temperate shallow water assemblages, which is consistent with predictions (Giorgi 2006; Calvo et al. 2011) that highlight the Mediterranean Sea as one of the ecosystems most sensitive to global change.

Acknowledgments

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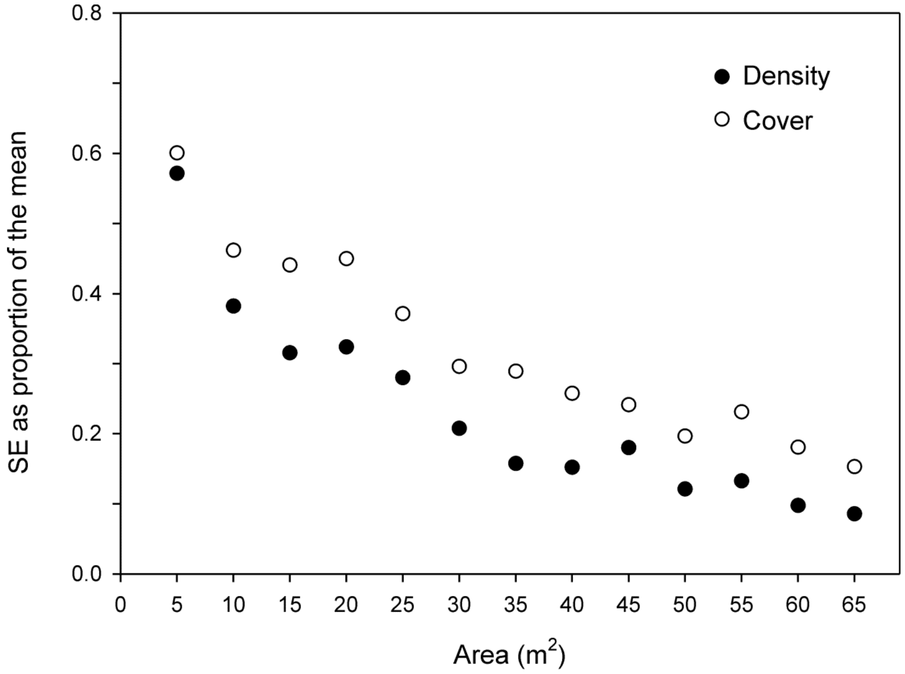
Supplementary Material (SM)

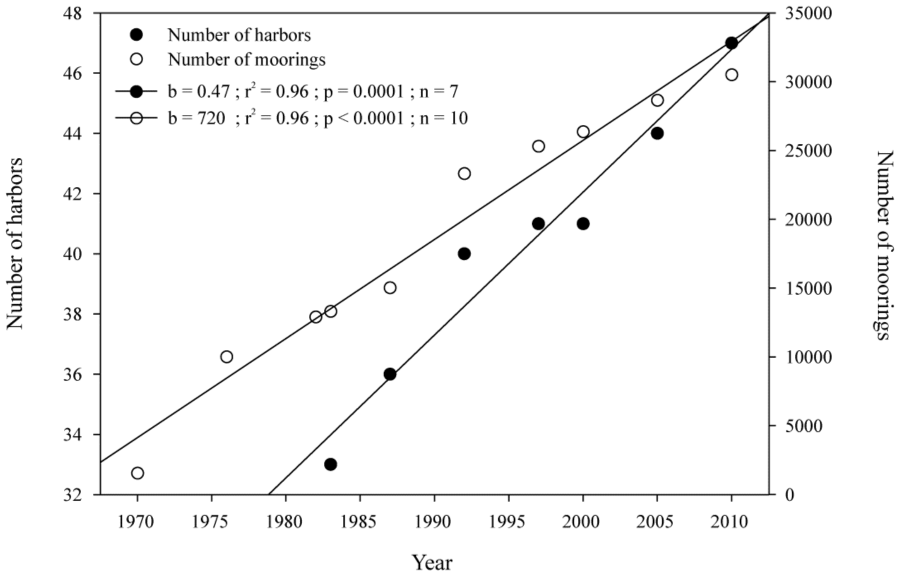
SM 4.3.1 *Oculina patagonica*. Minimal sampling area for colony density and cover estimates. Variation of the standard error (SE) as a proportion of the mean with sample size (area in square meters) to determine the minimum sample size for colony density and cover estimates.



SM 4.3.2 Studied locations for sea surface temperature (SST) in the Catalan coast. The cumulative distances between the locations for which temperature was examined, ordered from south to north, are indicated. *N*: number of valid daily SST measurements obtained from NASA satellite measurements over the last 8 years (2003–2010).

Zone	Locality	Code	Distance (km) south to north	Geographic coordinates		SST readings
				Latitude, N	Longitude, E	N
1	Les Cases d'Alcanar	CA	0	40°31'05"	0°32'25"	1089
	L'Ampolla	LA	40	40°50'00"	0°46'51"	1202
2	Vilanova i la Geltrú	VG	130	41°11'02"	1°42'05"	1454
	Premià de Mar	PM	200	41°29'28"	2°25'28"	1400
3	Platja d'Aro	PA	280	41°46'47"	3°04'52"	1385
	Medes Islands	MI	325	42°01'14"	3°13'47"	1397
4	Cadaqués	CD	370	42°15'00"	3°18'16"	1410
	Port de la Selva	PS	404	42°21'52"	3°12'19"	1237

SM 4.3.3 Trends on coastal development in the Catalan coast (1970–2010). Modified from Pla de Ports Catalunya 2007-2015 (2007). Generalitat de Catalunya. Departament de Política Territorial i Obres Públiques. ISBN 978-84-393-8417-5 (www.gencat.cat).



SM 4.3.4 Sea surface circulation in the Catalan Sea, implications for *Oculina patagonica* northward dispersal.

The sea surface circulation in the Catalan coast is dominated by a southwestward current (Northern Current, NC) flowing throughout the year along the continental shelf of the French and Catalan coasts (Font et al. 1988; Millot 1999). Although the direction of the NC flow is steady southward, its flux is maximum from December to May and its structure markedly changes seasonally. In summer, the NC is relatively wide and tends to flow closer to the coast, whereas in winter it becomes narrower and tends to flow closer to the continental slope (Albérola et al. 1995; Sammari et al. 1995; André et al. 2005). However, the NC displays significant mesoscale structures, mostly eddies and meanders, that affect the circulation at a local scale together with intermittent strong winds from the south (Alvarez et al. 1996; Salat et al. 2002; André et al. 2005). These mesoscale structures undergo a strong increase in autumn (Font et al. 1995; Sammari et al. 1995) which may have contributed to the northward dispersion of the species in the opposite direction to the main current. Nevertheless, the permanent southward sea surface circulation of the NC and its flow shoreward shift during the *O. patagonica* spawning and dispersion season in early autumn (Fine et al. 2001) is a hydrological factor that may have been diminishing the species rate of northward expansion documented along the Catalan coast.

4.4. Recurrent partial mortality events in winter shape the dynamics of the zooxanthellate coral *Oculina patagonica* at high latitude in the Mediterranean

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Abstract

Global warming has many biological effects on corals and plays a central role in the regression of tropical coral reefs; therefore, there is an urgent need to understand how some coral species have adapted to environmental conditions at higher latitudes. We examined the effects of temperature and light on the growth of the zooxanthellate coral *Oculina patagonica* (Scleractinia, Oculinidae) at the northern limit of its distribution in the eastern Iberian Peninsula (western Mediterranean) by transplanting colonies onto plates and excluding them from space competition over a ~4-yr period. Each year, most of the colonies (~70%) exhibited denuded skeletons with isolated polyps persisting on approximately half of the coral surface area. These recurrent episodes of partial coral mortality occurred in winter, and their severity appeared to be related to colony exposure to cold but not to light. Although *O. patagonica* exhibited high resistance to stress, coral linear extension did not resume until the coenosarc regenerated. The resumption of linear extension was related to the dissociation of the polyps from the coenosarc and the outstanding regenerative capacity of this species (10.3 mm^2 d^{-1}). These biological characteristics allow the species to survive at high latitudes. However, the recurrent and severe pattern of denuded skeletons greatly affects the dynamics of the species and may constrain population growth at high latitudes in the Mediterranean.

Introduction

Latitudinal variation in environmental parameters determines coral biogeography. Temperature, solar radiation, nutrients and the saturation state of seawater aragonite are critical factors for photosynthesis and the calcification of zooxanthellate corals, and these variables co-vary with increasing latitude, thus limiting coral growth at high latitudes (e.g., Kleypas et al. 1999; Muir et al. 2015). The scarcity of zooxanthellate corals in temperate areas is related to the effects of environmental parameters, competition with macroalgae and the synergistic interactions of biotic and abiotic factors (e.g., Miller 1998; Hoegh-Guldberg 1999). However, the current decline of coral reefs in both perturbed and unperturbed areas indicates that increasing temperature is a global stressor that is playing a crucial role in the regression of reef ecosystems (e.g., Hughes et al. 2010). Temperature has long been considered to be the primary factor controlling the distribution of coral species (e.g., Hoegh-Guldberg 1999; Kleypas et al. 1999), and exposure to both high and low stressful temperatures has been documented to reduce coral growth and cause bleaching and mortality (e.g., Saxby et al. 2003; Hoegh-Guldberg et al. 2005; Colella et al. 2012; Roth et al. 2012).

Global warming is affecting many biological aspects of coral species; even the more conservative warming projections indicate that many tropical reefs may enter a non-coral-dominant stage before the end of the century (Hoegh-Guldberg and Bruno 2010; Pandolfi et al. 2011; Frieler et al. 2013). Corals are among the organisms least expected to exhibit poleward movement because their capacity to adapt is usually outpaced by the current, rapid rate of environmental change due to human activities (Hoegh-Guldberg 2012). However, the distribution of some zooxanthellate scleractinian corals has shifted to higher latitudes in some areas, tracking the movement of suitable temperatures (e.g., Takao et al. 2015), and marginal habitats for coral reefs are predicted to expand in future climate scenarios (Freeman 2015). Understanding the ability of such coral species to adapt to environmental changes at high latitudes is crucial to predict shifts in coral communities in response to climate change.

In the shallow rocky assemblages of the temperate Mediterranean Sea, both local evidence of phase shifts from macroalgal to coral dominance and the rapid expansion of *Oculina patagonica* (Scleractinia, Oculinidae; Salomidi et al. 2013; Rodolfo-Metalpa et al. 2014; Chapters 4.1, 4.3) provide evidence that this zooxanthellate coral may be displaying invasive behavior that could challenge the current conceptual framework of the ecosystem (Miller 1998). Such behavior is consistent with the fact that *O. patagonica*, first documented in the Mediterranean in 1966, is currently found in many areas throughout the Mediterranean Sea (Rubio-Portillo et al. 2014a and references therein). A recent study indicated that the species is not a recent introduction, and thus its current taxonomic status is unclear because it cannot be reliably classified as either 'native' or 'introduced' (Leydet and Hellberg 2015). The most abundant *O. patagonica* populations have been recorded along the coast of the eastern Iberian Peninsula (Balearic Sea; Fine et al. 2001; Rubio-Portillo et al. 2014a; Chapters 4.1, 4.2, 4.3). However, although this coral has been expanding northward from the north Balearic Sea (40ºN) toward the Gulf of Lyon (42ºN) over the last two decades (Chapter 4.3), little is known about its growth dynamics in the expansion zone.

Similar to tropical corals, the growth rate of *O. patagonica* in the western Mediterranean is positively correlated with a certain temperature range (Rodolfo-Metalpa et al. 2008). Prolonged exposure to sublethal warm-temperature thresholds has been reported to damage *O. patagonica* colonies in short-term field studies (<2 yr) and surveys (Rodolfo-Metalpa et al. 2008, 2014; Rubio-Portillo et al. 2014b), and long-term studies in the eastern Mediterranean have shown that the species suffers severe annual bleaching and mortality events in summer (Fine et al. 2001; Shenkar et al. 2005) that are mainly related to exposure to high temperature (Ainsworth et al. 2008). In this study, we addressed the effect of temperature and light on *O. patagonica* growth dynamics in the expansion zone at the northern limit of its population distribution along the Iberian Peninsula (Chapter 4.3), a critical first step toward understanding the response of this species to climate change. We assessed the seasonal variation in growth and mortality of *O. patagonica* colonies over a ~4-yr period. Although long-term monitoring studies are labor intensive, they are fundamental to acquiring a thorough understanding of the factors that influence the life cycles of long-lived species such as corals, and they enable predictions of how such species might be affected by climate change. The effects of these abiotic factors were examined by transplanting coral colonies onto plates and excluding them from space competition with other organisms. The results of this study provide new insights into the seasonal and annual growth dynamics of *O. patagonica* at the northern limit of its distribution and contribute to an understanding of the biological characteristics that allow some zooxanthellate corals to thrive in temperate systems.

Materials and Methods

Sample collection

In August 2008, the encrusting colonial coral *O. patagonica* was sampled at L'Ampolla breakwater (40º49'N–0º43'E) in the north-Balearic Sea (northwest Mediterranean Sea; Fig. 4.4.1) by scuba diving at depths of 2–5 m. Coral fragments (~3 cm in diameter) were collected with a hammer and chisel from widely separated (>3 m) and healthy (<10% colony partial mortality) colonies (n = 29) that ranged between 25 and 40 cm in maximum diameter. The coral specimens were immediately placed in large seawater containers and transported to the Experimental Aquarium Zone at the Institute of Marine Sciences in Barcelona (<4 h). Shortly after, the coral samples were carefully cleaned of epiphytes and sediment, and each was glued onto a methacrylate plate (15 x 15 cm) with an inert mastic compound. The coral plates were placed in a 225-L acclimation tank equipped with a circulation pump and running natural seawater. The inlet and outlet pipes remained open so that the acclimation tank functioned as a flow-through open system, and the corals were maintained in aquaria under controlled conditions until the perimeter of the entire colony was growing onto the plastic plates. During the ~3-month acclimation period in the aquaria, the natural seawater temperature (ST) was gradually decreased from 25 to 18ºC, and the light conditions were adjusted to 150 µmol photons m^{-2} s^{-1} (12:12 light:dark photoperiod) to simulate late summer/early autumn conditions at the study area (Fig. 4.4.2).

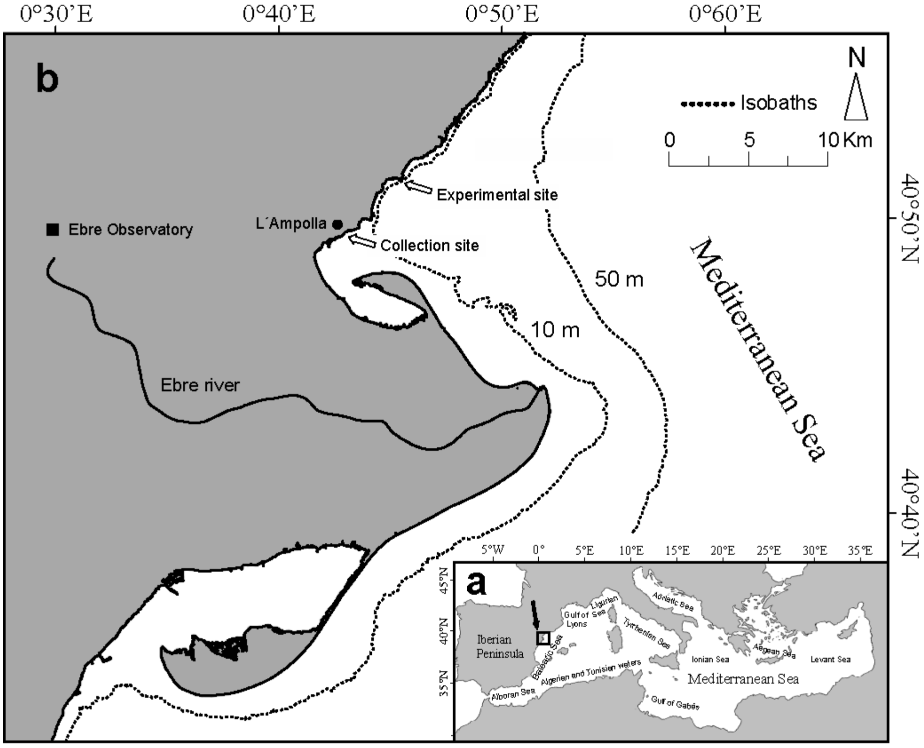

Fig. 4.4.1 Study area. **a** Map of the Mediterranean Sea showing the study area (L'Ampolla) in the north Balearic Sea. **b** Location of the collection site and the experimental site.

Study site and experimental design

In November 2008, the 29 coral plates were transported back and randomly fixed onto a rocky reef located ~5 km north of the collection site (Fig. 4.4.1). The thermal and light regimes did not differ between the collection and experimental sites (see SM 4.4.1 in supplementary material, SM). Therefore, we will generally refer to the study area as L'Ampolla. In the study area, *O. patagonica* has a patchy distribution on shallow rocky reefs with locally abundant populations (Chapter 4.3). All coral plates were installed on slightly inclined surfaces (<45º) at depths of 4–5 m within a ~400-m^2 rocky area oriented parallel to the shore (80 x 5 m). The coral plates were monitored over a ~4-yr period (November 2008–August 2012, n = 17 sampling dates) at an average sampling interval of 87 ± 8 d (SE, n = 16). The benthic community surrounding the plates was dominated by algal communities with a canopy height >2 cm. On each sampling date, the coral plates were cleaned of settling organisms (commonly turf algae <1 cm in height) to ensure that the corals were not exposed to algal competition, and any algae that settled on the coral skeleton were removed during the surveys.

Colony partial mortality and growth

On each sampling date, all coral plates were photographed *in situ* using a ruler as a size reference. Because colonies of *O. patagonica* have an encrusting morphology, the colony surface area from a planar view and the area experiencing partial mortality were measured from photographs using ImageJ software. Colony partial mortality was evaluated for each sampling date as the percentage of the colony area showing signs of mortality (i.e., denuded skeleton or coverage by sessile organisms). Partial mortality was further classified into three levels of severity: mild (<15%), moderate (15–85%) or severe (>85%). At the beginning of the study (November 2008), mean partial mortality was 2 ± 1% (SE, n = 29). Colony partial mortality rates between sampling dates were calculated by dividing the change in partial mortality from one sampling date to the next by the number of days in the sampling interval expressed as a percentage of the colony area (% d^{-1}) and as mm^2 d^{-1}. The rate of variation in planar area between sampling dates was calculated by dividing the accumulated colony surface area from one sampling date to the next by the number of days in the sampling interval (cm^2 d^{-1}). The change in arithmetic mean diameter appears to be the most appropriate method to standardize linear growth rate data of coral colonies *versus* the initial size, particularly for encrusting species that tend to grow primarily in the horizontal plane and have circular areas (Pratchett et al. 2015), such as *O. patagonica* (Fig. 4.4.3). Then, to provide a size-independent measure of the linear extension rate (cm diameter d^{-1}), the planar area (A, cm^2) was translated to the arithmetic mean diameter (D, cm) using the formula $D = 2 * \sqrt{A/\pi}$. The mean annual linear extension rate was estimated for each study year by integrating the mean daily values of the different sampling intervals.

Environmental data

Global solar radiation (J m^{-2}) throughout the study period was recorded by the Ebre Observatory (located 50 m above sea level; Fig. 4.4.1). The daily photosynthetically active radiation (PAR, mol photons m^{-2} d^{-1}) at a depth of 5 m was obtained from global irradiance and light attenuation coefficient data (SM 4.4.1). The mean annual and monthly PAR were determined based on the daily values averaged over the study period.

ST was recorded hourly throughout the study period using onset HOBO pendant temperature data loggers (UA-002–64) placed at a depth of 5 m, and the mean annual and monthly STs were determined based on the averaged daily values. We also calculated the number of days in which the mean daily ST was above and below different thresholds (≥20 to ≥28ºC and ≤19 to ≤11ºC, respectively).

Statistical analysis

The individual and combined relationships between coral performance (partial mortality and linear extension rates) and environmental parameters (PAR and ST) were assessed by multiple regression using the mean PAR and ST calculated for each sampling interval. Cross-correlation analyses were used to establish relationships between the environmental parameters (PAR and ST) over time and to determine the relationship between *O. patagonica* performance and ST. One-way repeated-measures ANOVA was used to test the interannual differences in mean partial mortality and linear extension rates, combined with Tukey's test for post hoc comparison. A Chi-squared (χ^2) test was used to examine the interannual variability in ST thresholds. We used STATISTICA version 7.0 for the analyses, and the results are expressed as the mean ± SE.

Results

Environmental parameters

The mean annual PAR at L'Ampolla (5 m depth) during the study period was 19.5 ± 0.7 mol photons m^{-2} d^{-1} (2009–2011, n = 3) and ranged between 18.3 and 20.8 mol photons m^{-2} d^{-1} (Fig. 4.4.2a). The light regime was characterized by marked seasonality, with monthly mean PARs ranging from 6.1 mol photons m^{-2} d^{-1} in December 2009 to 36.6 mol photons m^{-2} d^{-1} in July 2010 (Fig. 4.4.2a; daily mean PAR values are shown in SM 4.4.2a). Two periods were distinguished based on the monthly mean PARs: (1) a high-radiation period from April to September (27.3 ± 1.0 mol photons m^{-2} d^{-1}, n = 3) and (2) a low-radiation period from October to March (12.1 ± 0.6 mol photons m^{-2} d^{-1}, n = 3; Fig. 4.4.2a).

The mean annual ST at L'Ampolla was 18.5 ± 0.4ºC (2009–2011, n = 3) and ranged between 17.7 and 18.9ºC (Fig. 4.4.2b). The thermal regime was characterized by marked seasonality with monthly mean STs ranging from 11.7ºC in February 2010 to 27.1ºC in August 2009 and a mean thermal amplitude of 13.9 ± 0.2ºC during the annual cycle. The minimum mean daily ST was observed in February 2010 (10.1ºC), and the maximum occurred in August 2009 (28.6ºC; SM 4.4.2b). Based on the monthly mean STs, two periods were identified (each separated by a 1-month shift): (1) a cold period from December to April (13.5 ± 0.1ºC, n = 4) with a warming shift in May (18.1 ± 0.4ºC, n = 4) and (2) a warm period from June to October (23.6 ± 0.5ºC, n = 3) with a cooling shift in November (17.4 ± 0.6ºC, n = 4; Fig. 4.4.2b).

The PAR and thermal regimes exhibited similar seasonal trends but with a time delay (i.e., the maximum seasonal peaks in ST shifted to the right relative to the maximum peaks in PAR; Fig. 4.4.2). Based on the daily means, cross-correlation analysis revealed that the highest positive Pearson correlation coefficients were between the ST and the PAR measured 1–2 months earlier (the maximum correlation at –40-d lag, r = 0.79; SM 4.4.2c). The wave-like form of the cross-correlation plot, with peaks separated by ~6 months, reflected the seasonal nature of the changes in PAR and ST.

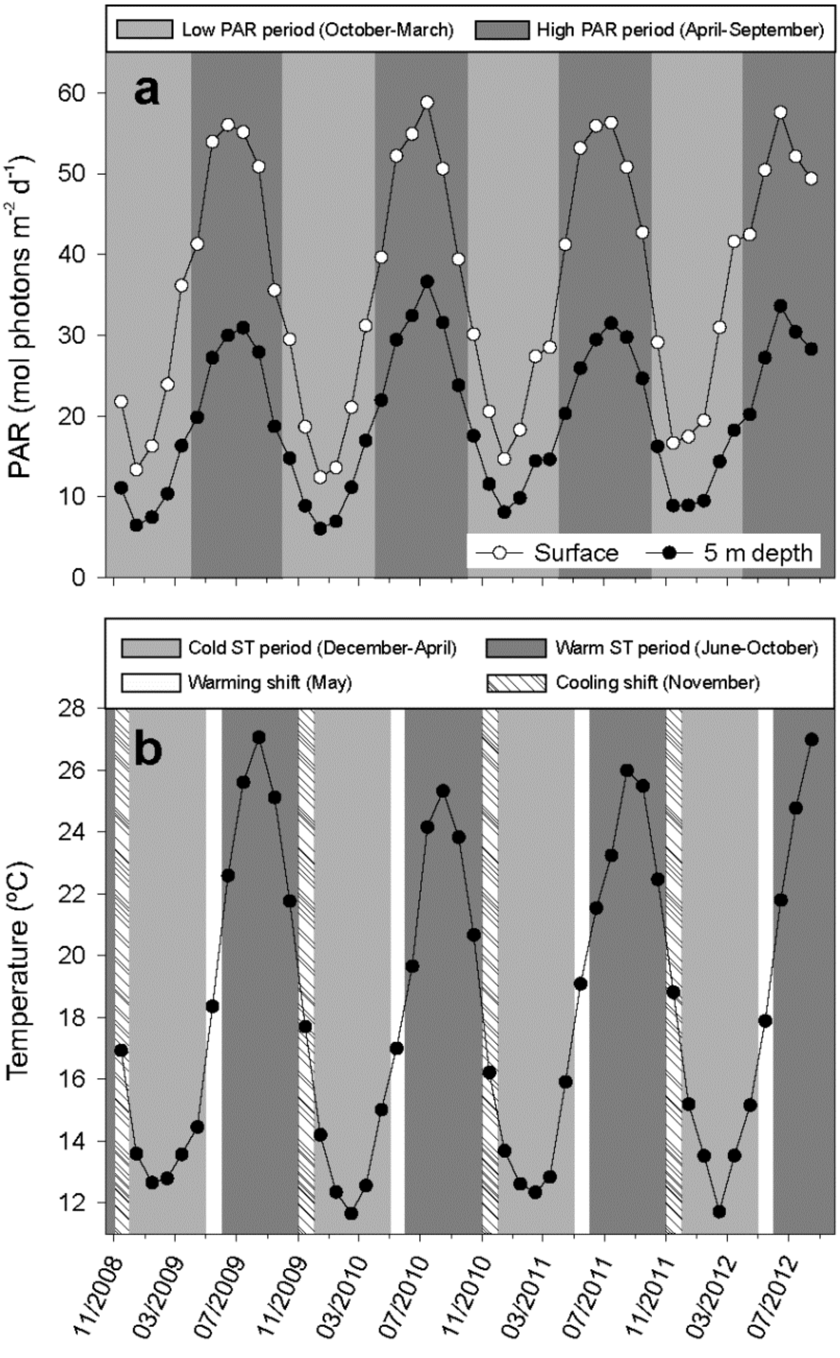

Fig. 4.4.2 Environmental parameters. **a** Monthly mean photosynthetically active radiation (PAR) at sea surface and 5 m depth at L'Ampolla. **b** Monthly mean seawater temperature (ST) at 5 m depth at L'Ampolla.

Annual cycle of coral partial mortality

The seasonal advent of partial mortality (i.e., tissue loss resulting in a denuded skeleton) and recovery in the *O. patagonica* colonies was the most predominant process and occurred each year throughout the four annual cycles examined at L'Ampolla (Fig. 4.4.3). The phenomenon of partial mortality began affecting small, unconnected parts of the coenosarc, exposing the denuded coenosteum in different (central and peripheral) but isolated parts of the colony (i.e., multifocal distribution; e.g., January in Fig. 4.4.3). In this first phase, partial mortality usually followed a progressive coalescence of the multifocal denuded skeleton that was conducive to the loss of nearly the entire coenosarc, but the remaining polyps remained healthy (alive and brown in color) and isolated within the calyx (e.g., April in Fig. 4.4.3). The phenomenon was rarely observed in the final phase, in which the isolated polyps disappeared from parts of the colony, leaving a completely denuded skeleton.

The first symptoms of denuded partial mortality were detected in December, and the symptoms increased until April of each year when the highest values were detected (49 ± 9%, 2009–2012, n = 4; Fig. 4.4.4a). The April peak in partial mortality resulted in the highest percentage of colonies with moderate and severe partial mortality (>15%, 75 ± 10%; SM 4.4.3). The mean rate of partial mortality from December to April was 0.32 ± 0.08% d^{-1} (n = 7; Fig. 4.4.4b,c), which is equivalent to 10.0 ± 3.1 mm^2 d^{-1}. The colonies started to exhibit signs of recovery in May, when the tissue surrounding the denuded skeleton began to recover. The mean annual peak in the tissue regeneration rate from May to July was –0.35 ± 0.02% d^{-1} (2009–2012, n = 4; Fig. 4.4.4b,c), which is equivalent to –10.3 ± 2.7 mm^2 d^{-1}. By July, the mean extent of partial mortality was reduced to 24 ± 4% of the April peak each year (2009–2012, n = 4; Fig. 4.4.4a). Some overgrowth of the denuded coral skeleton by filamentous and foliose algae and deposition of sediment particles occurred during the mortality and recovery periods (Fig. 4.4.3), so after this rapid recovery phase, tissue regeneration of the remaining areas of partial mortality continued at a slower pace from August to November (–0.05 ± 0.03% d^{-1}, n = 5; Fig. 4.4.4b,c). Partial mortality rate values from this slow recovery phase were excluded in the regression analysis with environmental parameters, because lesion regeneration was already completed or affected by algae overgrowth. Overall, the regeneration process led to the lowest mean extent of partial mortality (4–8%, 2009–2011, n = 3) and the lowest percentage of colonies with mild partial mortality (<15%, 96 ± 2%) in November; these values remained low until the initiation of the subsequent partial mortality event in December (Fig. 4.4.4a; SM 4.4.3). The occurrence of a recently denuded skeleton and/or visually apparent bleaching was not observed from May to November in any of the study years (Fig. 4.4.3; Fig. 4.4.4).

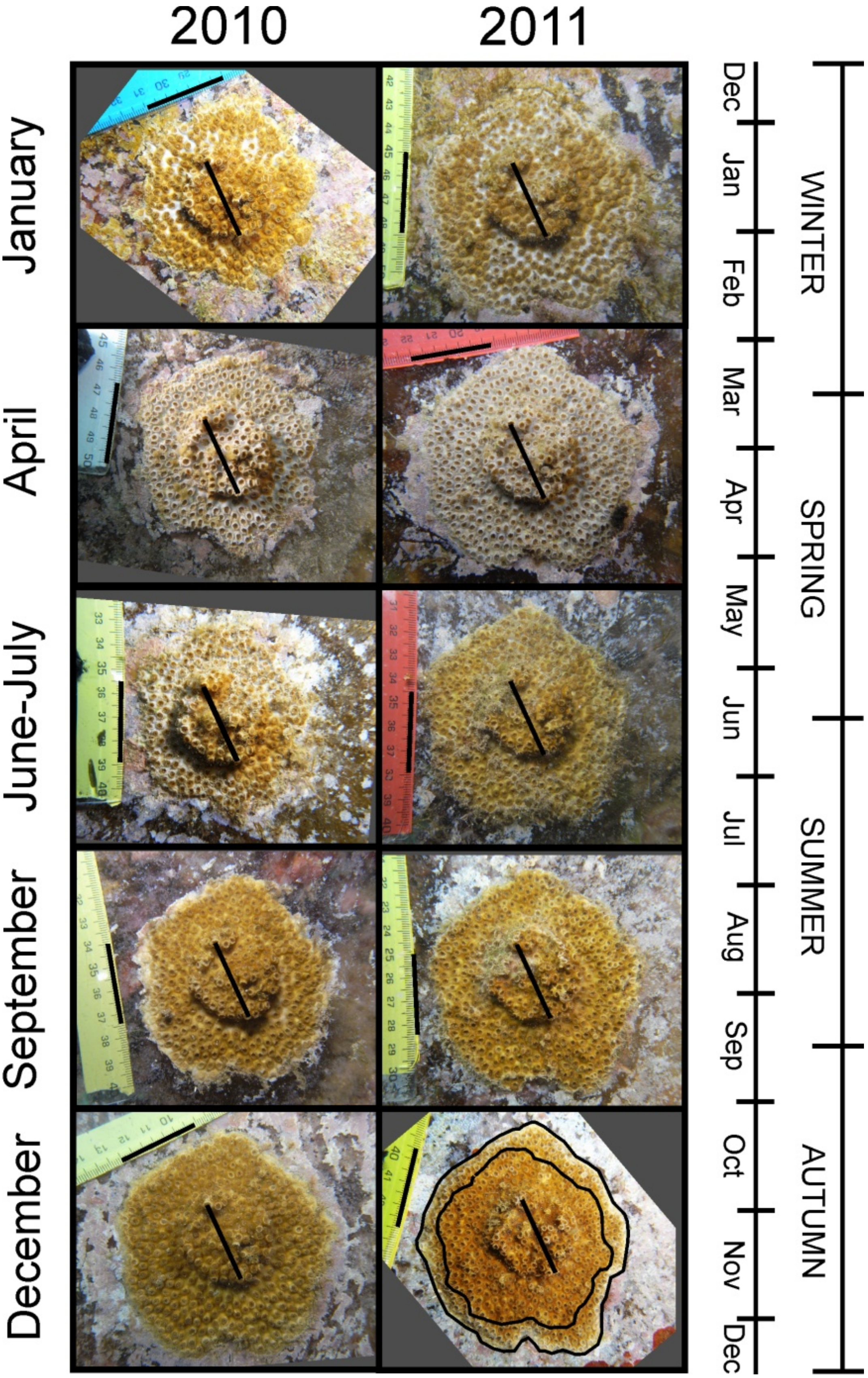

Fig. 4.4.3 Monitoring of a colony of *Oculina patagonica* from January 2010 to December 2011. Partial mortality occurred during winter and early spring, followed by recovery in late spring and linear extension during summer and autumn. The *perimeter* from January 2010 is superimposed on that from December 2011. *Scale bars* 3.40 cm.

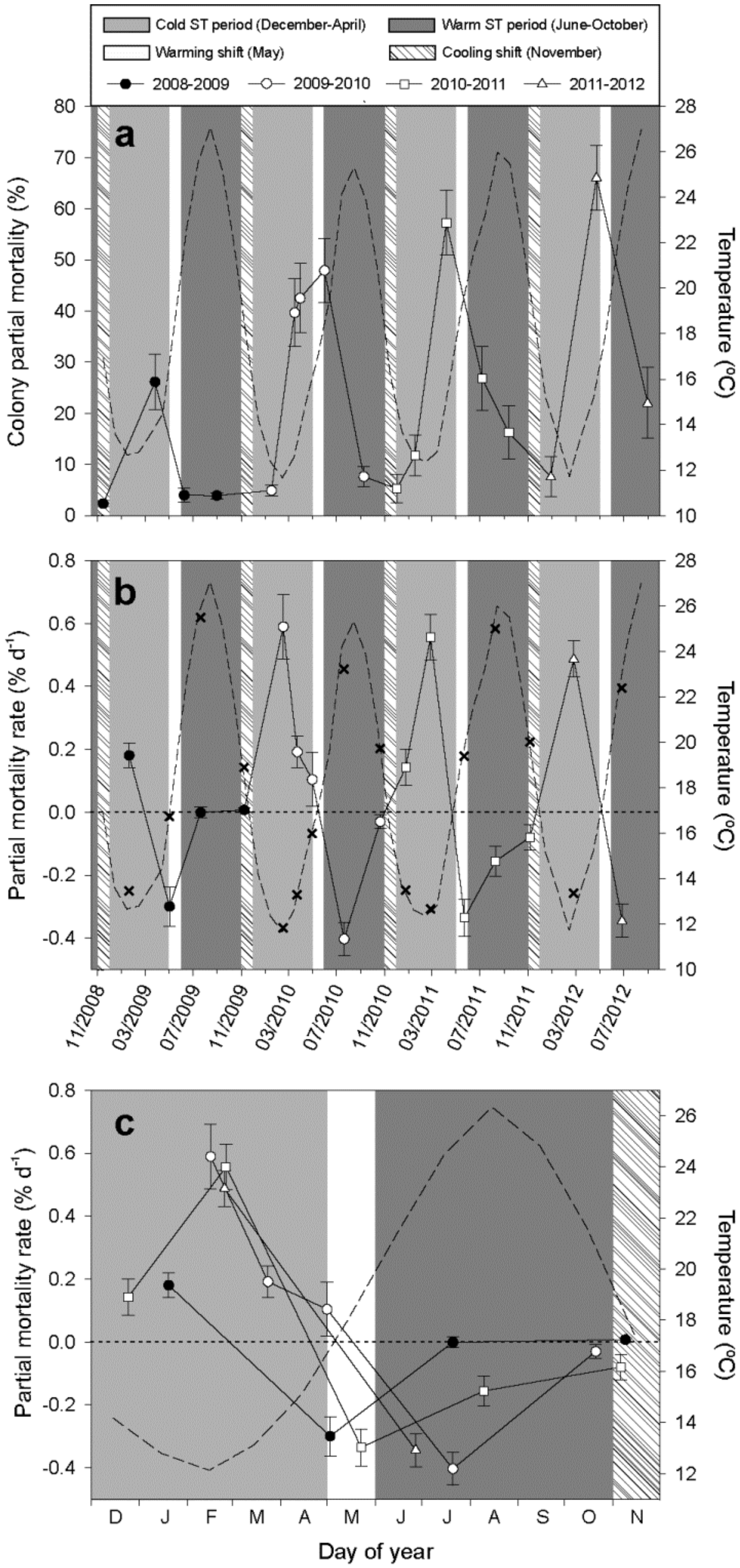

Fig. 4.4.4 Partial mortality of *Oculina patagonica* and seawater temperature (ST, *dashed lines* and *crosses*) at L'Ampolla. **a** Proportion of colony partial mortality on each sampling date (n = 17). Colony partial mortality rate **b** over the study period and **c** on an ordinal date for each sampling interval (n = 16). Values are mean ± SE.

Annual cycle of coral growth

The mean size of the *O. patagonica* colonies increased from 10 ± 1 cm^2 in November 2008 to 60 ± 12 cm^2 in August 2012 at a mean linear extension rate of 13.27 ± 2.95 cm^2 yr^{-1} (Fig. 4.4.5a), which is equivalent to a mean increase in colony diameter of 1.27 ± 0.19 cm yr^{-1}. The maximum linear extension rate of an individual colony was 2.47 cm diameter yr^{-1}. Coral growth exhibited a marked pattern of seasonal variation that repeatedly occurred during the ~4-yr study period (Fig. 4.4.5). The mean linear extension rate reached a minimum during the 6 months from December to May (0.0016 ± 0.0007 cm diameter d^{-1}, n = 9; Fig. 4.4.5b,c), which coincided with a decrease in living colony size (i.e., the extent of the coral tissue, which is complementary to the proportion of partial mortality) between December and April (Fig. 4.4.5a). Despite this decline in live tissue, coral skeleton growth resumed in June following the rapid tissue regeneration that started in May (Fig. 4.4.5a). The mean linear extension rate during the ~6 months from June to November (growing period) was 0.0058 ± 0.0007 cm diameter d^{-1} (n = 7; Fig. 4.4.5b,c).

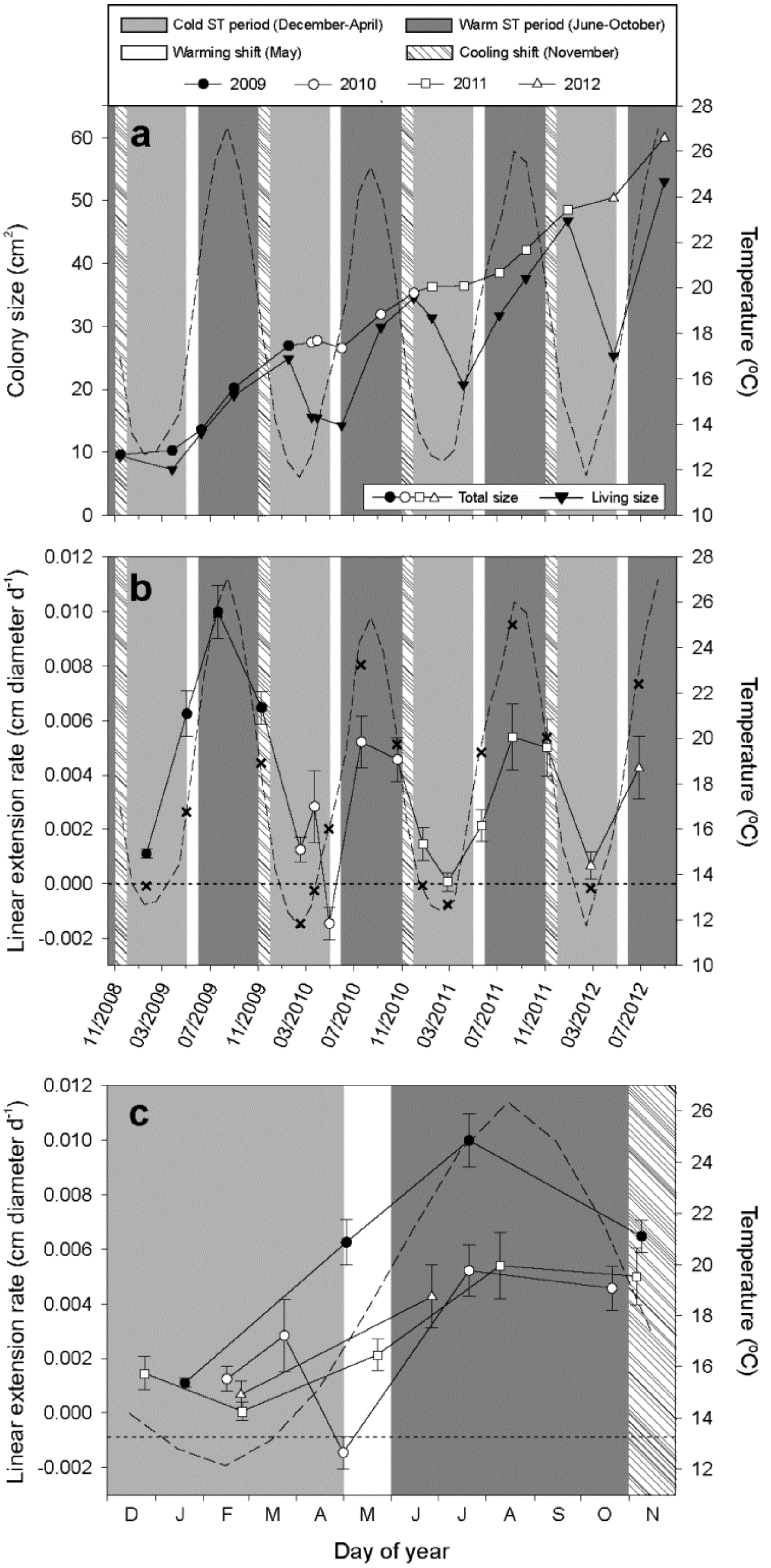

Fig. 4.4.5 Linear extension of *Oculina patagonica* and seawater temperature (ST, *dashed lines* and *crosses*) at L'Ampolla. **a** Total and living colony size on each sampling date (n = 17). Colony linear extension rate **b** over the study period and **c** on an ordinal date for each sampling interval (n = 16). Values are mean ± SE.

Coral mortality and growth in relation to environmental variables

The rate of *O. patagonica* partial mortality was negatively related to ST ($p = 0.0290$) but did not exhibit a significant relationship with PAR ($p = 0.64$) (multiple regression: $F_{2,8} = 15.79$, $r^2 = 0.80$, $p = 0.0017$, $n = 11$; values from the slow recovery phase were excluded). The proportion of colony partial mortality and ST displayed opposite trends but with a time delay (i.e., the maximum seasonal peaks in partial mortality shifted right relative to the minimum peaks in ST; Fig. 4.4.4a), and cross-correlation analysis indicated that ST and the proportion of partial mortality were negatively correlated and that the highest Pearson correlation coefficient was associated with a lag of –78 d ($r = –0.68$; SM 4.4.4a). These results indicated that the pattern of increased partial mortality was preceded by the minimum ST values 2–3 months earlier (i.e., the April peak in partial mortality was related to the lowest ST in January–February; Fig. 4.4.4a). The rate of partial mortality and ST exhibited opposite trends with no time delay (i.e., the maximum seasonal peaks in partial mortality rate coincided with the minimum peaks in ST; Fig. 4.4.4b; SM 4.4.4b), and there was a negative relationship between the two variables ($r^2 = 0.79$, $p = 0.0002$, $n = 11$), indicating that the positive mortality rate values might be related to the <14ºC threshold that commonly occurred from December to April (Fig. 4.4.6a). These results suggest that cold STs are an important factor influencing *O. patagonica* partial mortality in the study area.

The linear extension rate of *O. patagonica* colonies was positively related to ST ($p = 0.0008$) but did not have a significant relationship with PAR ($p = 0.10$) (multiple regression: $F_{2,13} = 12.63$, $r^2 = 0.66$, $p = 0.0009$). The linear extension rate and ST exhibited similar trends with no time delay (i.e., the maximum peaks in the linear extension rate coincided with the maximum peaks in ST; Fig. 4.4.5b; SM 4.4.4c), and there was a positive relationship between the two variables, with higher linear extension rates related to the >16ºC threshold that commonly occurred from May to November (Fig. 4.4.6b). These results suggest that warm STs are an important factor increasing *O. patagonica* linear extension in the study area.

These results demonstrate that ST is related to both partial mortality and linear extension of the species. Consequently, a cross-correlation analysis was conducted to examine the potential trade-offs between the two processes. The highest negative correlation between colony partial mortality and linear extension rates occurred at a –48-d lag (SM 4.4.4d), indicating that the high partial mortality rate from the previous 1–2 months negatively affected linear extension of the colonies.

Interannual variability in coral mortality and growth in relation to ST

The yearly peak in mean denuded partial mortality observed in April was always associated with similarly low values of partial mortality due to overgrowth in November (2–8%, 2008–2011), despite the fact that the April peak in 2009 (26%) was approximately half as large as those in 2010, 2011 and 2012 (48, 57 and 66%, respectively; Fig. 4.4.4a). Similarly, the percentage of colonies suffering from moderate to severe partial mortality (>15%) in April 2009 (45%) was 45–51% lower than those in 2010, 2011 and 2012 (83, 82 and 91%, respectively; SM 4.4.3). The annual peak in the partial mortality rate was also lower in 2009 (0.18 ± 0.04% d^{-1}) than in 2010, 2011 and 2012 (0.54 ± 0.03% d^{-1}; one-way repeated-measures ANOVA, $F_{3,84} = 10.62$, $p < 0.0001$). The number of days that ST was ≤19 to ≤13ºC did not vary significantly among the cold periods studied (2008–2009 to 2011–2012, n = 4; χ^2, p >0.05). However, the mean number of days that ST was ≤12ºC was 20 ± 4 d in 2009–2010, 2010–2011 and 2011–2012, a threshold that was not reached during the cold period of 2008–2009 (χ^2, p <0.05; SM 4.4.5). These results indicate that the occurrence of partial mortality was lower during the less severe cold period of 2008–2009 than during the other three more severe cold periods.

Generally, colony partial mortality occurred during the cold period (December–April) and was followed by tissue regeneration and linear extension. The annual peak in the regeneration rate was similar among the studied years (0.35 ± 0.02% d^{-1}, 2009–2012; one-way repeated-measures ANOVA, $F_{3,84} = 0.84$, p >0.05). Hence, the time required for nearly complete regeneration of the tissue (i.e., when the lowest partial mortality values, of 4–8%, were first reached) appeared to be related to the severity of the annual partial mortality episodes (i.e., the time required for regeneration was longer in years showing high denuded partial mortality in April), which contributed to the interannual variation of the duration of the negative effect of partial mortality on the linear extension rate. As a result, the lower incidence of partial mortality in 2009 resulted in complete regeneration by June, but as the incidence of partial mortality increased in the following years (2010 and 2011), the regeneration time was longer (September and December, respectively; Fig. 4.4.4). This pattern is consistent with the higher linear extension rate observed in May 2009 (0.0063 ± 0.0008 cm diameter d^{-1}) compared to May 2010 and 2011 (0.0003 ± 0.0018 cm diameter d^{-1}, n = 2) and the twofold higher peak in the linear extension rate in July–August in 2009 (0.0100 ± 0.0010 cm diameter d^{-1}) compared with 2010 and 2011 (0.0053 ± 0.0001 cm diameter d^{-1}, n = 2; Fig. 4.4.5b,c). The mean annual linear extension rate of *O. patagonica* was twofold higher in 2009 (1.91 ± 0.25 cm diameter yr^{-1}) than in 2010 and 2011 (0.86 ± 0.22 and 1.03 ± 0.27 cm diameter yr^{-1}, respectively; one-way repeated-measures ANOVA, $F_{2,56} = 19.36$, $p < 0.0001$). These results indicate that ST may be exerting a direct effect on the growth dynamics of the species as well as an indirect effect through partial mortality. The number of days in which the ST was ≥20 to ≥24ºC did not vary significantly among the warm periods during the study (2009–2011, n = 3; χ^2, p >0.05), whereas the ≥25 to ≥27ºC thresholds in the 2009 warm period were higher than those in 2010 and 2011 (χ^2, $p < 0.05$; SM 4.4.5). For instance, the number of days in which the ST was ≥25ºC was 25 and 60% higher in 2009 than in 2010 and 2011, respectively. However, recently denuded skeletons and/or visually apparent bleaching were not observed during the summer and fall in any of the study years.

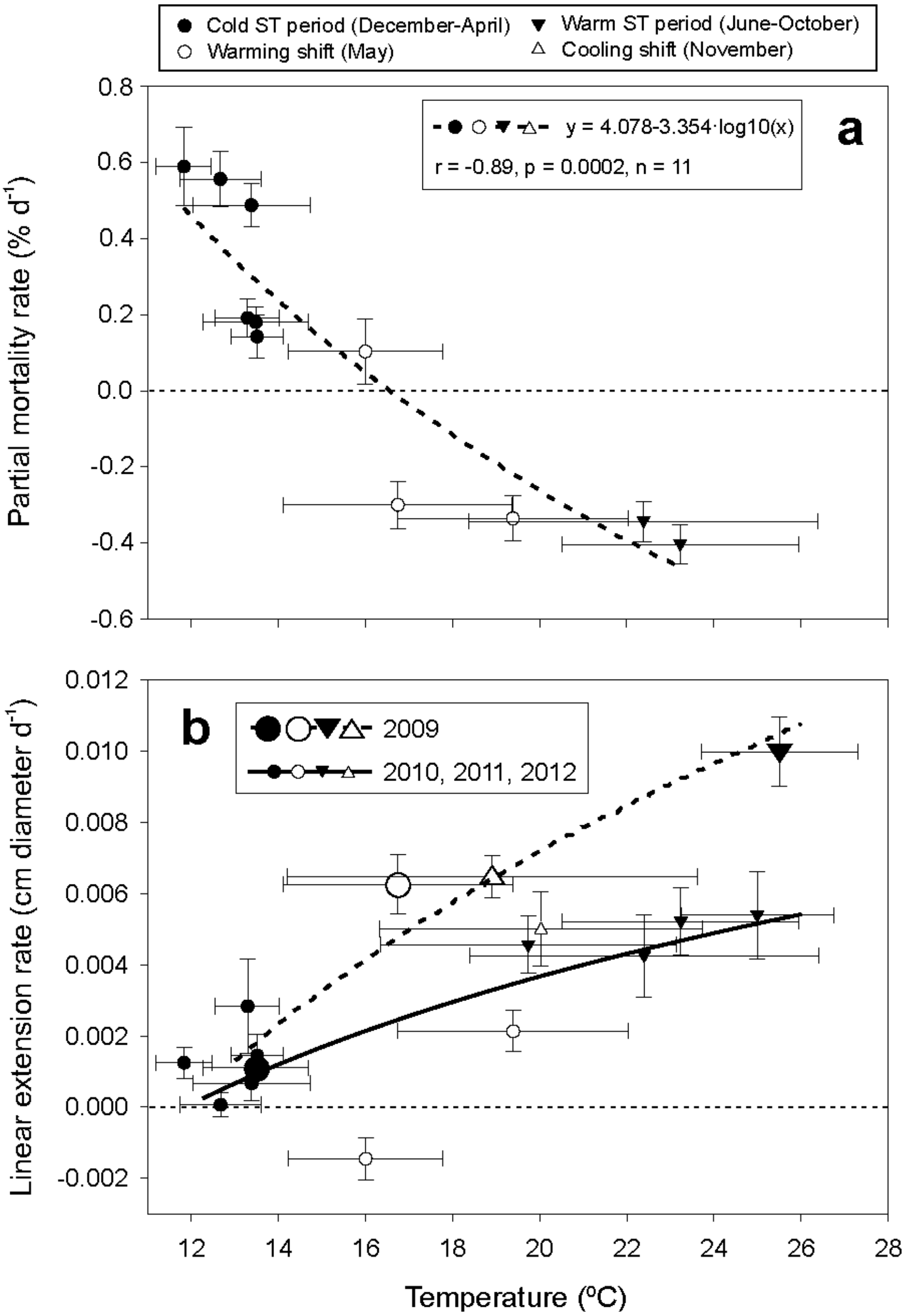

Fig. 4.4.6 Pearson product-moment correlations between *Oculina patagonica* performance and seawater temperature (ST) for each sampling interval. **a** Colony partial mortality rate. Values from the late warm ST and cooling shift periods were not included because lesion regeneration was already completed or was strongly affected by algal overgrowth. **b** Colony linear extension rate. Values are mean ± SE for coral performance and mean ± SD for ST. Two linear extension patterns depending on the severity of the annual event of denuded partial mortality are depicted: the pattern observed in 2009 (*dashed line*) and that observed in 2010, 2011 and 2012 (*solid line*). Data were fitted to logarithmic functions.

Discussion

Pattern of partial mortality and tissue regeneration

The yearly occurrence of denuded partial mortality in the *O. patagonica* colonies in winter (December–April) was the most distinctive process observed during the study. The denuded skeleton resulted from progressive tissue loss, which caused a loss of coloniality (i.e., dissociation of polyps from their connective coenosarc). The presence of colonies with brown, isolated polyps within the calyx distributed over a white coenosteum was a sign of the observed partial mortality, which we usually refer to as a Dalmatian mortality pattern (Fig. 4.4.7). The usual persistence of isolated brown polyps on the colonies distinguished the observed pattern of mortality from the pattern of tissue loss documented at the end of summer in colonies from Albissola, Monaco and Portman; although these colonies also exhibit areas of isolated brown polyps, they commonly display patches of completely denuded skeleton (i.e., the coenosteum and calyx; Rodolfo-Metalpa et al. 2008, 2014) that were rarely observed in our study. The process of denuded partial mortality that affected the colonies at our study site during winter resembled that observed in February 2006 in Monaco (Rodolfo-Metalpa et al. 2008). Colonies responded a similar way to reduced pH conditions in aquaria (Kvitt et al. 2015). The process observed in February 2006 did not appear to impact the dynamics of the species because the colonies completely regenerated by May, and the process was only observed during one year (Rodolfo-Metalpa et al. 2008). The dissociation of polyps from the coenosarc at low pH appears to be an essential mechanism mediated by apoptosis by which the species withstands acidification (Kvitt et al. 2015). Although addressing the mechanisms of tissue loss was outside the scope of this study, we did not observe any evidence of tissue necrosis that might have indicated that apoptosis was involved. As observed in other zooxanthellate coral species, the symptoms of the responses to different types of stress can be similar (e.g., Gates et al. 1992; Roth et al. 2012).

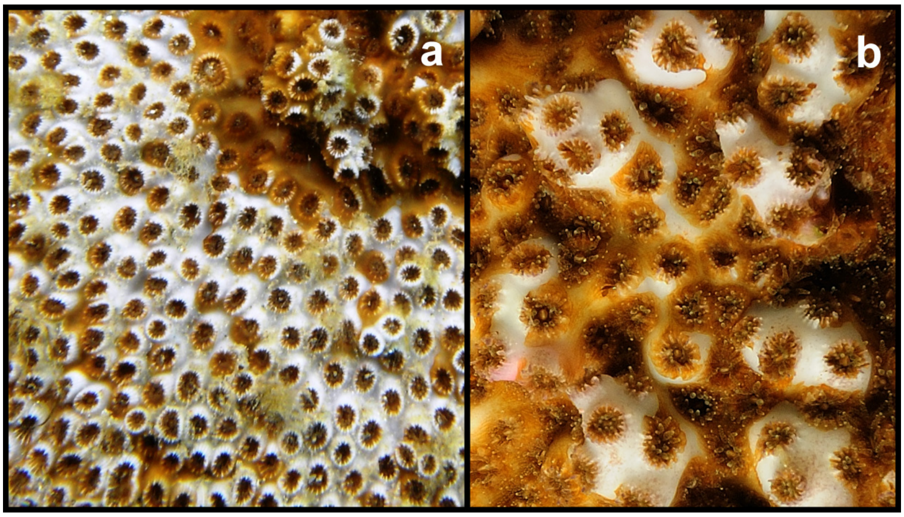

Fig. 4.4.7 Dalmatian mortality pattern in *Oculina patagonica*: a general view and **b** close-up view.

Lesion recovery is fundamental to coral survival, and during this 4-yr study, the *O. patagonica* colonies began to recover shortly (a few days) after the peak of partial mortality in April and were nearly fully recovered (down to 4–8%) from the yearly, recurrent partial mortality episodes. Over the ~4-yr study, the average regeneration rate was 10.3 mm^2 d^{-1}, a rate that occurred in the absence of competition with other organisms (Fine and Loya 2003). This rate was 2.5-fold faster than the recovery rate of unbleached colonies documented in the Levant Sea (4.09 mm^2 d^{-1}; Fine et al. 2002). Fine et al. (2002) observed that lesion regeneration in unbleached *O. patagonica* colonies resulted in intracolonial translocation of resources toward recuperating lesions 4–5 cm away, whereas bleached colonies exhibited no lesion regeneration. These observations are consistent with tissue regeneration as an energetically costly process, as has been documented in other species (Oren et al. 2001). Thus, the more rapid regeneration rate at L'Ampolla might be attributable to the timing of the recovery of the lesions during the favorable growing season, whereas in the Levant Sea, recovery was examined during the unfavorable bleaching season (Fine et al. 2001, 2002). The denuded partial mortality of *O. patagonica*, which usually left polyps alive but isolated within the calyx, represents a characteristic pattern that may favor regeneration because (1) it increases the relationship between the wound perimeter and lesion size, which has been shown to positively correlate with the regeneration rate (Meesters et al. 1997), and (2) it rids the colony of energetically costly processes, such as calcification, and tissues (Kvitt et al. 2015). Moreover, the small polyp size and encrusting morphology of *O. patagonica* colonies may help to maintain mass transfer, which also favors lesion regeneration (e.g., van Woesik et al. 2012). The immediate initiation of regeneration at the end of the partial mortality event points to the prioritization of this life-preserving process that helps to reduce the detrimental effects of the settlement of algae and other organisms on the skeleton and the disruption of the physiological integration of the colony (Oren et al. 2001).

Potential causes of the observed pattern of partial mortality and growth

The complex interaction between ST and light on zooxanthellate corals (Lesser 1996) suggests that both factors are relevant to the seasonal dynamics of colony partial mortality in *O. patagonica*. However, although the loss of tissue in the coenosarc but not in the polyps might suggest a light effect, two sources of evidence suggest a secondary role of light in the observed pattern of partial mortality. First, the process of partial mortality started in December, the period with the lowest PAR levels. Second, the annual pattern of partial mortality exhibited a negative relationship with ST but not PAR.

The linear extension of *O. patagonica* colonies was positively related to ST but not to PAR, which also indicates that light might play a secondary role in the growth pattern of *O. patagonica*, in accordance with the results of previous studies (Shenkar et al. 2005; Rodolfo-Metalpa et al. 2008;

Rubio-Portillo et al. 2014b). This finding is also consistent with the lack of a negative effect of turbidity on colony growth observed by Rubio-Portillo et al. (2014b), who observed that growth of the colonies did not differ between a harbor and a marine protected area, despite the much greater sedimentation in the harbor and the consequent reduction in light due to turbidity. This observation supports the hypothesis that *O. patagonica* may have a high capacity for photoacclimation to distinct and variable light regimes that may allow it to function as a facultative zooxanthellate and thrive in a wide range of light conditions, as has been observed (Fine et al. 2001; Rodolfo-Metalpa et al. 2014). Such characteristics would be consistent with the secondary role that light usually plays in promoting coral growth at high latitudes (Miller 1998; Rodolfo-Metalpa et al. 2008; Dimond et al. 2013). The absence of bleaching and/or mortality in the study area in summer might be related to the relatively low PAR levels caused by river runoff, which has also been suggested to contribute to the lack of partial mortality in response to warming in the laboratory (Rodolfo-Metalpa et al. 2014).

During the four annual cycles that were examined, the partial mortality episodes at L'Ampolla occurred during the cold periods, and thus we estimated the extent of exposure of this coral species to low ST based on data from this study and previous field studies to examine whether the intensity of the partial mortality episodes was related to the severity of the cold ST period. During the warmest winter at L'Ampolla, 2008–2009 (63 d ≤ 13ºC, 0 d ≤ 12ºC; SM 4.4.5), the peak in partial mortality (26%) was similar to that reported during the winter of 2005–2006 in Monaco (5–20%) under similarly cold ST conditions (66 d ≤ 13ºC, 0 d ≤ 12ºC; Rodolfo-Metalpa et al. 2008). By contrast, the higher incidence of partial mortality (48–66%) during the more severe cold ST periods (2009–2010 to 2011–2012) at L'Ampolla could be related to exposure to the ≤12ºC threshold (15–29 d; SM 4.4.5), suggesting that years with severely cold ST periods increased partial mortality in *O. patagonica*. The analysis of published data is consistent with this hypothesis because coral populations in the mid-Balearic Sea did not suffer from partial mortality and/or visually apparent bleaching during the winter of 2010–2011 (0 d ≤13ºC; Rubio-Portillo et al. 2014b) nor during the examined winters since 1993 in the Levant Sea (0 d ≤16ºC; e.g., Fine et al. 2001; Shenkar et al. 2005, 2006). Thus, the degree of exposure to cold ST appears to be related to the occurrence and severity of partial mortality events. However, although the cold thermal regimes at L'Ampolla were similar between 2010 and 2012, our results showed that the yearly peak in *O. patagonica* partial mortality gradually increased during this time period (Fig. 4.4.4a; SM 4.4.5). As observed during consecutive extreme summers in *Porites astreoides* (Schoepf et al. 2015), we hypothesize that the cumulative impact of consecutive winter events of partial mortality may have affected the physiological status (energy budget) of the colonies, thus diminishing their recovery capacity.

The recurrent and severe partial mortality of the colonies in winter indicates that cold ST may be exerting both a direct effect on the linear extension dynamics of the species and an indirect effect *via* partial mortality, as the growth of the colonies did not resume until the colonies recovered from their lesions. Such direct and indirect effects are consistent with (1) the lower incidence of partial mortality during the warmest first winter period at L'Ampolla (2008–2009), which reduced the time needed for complete tissue regeneration, and (2) the twofold higher linear extension detected in 2009 compared to 2010 and 2011. Our interpretation is that the high linear extension observed in summer 2009 was not an isolated estimate that could be considered an outlier because compared to the other years, linear extension in that year was also higher in spring and fall. Although the colonies in 2009 were exposed to 27ºC during summer, the linear extension in fall suggested no detrimental effect on the colonies (probably due to the low PAR levels, see above). The lack of a detrimental effect may be related to the lower impact of partial mortality in winter 2008–2009, which permitted rapid recovery and an earlier onset of the linear extension period (Fig. 4.4.4; Fig. 4.4.5). These results suggest the occurrence of two linear extension patterns depending on the severity of the annual event of denuded partial mortality: the pattern observed in 2009, i.e., an increase with ST up to ~26ºC, and that observed in the other years, i.e., an increase with ST up to ~20ºC and then a plateau, which may be related to the cost of the regeneration process (Fig. 4.4.6b). Thus, cold STs may be playing an important role in constraining the growth dynamics of *O. patagonica* at the northern limit of its distribution, in contrast to the dynamics documented in the Levant Sea, where growth occurs during the cold period (16–26ºC, November–May) and bleaching recurrently affects the colonies in summer (>26–32ºC, June–October; Fine et al. 2002; Shenkar et al. 2005). The *O. patagonica* linear extension rate at L'Ampolla during the study period (1.27 cm in diameter yr^{-1}) was 69–112% higher than those in natural populations from the Levant Sea (0.60–0.75 cm in diameter yr^{-1}; Fine et al. 2001), suggesting that the negative effects of high ST stress occurring at the Levant Sea are more harmful than the cold ST stress occurring at the north Balearic Sea. This conclusion is consistent with previous studies documenting the effect of cold STs on corals (Gates et al. 1992; Saxby et al. 2003; Hoegh-Guldberg et al. 2005; Colella et al. 2012) and the differential effect of low- and high-ST stress on *Acropora yongei* (Roth et al. 2012). However, the detrimental effect of competition on scleractinian corals (e.g., Fine and Loya 2003), which may diminish coral linear extension in natural populations, was excluded in our study.

Our results also indicate a trade-off between regeneration and linear extension that is consistent with the priority of energy allocation to recovery rather than to other biological processes. This trade-off is in agreement with previous studies from the Levant Sea, where bleaching and mortality events in *O. patagonica* during summer result in a low-energy state of the colonies that is responsible for the cessation of resource translocation and a reduction in gametogenesis and colony growth (Fine et al. 2001, 2002; Armoza-Zvuloni et al. 2011). The recurrent mortality events at L'Ampolla peaked in April and overlapped temporally with the gametogenesis of *O. patagonica* (March–September; Fine et al. 2001), suggesting that this energy shortage might also impair species reproduction and population growth.

The results of this study have demonstrated that *O. patagonica* at this northern limit of its distribution can survive and grow under wide seasonal variation in ST (monthly mean ranging from 11.7 to 27.1ºC). The coral exhibits a strong seasonal cycle that includes partial mortality and cessation of linear extension during winter (December to April), tissue regeneration starting in late spring (May) and linear extension during summer and fall (June to November), a cycle that appears to be primarily driven by ST. However, our data provide only correlational evidence, and causation of the observed pattern of denuded skeleton cannot be determined without additional experimental work. Partial mortality affected approximately half of the surface area and most of the colonies (~70%) and occurred repeatedly in all four years studied, indicating that partial mortality is a crucial process affecting the dynamics of the species, the relevance of which is comparable to that of the recurrence of summer bleaching in the Levant Sea (e.g., Fine et al. 2001).

Due to concerns regarding the threat of global warming to tropical coral reefs, understanding the resilience of zooxanthellate corals at high latitudes is crucial for predicting shifts in coral communities and their responses to climate change. The results of our experimental exclusion from competition indicate that the recurrent and severe pattern of denuded skeletons results from unfavorable environmental conditions that may constrain the population dynamics of the coral and affect the poleward expansion of the species. However, *O. patagonica* can withstand harsh environments because of its high regeneration capacity, which is among the highest reported for a coral species, particularly at high latitudes (Henry and Hart 2005). The stress response of polyp dissociation from the coenosarc appears to be a crucial pattern favoring the rapid regeneration of the species. The combination of the dissociation stress response and the rapid regeneration of the species appears to be a decisive biological characteristic that enables the species to withstand unfavorable environmental conditions affecting zooxanthellate coral species at high latitudes.

Acknowledgments

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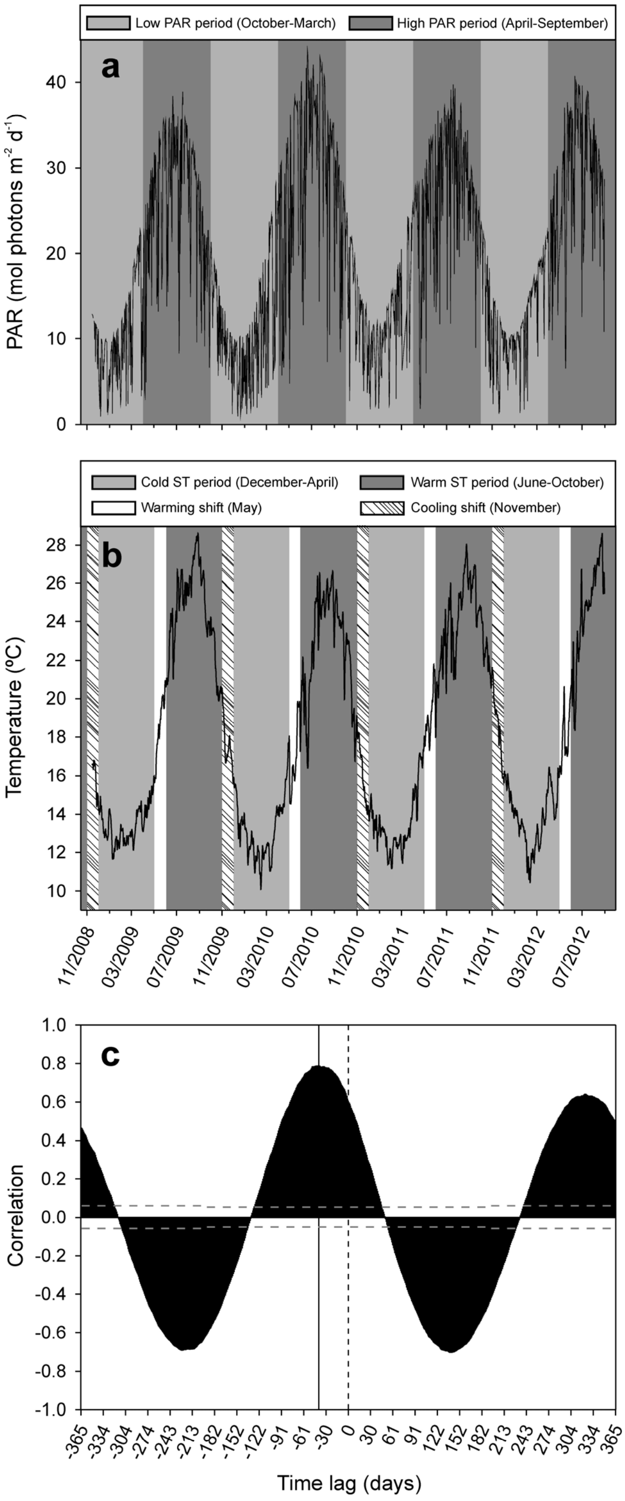
Supplementary Material (SM)

SM 4.4.1 Supplementary methods

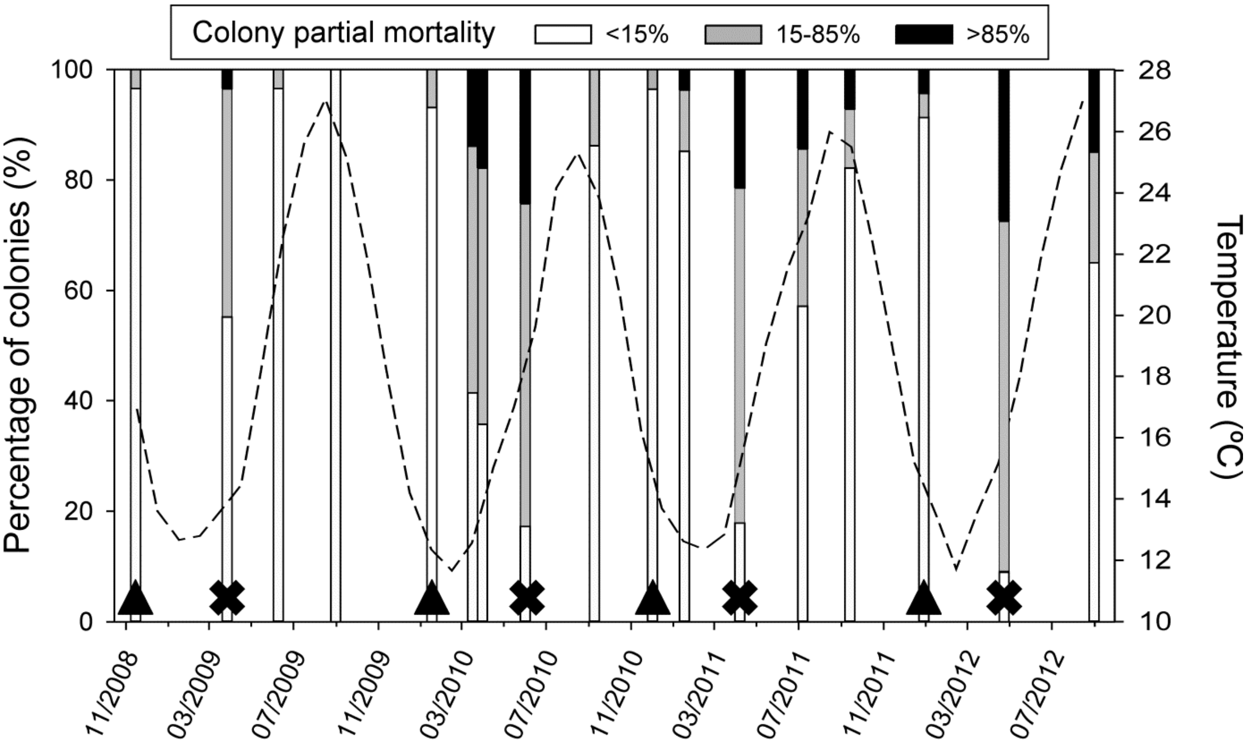
The integrated daily irradiance (J m^{-2} d^{-1}) throughout the study period was determined based on the cumulated hourly values averaged for each daily cycle (Ebre Observatory, Spanish State Meteorological Agency). The daily photosynthetically active radiation (PAR, mol photons m^{-2} d^{-1}) was obtained from global irradiance using a conversion coefficient of 4.57×10^{-6} mol J^{-1} (Thimijan and Heins 1983) and a ratio of PAR to total radiation of 0.50 (Monteith 1969). Light attenuation coefficient data were regularly recorded by the Catalan Water Agency at both the collection and the experimental sites within the study area and were employed to calculate the PAR at 5 m depth. Mean annual and monthly PAR were determined based on the daily values averaged over the study period.

The study area is a homogeneous shallow-water coast influenced by the Ebre river runoff. The comparison of the seawater temperature from data loggers (Onset HOBO UA-002–64) between the collection and the experimental sites revealed no differences (Pearson product-moment correlation, $r^2 = 0.99$, $p < 0.0001$). There was also no difference in the light attenuation coefficient values between sites (Chi-square, $\chi^2 = 11.99$, $p = 0.52$).

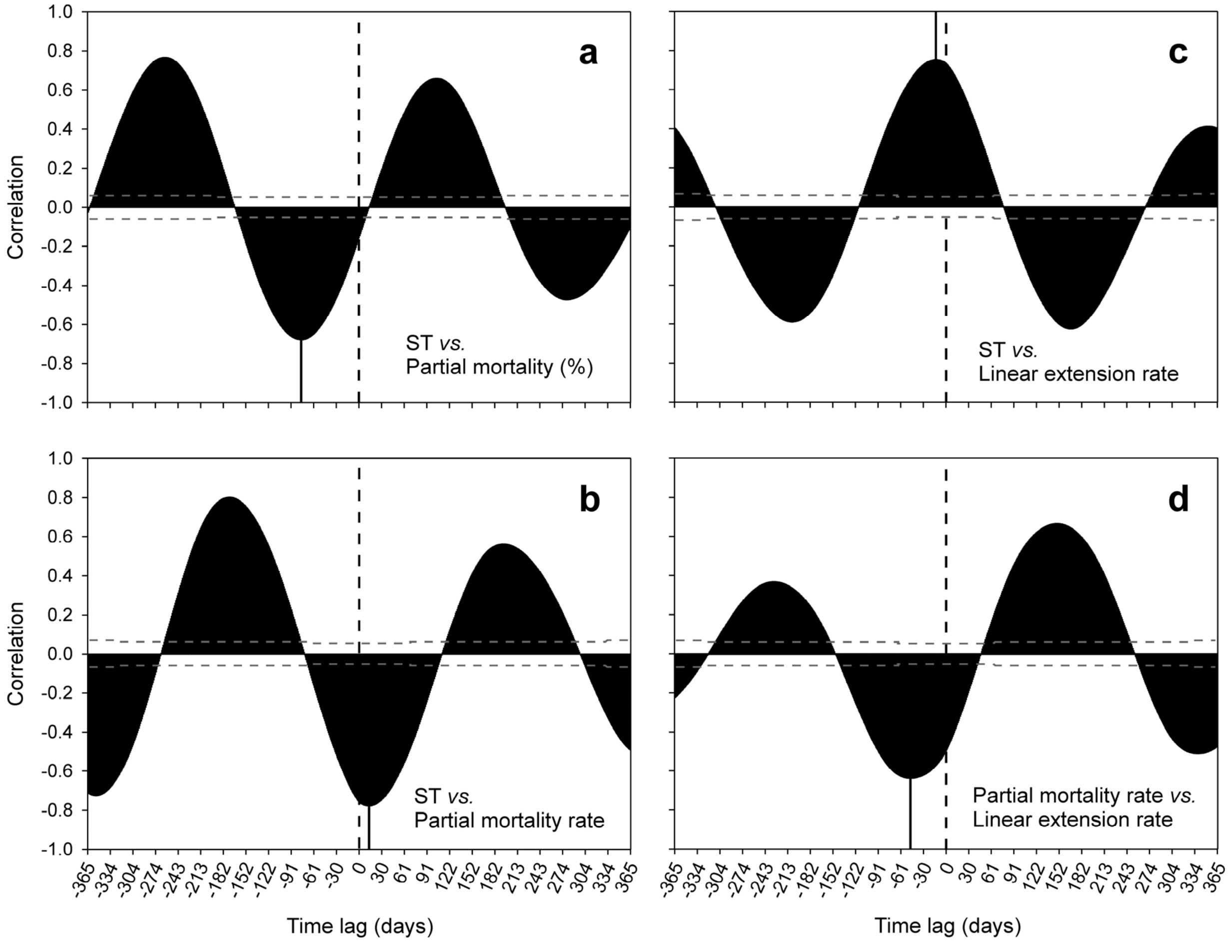
SM 4.4.2 Environmental parameters measured during the study period (November 2008–August 2012) at 5-m depth at L'Ampolla. **a** Daily mean photosynthetically active radiation (PAR). **b** Daily mean seawater temperature (ST). **c** Cross-correlation analysis between PAR and ST. The *solid vertical line* indicates the maximum significance at a lag of -40 d (r = 0.79), whereas the *dashed vertical line* indicates the correlation coefficient at a lag of 0 d (r = 0.60). Bars that reach or pass the *dashed horizontal lines* have significant (p <0.05) positive (upper) or negative (lower) correlation values.



SM 4.4.3 Proportion of colony partial mortality in the coral *Oculina patagonica* classified into three levels of severity: mild (<15%), moderate (>15–85%) or severe (>85%) throughout the study period (November 2008–August 2012, n = 17 sampling dates) at L'Ampolla. Mean monthly seawater temperature data (*dashed line*) are superimposed. Sampling dates with minimum (*black triangles*) and maximum (*black crosses*) incidence of partial mortality are highlighted for each annual cycle.



SM 4.4.4 Cross-correlation analyses between coral performance and seawater temperature (ST) throughout the study period (November 2008–August 2012) at L'Ampolla. **a** ST and proportion of colony partial mortality (%). The *solid vertical line* indicates the maximum significance at a lag of –78 d (r = –0.68); the *dashed vertical line* indicates the correlation coefficient at a lag of 0 d (r = –0.16). **b** ST and colony partial mortality rate (% d^{-1}). The *solid vertical line* indicates the maximum significance at a lag of +13 d (r = –0.78), which does not differ from the *dashed vertical line* indicating the correlation coefficient at a lag of 0 d (r = –0.76). **c** ST and colony linear extension rate (cm diameter d^{-1}). The *solid vertical line* indicates the maximum significance at a lag of –13 d (r = 0.75), which does not differ from the *dashed vertical line* indicating the correlation coefficient at a lag of 0 d (r = 0.73). **d** Colony partial mortality rate (% d^{-1}) and colony linear extension rate (cm diameter d^{-1}). The *solid vertical line* indicates the maximum significance at a lag of –48 d (r = –0.64); the *dashed vertical line* indicates the correlation coefficient at a lag of 0 d (r = –0.50). Bars that reach or pass the *dashed horizontal lines* have significant ($p < 0.05$) positive (upper) or negative (lower) correlation values.



SM 4.4.5 Seawater temperature (ST) thresholds obtained from temperature sensors placed in situ at a depth of 5 m at L'Ampolla. **a** Number of days on which the ST was ≤19 to ≤11ºC during the cold seasons of 2008–2009 to 2011–2012 (n = 4). **b** Number of days on which the ST was ≥20 to ≥28ºC during the warm seasons of 2009 to 2011 (n = 3). The mean proportion of colony partial mortality documented on *Oculina patagonica* is indicated for each season.

a Cold season	≤19ºC	≤18ºC	≤17ºC	≤16ºC	≤15ºC	≤14ºC	≤13ºC	≤12ºC	≤11ºC	Partial mortality (%)
2008–2009	202	185	175	162	143	94	63	0	0	26
2009–2010	199	196	176	161	129	104	73	29	0	48
2010–2011	207	175	165	151	135	108	63	15	0	57
2011–2012	192	189	163	141	112	81	44	17	0	66
b Warm season	≥20ºC	≥21ºC	≥22ºC	≥23ºC	≥24ºC	≥25ºC	≥26ºC	≥27ºC	≥28ºC	Partial mortality (%)
2009	164	135	125	109	90	75	41	22	0	0
2010	136	111	105	88	69	60	0	0	0	0
2011	165	148	128	83	66	47	34	0	0	0

ST thresholds are based on mean daily values. To examine whether exposure to cold ST thresholds (≤19 to ≤11ºC) impacted the species, we determined the fall/winter days on which ST dropped below each threshold and the days in spring/early summer of the next year on which it rose above each threshold. To examine whether exposure to warm ST thresholds (≥20 to ≥28ºC) affected the species, we determined the days in spring/summer on which the ST reached each threshold and the days in late summer/fall on which it dropped below each threshold. To avoid any bias introduced by short-term ST oscillations, we determined that the daily mean ST values had to remain ≤ or ≥ each threshold on at least 80% of the days throughout the following two weeks (i.e., 11 of 14 d) after the date on which the ST crossed the threshold to be considered.

4.5. Variation in demographics of the zooxanthellate coral *Oculina patagonica* along the Mediterranean Iberian coast in relation to environmental parameters

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Photograph by Juan Carlos Calvín

Chapter 4.5

Abstract

Extensive baseline data and understanding the effects of environmental factors at high latitudes on indicator species such as corals is fundamental to predict species and temperate ecosystems response to global change. In the Mediterranean Sea, the zooxanthellate coral *Oculina patagonica* (Scleractinia, Oculinidae), a range-expanding species able to turn algal forests into coral dominated ecosystems, provides a good example of how zooxanthellate corals can impact the algal-dominated structure of shallow-water rocky ecosystems in temperate areas. Our goal was to provide a baseline quantitative assessment of the occurrence and demographics of *O. patagonica* along the ~1300 km Mediterranean coast of the Iberian Peninsula and to relate them to environmental parameters. A combination of analytical approaches was used to identify spatial regimes of coral demographics and the key environmental correlates of this variation at studied natural locations along the Iberian coast. The South-Balearic Sea constituted the core zone of *O. patagonica* distribution, with populations having up to 6-fold higher mean living coral cover (3.4%, up to 13%), lower colony partial mortality and colony size-structure indicating faster growing populations, when compared to the peripheral southwest (North-Alborán Sea) and northeast zones (Mid- and North-Balearic Sea, and West Gulf of Lyons). The coral demographics (i.e., density, total and living cover, skewness and kurtosis coefficients) were positively correlated among them and with annual mean seawater temperature (ST), percentiles 10th-ST and 90th-ST, and photosynthetic active radiation at 3-m depth (PAR-3m), but negatively correlated with chlorophyll-a. On this basis, we identified thresholds that may constrain the growth of *O. patagonica* colonies and populations, including annual mean ST <19-20ºC, percentile 10th-ST <14ºC, percentile 90th-ST <25ºC and >27ºC, and PAR-3m <30 mol photons m^{-2} d^{-1}. The results obtained showed that the Iberian coast is the region with the highest *O. patagonica* abundance across the Mediterranean, and provide a baseline quantitative assessment of its current demographics. The species abundance conforms to the general pattern of the 'abundance-center' hypothesis (i.e., a most abundant center that declines toward the edges of a geographic range). However, the results on coral demographics showed that this pattern is not only related to the timing of arrival but points to the relevant role of differences in coral population growth that correlate with key environmental parameters. Our present correlational results support the hypothesis of an ongoing coral-mediated tropicalization of temperate shallow-water rocky ecosystems.

Introduction

Marine ecosystems are highly threatened by human-related impacts such as seawater warming, acidification, habitat destruction, pollution and invasive species, that can cause structural and functional alterations (Walther et al. 2009; Hoegh-Guldberg et al. 2014; Poloczanska et al. 2016). A striking example of cumulative impacts on the function of marine ecosystems is the ongoing mortality of tropical coral reefs that has led to widespread phase shifts from coral- to algal-dominance (Bruno et al. 2009; De'ath et al. 2012; Graham et al. 2015). In turn, sea warming has facilitated the poleward expansion of tropical zooxanthellate corals into algal-dominated subtropical and temperate areas, which is predicted to expand in future climate scenarios (Burrows et al. 2011; Couce et al. 2013; Vergés et al. 2014a; Freeman 2015; Takao et al. 2015; Wernberg et al. 2016). Despite a poleward migration of whole coral reef ecosystems is generally not expected (Hoegh-Guldberg 2012), several evidences indicate that the coral-mediated tropicalization of high-latitude ecosystems is an ongoing phenomenon occurring at a global scale (reviewed in Vergés et al. 2014a). For example, benthic communities in Tosa Bay (southern Japan, 33ºN) were dominated by kelp forests in the 1980s, by barrens in the 2000s and currently by reef-building scleractinians such as *Acropora* species (Denis et al. 2013). Understanding the ability of such tropical coral species to adapt to environmental changes at high latitudes is crucial to predict ecosystem shifts in response to climate change, but requires from extensive baseline data.

The growth of zooxanthellate corals is mainly determined by the lower limits of temperature and light, which constrain the global distribution of zooxanthellate corals at latitudes <40º north or south of the equator and restrict their depth limit to shallower depths at higher latitudes (Kleypas et al. 1999; Muir et al. 2015; Veron et al. 2015). The scarcity of zooxanthellate corals in temperate areas is related to the synergistic interactions of abiotic factors (i.e., temperature, solar radiation, nutrients and the saturation state of seawater aragonite) and biotic interactions (i.e., competition with macroalgae; Miller and Hay 1996; Miller 1998; Kleypas et al. 1999). Macroalgae dominate shallow-water rocky reefs in temperate areas, where they are among the most productive and diverse communities, whilst zooxanthellate corals are extremely rare (Ballesteros 1989; Zabala and Ballesteros 1989; Miller 1998). Healthy shallow ecosystems at high latitudes are generally dominated by canopy-forming macroalgae, but a variety of human-related impacts (e.g., sea warming, pollution and habitat alteration) are shifting canopy forests to less structurally complex benthic assemblages, such as turf-forming algae or barren grounds, which in turn facilitate the establishment of zooxanthellate corals (e.g., Miller and Hay 1996; Vergés et al. 2014a; Wernberg et al. 2016; Thibaut et al. 2017). In this framework, it is noteworthy that the zooxanthellate coral *Oculina patagonica* (Scleractinia, Oculinidae), first recorded in 1966 (Zibrowius 1974), is currently documented to be present throughout the temperate Mediterranean Sea (reviewed in Rubio-Portillo et al. 2014a). Furthermore, outbreaks of the coral populations, geographic range expansion, and local phase shifts from macroalgal to coral dominance have been documented in several areas (Salomidi et al. 2013; Chapters 4.1, 4.2, 4.3), providing evidences of an invasive behavior (Blackburn et al. 2011) that may challenge the current conceptual framework (Zabala and Ballesteros 1989). Although *O. patagonica* was first described based on fossils of western Atlantic origin (Zibrowius 1974), it has not been found alive anywhere else in the world other than in the Mediterranean, so it cannot be reliably classified as either native or introduced and, therefore, it is considered a cryptogenic species (Zenetos et al. 2017).

Current direct and indirect evidences of expansion of the coral *O. patagonica* on shallow rocky reefs throughout the Mediterranean (e.g., Fine et al. 2001; Salomidi et al. 2013; Chapters 4.2, 4.3) have been related to its life-history strategies, characteristic of an opportunistic colonizer (Harrison 2011; Darling et al. 2012; Cardeccia et al. 2016), such as: (i) its capacity to reproduce both sexually (i.e., gonochoric broadcast spawning coral with small gametes and high gonadal production, and an age of first reproduction of 1-2 years; Fine et al. 2001; Armoza-Zvuloni et al. 2011) and asexually via polyp expulsion (Kramarsky-Winter et al. 1997); (ii) its ability to function as a facultative zooxanthellate species; (iii) its ability to survive, grow and reproduce under a wide range of environmental conditions, such as in tide pools at temperatures of 10-40ºC and at salinities of 28-50‰, polluted areas and in areas affected by severe sand scouring, as well as on algal-dominated rocky bottoms (Fine et al. 2001; Armoza-Zvuloni et al. 2011, 2012; Chapters 4.1, 4.2, 4.3); and (iv) its high dispersal capacity that has been related to the interplay of two spatial scales of dispersal: neighborhood and long-distance (Chapter 4.3). In comparison to the surrounding natural rocky reefs, man-made structures (i.e., artificial reefs) foster the abundance of *O. patagonica* and likely act as a focus for successful coral reproduction and dispersal (Salomidi et al. 2013; Chapter 4.3).

Ocurrence of *O. patagonica* has been long described along the Mediterranean coast of the Iberian Peninsula (Zibrowius and Ramos 1983; Rubio-Portillo et al. 2014a; Terrón-Sigler et al. 2015; Chapters 4.1, 4.2, 4.3). However, these previous surveys have focused on a local scale and/or are qualitative. Examination of the variation in the demographics of zooxanthellate corals at a regional scale may contribute to understand the environmental parameters that affect the establishment, survival, growth and reproduction of corals as individuals, and become integrated in the abundance and colony size-frequency distribution of the coral populations (Bak and Meesters 1998; Meesters et al. 2001; Goffredo et al. 2008; Gaston 2009; Kružić et al. 2012; Airi et al. 2014). In this sense, the Iberian coast, which encompasses three distinct water masses separated by oceanographic fronts (Alborán Sea, Balearic Sea and Gulf of Lyons; Millot 2005; Pascual et al. 2017), represents an excellent region to investigate the role of environmental conditions in determining coral demographics. In this study, we aim to provide a baseline quantitative assessment of current demographics of *O. patagonica* along the Mediterranean Iberian coast and to contribute understanding the main factors affecting the geographic range structure and population growth dynamics of the species. This knowledge is fundamental towards the determination of the future rate of change of *O. patagonica* and whether its current invasive behavior could substantially affect shallow rocky habitats in the temperate Mediterranean Sea.

Materials and Methods

Study area and distribution surveys

In this study, we examined the demographics of the coral *O. patagonica* along the ~1,000 km coastline of the southern Iberian Peninsula in the western Mediterranean Sea (Fig. 4.5.1). A total of 90 locations were selected randomly and examined during summer-autumn of 2009-2011. We surveyed both natural (n = 64) and artificial (n = 26) locations. In a previous study, we documented the gradual northward expansion of this species along the ~400 km northeastern Iberian coast over 19 years (1992 to 2010; Chapter 4.3). The recent occurrence of *O. patagonica* on this range-expanding area suggests that its demographics may be affected by the randomness associated to the initial stages of colonization. However, data from this range-expanding area obtained in 2010 by using the same methods (169 natural locations and 54 artificial locations; Chapter 4.3) has been incorporated in some analyses of this study to provide a full integrative picture of the demographics of *O. patagonica* along the whole Mediterranean coast of the Iberian Peninsula (spanning ~6º of latitude and 8º of longitude from the southwest: 36º30'N–4º52'W, to the northeast: 42º26'N–3º10'E; Fig. 4.5.1). The natural locations were rocky reefs, while the artificial locations included the wave-exposed side of man-made structures (i.e., harbor dikes and breakwaters made of boulders). Preliminary sampling to study the bathymetric distribution pattern of *O. patagonica* was conducted in 2007 at El Hormigón (37º39'N, 0º39'W; Chapter 4.2) by using three replicates of randomly positioned 40 m^2 transects (40 x 1 m; for minimal sampling effort estimates see SM 4.5.1 in supplementary material, SM; and Chapter 4.3) at 6 selected depths (1, 3, 6, 9, 12 and 15 m). The abundance (density and cover) of the species exhibited a bell-shaped curve that peaked at depths of 3 and 6 m, and declined sharply either towards 1 m and towards 9 m and deeper (SM 4.5.2), a bathymetric distribution pattern similar to those documented in previous studies (e.g., Salomidi et al. 2013). Therefore, the occurrence of *O. patagonica* at each studied location (i.e., natural and artificial) was determined by means of the close examination of ~1500 m^2 of rocky bottom between ~2 and 7 m depth. The mean depth of the locations examined in this study was 3.1 ± 0.4 m (± SE, n = 313). Two scuba divers counted all colonies found until ranked the coral density at each of three categories: absence, presence (<0.05 colonies m^{-2}) or populations (>0.05 colonies m^{-2}, equivalent to >75 colonies in 1500 m^2). The colonies of *O. patagonica* displayed a predominantly encrusting growth form with a circular-ellipsoidal shape. Individual colonies were defined as any autonomous, free-standing coral skeleton. A colony divided by partial mortality into separate patches of living tissue, but that was morphologically still one entity, was considered a single colony. Neighboring colonies in touch had a visually apparent contact front (Chapter 4.1) and were counted as distinct.

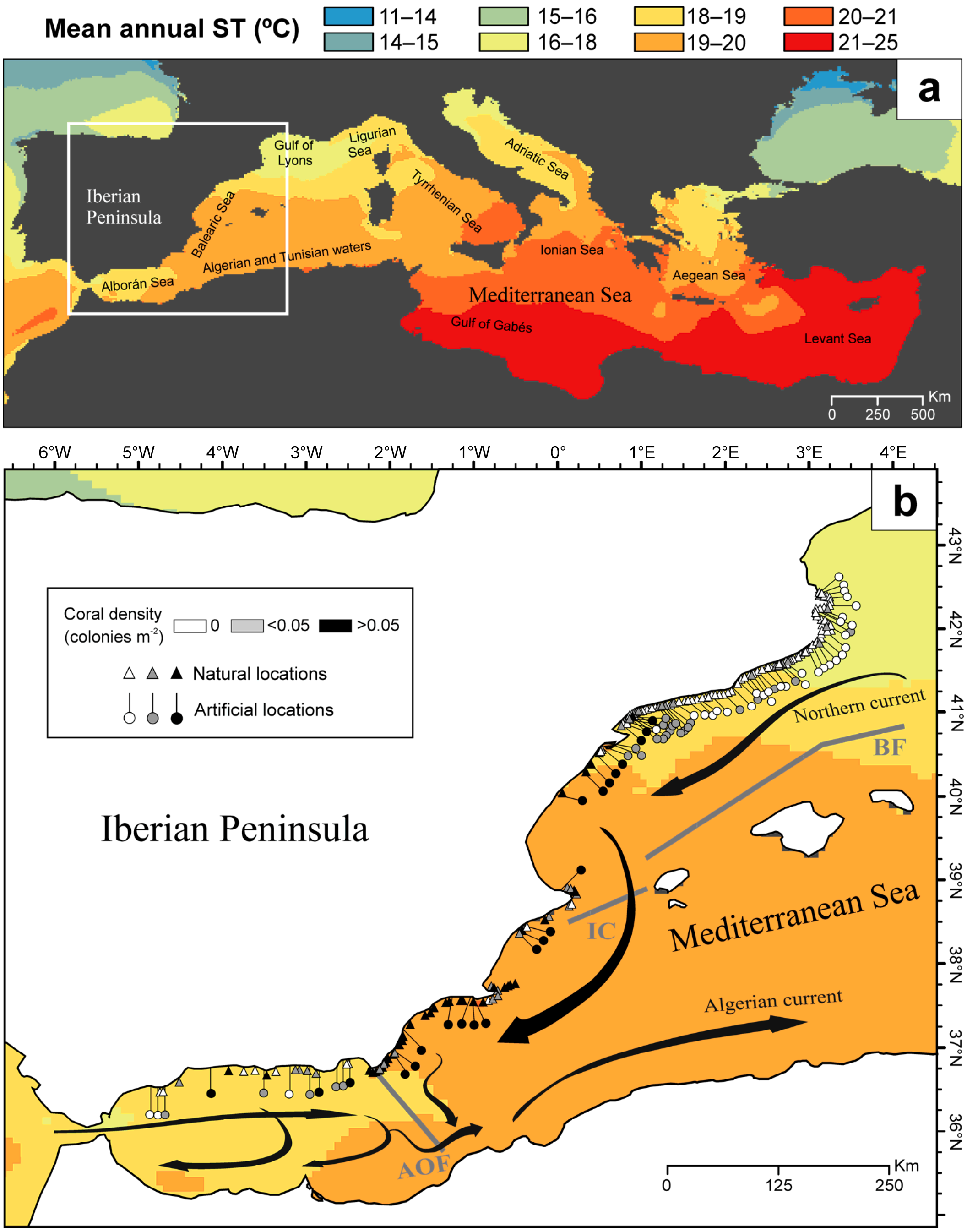

Fig. 4.5.1 Study locations. a Map of the Mediterranean Sea showing the study area in the coast of the Iberian Peninsula. **b** Map of the study area with the positions of the 313 surveyed locations displaying three categories of abundance (i.e., density) of *Oculina patagonica* and distinguishing between location type (i.e., natural and artificial reefs). The main mesoscale sea surface circulation and locations of the oceanic fronts (*BF*: Balearic front, *AOF*: Almeria-Oran front, *IC*: Ibiza Channel) are indicated. The study area is characterized by a well-defined seawater temperature (ST) gradient, represented here by mean annual surface-ST (2002-2009, obtained from Bio-Oracle dataset; Tyberghein et al. 2012).

Demographics of *O. patagonica*

Two methods were used to estimate *O. patagonica* demographics on natural locations in which the species was found. At locations ranked as coral presence we assessed its abundance by counting and measuring all colonies found within ~1500 m^2 of rocky bottom, whereas at locations ranked as coral population we conducted three replicates of randomly positioned 40 m^2 transects (40 x 1 m). Only colonies with at least 50% of their surface area lying within the belt transect were counted to avoid boundary effect biases in the spatial sampling method (Nugues and Roberts 2003). The surface area of the colonies was estimated by means of *in situ* measurements of the longest axis of the colony skeleton (length, L) and its longest perpendicular axis (width, W) to the nearest half-centimeter. The colony surface area (S, cm^2) was calculated using the formula $S = \pi[(L+W)/4]^2$ according to Fine et al. (2001). The percentage of the colony area showing signs of mortality (i.e., colony partial mortality) was visually estimated in increments of 5% and differentiating recent (i.e., denuded skeleton with very little to no turf algae colonization on non-eroded calices) and old mortality (i.e., denuded skeleton with eroded calices and/or overgrown by thick turf, erect algae or sessile invertebrates). Colony old partial mortality was further classified into 4 levels of severity: 0-10, 11-40, 41-70 and >70%. Coral data was standardized based on the area surveyed, and the density (colonies m^{-2}) and percentage of the bottom occupied by the species (total and living cover, %) values were calculated for each location.

Environmental parameters and benthic composition

To determine whether the geographical variability in environmental conditions along the whole Iberian coast may shape patterns on *O. patagonica* demographics on natural locations, we considered five environmental parameters in this study: annual mean seawater temperature (ST), percentiles 10^{th}-ST and 90^{th}-ST ($P10^{th}$-ST and $P90^{th}$-ST, respectively), photosynthetic active radiation at 3-m depth (PAR-3m) and chlorophyll-a (Chl-a). These parameters have previously been shown to effectively explain the spatial distribution of zooxanthellate coral species (e.g., Kleypas et al. 1999). Surface-ST time series over 2003-2010 were obtained from MODIS-Aqua sensor (Ocean Level-2) satellite-derived measurements performed by NASA's Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov). A ST time series was obtained on a 9-km^2 area (~3 x 3 km) for 20 sites located ~2 km offshore and regularly distributed along the ~1300 km studied coastline (one ST-site each ~70 km coastal length; SM 4.5.3). Satellite MODIS-ST data has proved to be a reliable proxy for studies requiring ST regime reconstruction in shallow (<10 m depth) near-shore habitats in the study area (Bernardello et al. 2016). The ST time series were filtered to detect outliers, and valid values were linearly interpolated to fill the days without data and obtain continuous series with daily values (as in Bernardello et al. 2016). The ST regime (annual mean ST, $P10^{th}$-ST and $P90^{th}$-ST) was determined for each ST-site. For each studied natural location along the Iberian coast, we obtained a ST regime data by linear interpolation between coastal length (km) and the ST data for each pair of neighboring ST-sites. The annual mean climatology of PAR-3m (estimated from surface PAR and light depth-diffuse attenuation coefficient data, 1997-2009) and Chl-a on seawater surface (2002-2009) were obtained for each studied natural location from the Bio-Oracle dataset (Tyberghein et al. 2012).

Percentage cover of major benthic components was estimated at natural locations ranked as coral population by using 0.25-m^2 quadrats (n = 30) that were located randomly along the same belt-transects used for the quantitative surveys on coral populations. Four large categories were distinguished: i) bare rock and crustose coralline algae, ii) turf algae (i.e., sparse algae with a canopy height of <1 cm), iii) erect algae (i.e., crowded algae with a canopy height of >1 cm), and iv) sessile invertebrates (e.g., sponges, bryozoans and tunicates). Quadrats were subdivided into 25 squares (each representing 4% of the quadrat) and the benthic component dominating each subdivision was recorded. The percentage cover of the benthic components was standardized to that of space without *O. patagonica*. The effects of algae on coral settlement and growth vary depending on the macroalgal functional-form, so erect algae constrain larval settlement and coral population growth, while the turf algae and the crustose coralline algae and bare rock groups (i.e., open space availability) facilitate coral growth (e.g., McCook et al. 2001; Chapter 4.2). The abundances and sizes of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* were quantified along the same belt-transects used for the quantitative coral surveys. All individuals >2 cm in test diameter were counted and measured to the nearest centimeter with a plastic caliper, and biomass was estimated using wet-weight/size conversion rates from Pais et al. (2007). To examine whether the presence of nearby artificial reefs could determine the abundance of *O. patagonica* at the study area, we estimated the number and length of artificial reefs present along the Iberian coast, and the distance between each studied natural location and the nearest artificial reef with >500 m in length, by using Google Earth images between 2003 and 2004 at a scale of 1:1,000.

Data analyses

(i) Spatial categorization of *O. patagonica* and environmental regimes

We used correlation-based principal component analysis (PCA) using *O. patagonica* demographics (density, living cover, colony partial mortality and size) and environmental parameters (annual mean ST, P90th-ST, P10th-ST, PAR-3m and Chl-a) among the examined natural locations to provide insights into the relationships between species demographics and environmental parameters. Data was transformed to Z-scores (calculated as: $[X_i - X_{avg}]/SD$; where X_i is the value of a given type in a given sample, X_{avg} is the average of the population and *SD* is the standard deviation) to avoid the scaling effect and obtain average-centered distributions. The extent to which values of *O. patagonica* demographics (i.e., using living cover as an integrating measure of population abundance) were affected by corresponding values in nearby locations (i.e., autocorrelation) was examined with a spatial correlogram (Moran's Index coefficient, Moran 1950) using data from the whole Iberian coast. The row-standardized distance matrix used for the correlogram was obtained from the coastal length axis and the distance classes were set at intervals of 10 km. The results from the PCA analysis and that of the spatial correlogram were used to conduct a K-means partitional clustering process of the locations (Rai and Singh 2010) oriented to identify spatial autocorrelation in the demographics of *O. patagonica* along the studied coast. The K-means partitional clustering process of the locations with regards to their coral demographics (standardized as $[X_i-X_{min}]/[X_{max}-X_{min}]$) and key environmental correlates of this variation was carried out with 10,000 iterations. Then, locations were grouped in zones on the basis of the above-mentioned analyses.

(ii) Spatial variation in *O. patagonica* demographics and environmental parameters

The proportion of locations on each of the three categories of coral density (absence, presence or population) was calculated separately for each zone and location type (i.e., natural and artificial). Differences in coral occurrence among zones were tested for each location type and between location types within zones, using Chi-square (χ^2) test.

Colony partial mortality and size data of *O. patagonica* from natural locations that had less than 25 measured colonies were pooled among neighboring locations within each zone to accomplish minimal sampling effort estimates (see SM 4.5.1). The colony-size structure was analyzed on untransformed data by calculating mean colony size, the proportion of small colonies (% colonies <100 cm^2 in surface area) and the percentile 90th of colony size (P90th-size). The colony size data was then logarithmically transformed (ln) to normalize colony size distributions and increase resolution among smaller size classes (Bak and Meesters 1998). The skewness ($g_{1)}$ and kurtosis (g_2) coefficients of colony size distributions were analyzed on both untransformed and ln-transformed data, and were considered significant if absolute value of coefficient SE^{-1} >2 (Sokal and Rohlf 1995). The colonies were categorized into 21 size classes of 100-cm^2 (untransformed data) or 0.5-cm^2 (ln-transformed data) intervals to visualize the general structure of size-frequency distributions.

Variation in maximum and mean colony size, old partial mortality, % colonies <100 cm^2, P90th-size, sea urchin biomass and open space availability were compared among zones using one-way ANOVA followed by unequal N HSD Tukey's post hoc test. Data was tested for assumptions of normality and homoscedasticity and, whenever necessary, data was transformed prior to analyses. The Kruskal-Wallis test was used to assess the interzonal differences in environmental parameters (annual mean

ST, P10th-ST, P90th-ST, PAR-3m and Chl-a) and in coral density, total and living cover, because transformations did not achieve normality.

The pairwise relationships between coral demographics and environmental parameters among the examined natural locations were assessed by Spearman's rank correlation coefficient (r), which does not assume bivariate normality. Pearson correlation analysis was used to assess relationships between P10th-ST and coastal length, between living coral cover and the distance between natural locations and the nearest artificial reef, and between sea urchin biomass and open space availability. All analyses were computed using STATISTICA 10.0, except for the Moran's Index and the K-means analyses that were implemented with R (R Development Core Team 2012). The results are expressed as mean ± SE.

Results

Spatial categorization of regimes for *O. patagonica* demographics and environmental parameters

The coral *O. patagonica* was found in shallow-water rocky reefs along the whole Mediterranean coast of the Iberian Peninsula (~1300 km; Fig. 4.5.1). Within the 233 natural locations examined along the coast there was a positive autocorrelation (i.e., contagious distribution) of living coral cover at distance classes of <200 km, whereas a random distribution dominated at larger spatial scales (Moran's Index, $p < 0.0001$). The combination of analytical approaches using *O. patagonica* demographics and the key environmental correlates of this variation detected a heterogeneous regime (i.e., the species was scarce and the environmental correlates highly variable) at the range-expanding area from the northeastern Iberian coast: West-Gulf Lyons zone (WLYO, 137 locations, northernmost ~300 km; Chapter 4.3; SM 4.5.4) and therefore, only the pattern for the southern Iberian coast (96 locations, ~1,000 km) is shown in Fig. 4.5.2. The PCA using *O. patagonica* abundance (density and living coral cover) and environmental parameters (annual mean ST, P90th-ST, P10th-ST, PAR-3m, Chl-a) showed a clear pattern of 4 distinct regimes. Two principal components (PC) axis explained 75% of the total variance among locations (Fig. 4.5.2a). PC1 accounted for 50% of total variance and explained the variation in *O. patagonica* abundance in relation to environmental parameters, with higher coral abundance at higher mean ST, P10th-ST and PAR-3m, and lower Chl-a (at positive PC1 scores, loadings |0.62–0.89|); P90th-ST has a low positive loading (+0.18) in PC1. PC2 accounted for 25% of total variance and best explained the variability of seasonal STs, with higher P90th-ST and lower P10th-ST at positive PC2 scores (loadings |0.74–0.96|; Fig. 4.5.2b). Based on the contagious distribution of living coral cover at distance classes of <200 km coastal length, the K-means partitional clustering using coral abundance and the two ST extremes identified to be selective in PC2 (P90th-ST and P10th-ST) was used to differentiate the locations along the southern Iberian coast, which yielded a map with three boundaries that defined four zones with the groups of locations occurring with 100% similarity (Fig. 4.5.2c). The PCA diagram overlaid with the K-means clustering of the locations indicated that *O. patagonica* abundance and environmental correlates group into four clusters consistently separated in space (i.e., zones) that were named as: North-Alborán Sea (NALB), South-Balearic Sea (SBAL), Mid-Balearic Sea (MBAL) and North-Balearic Sea (NBAL; Fig. 4.5.2d). The combination of analytical approaches using all locations (i.e., five zones, NALB to WLYO) yielded similar results, with PC1 explaining 55% of total variance and showing higher coral abundance at lower Chl-a and higher PAR-3m, mean ST and P10th-ST, but also higher P90th-ST (at positive PC1 scores, loadings |0.70–0.88|; SM 4.5.4).

A total of 43 natural locations (or group of neighboring locations) were considered for *O. patagonica* colony data estimates (partial mortality and size) within the southern Iberian coast (NALB to NBAL). The PCA using coral colony data and environmental parameters explained 58% of the total variance among locations with the first two PC (Fig. 4.5.2e). PC1 accounted for 30% of total variance and is characterized by higher values of % colonies <100 cm^2, g_1 $SE^{-1}$and g_2 SE^{-1}, and lower P90th-size and mean size, at higher mean ST and P90th-ST, and lower Chl-a (at positive PC1 scores, loadings |0.43–0.84|). PC2 accounted for 28% of total variance and is characterized by higher mean size, maximum size, P90th-size, g_1 $SE^{-1}$and g_2 SE^{-1}, and lower partial mortality and % colonies <100 cm^2, at higher P10th-ST and PAR-3m, and lower Chl-a (at negative PC2 scores, loadings |0.43–0.70|; Fig. 4.5.2f). The spatial grouping of the locations based on coral colony data (i.e., PCA diagram and an overlaying K-means partitional clustering of the locations) showed a spatial aggregation that generally matched that obtained using coral abundance (Fig. 4.5.2d,f). Therefore, the results highlighted the existence of five primary regimes of *O. patagonica* demographics and the key environmental correlates of this variation within the five zones (i.e., NALB to WLYO) distinguished along the whole Iberian coast.

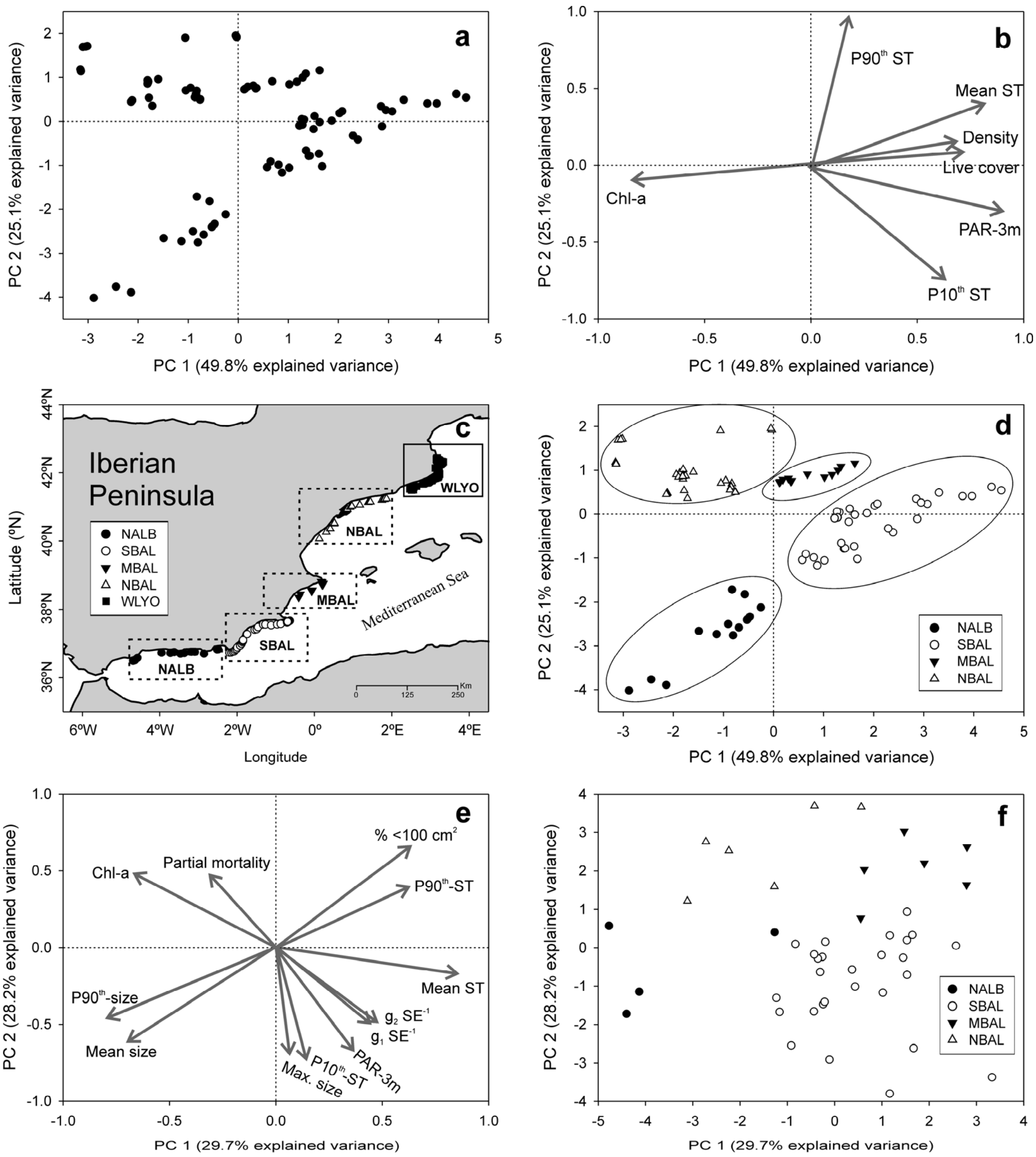

Fig. 4.5.2 Combination of analytical approaches used to identify regimes of *Oculina patagonica* demographics and the key environmental correlates of this variation at studied natural locations in the southern Iberian coast (NALB to NBAL). **a** Principal component analysis (PCA) diagram showing the spatial variation in coral abundance (density and living cover) and environmental parameters [*Mean-ST*: mean annual seawater temperature (ST), *P90th-ST*: percentile 90th ST, *P10th-ST*: percentile 10th ST, *PAR-3m*: photosynthetically active radiation at 3 m depth, *Chl-a*: chlorophyll-a] along the first two principal components (PC, n = 96 locations). **b** Ordination categories of coral abundance and the roles of environmental variables. **c** Map of the study area with an overlaying K-means partitional clustering of the locations (*dashed polygons lines*) using coral abundance and the environmental parameters identified to be selective in PC2 (P90th-ST and P10th-ST). The cluster for the range-expanding zone in northeastern Iberia (West Gulf of Lyons: WLYO, *solid polygon line*) is indicated to provide an integrated view of the whole Iberian coast (see SM 4.5.4). **d** PCA diagram with an overlaying K-means clustering of the locations. The polygons in **c,d** encompass 100% of the locations associated with each cluster. *Symbols* represent categorization of the locations matching the four zones defined by the K-means clustering: North-Alborán Sea (NALB), South-Balearic Sea (SBAL), Mid-Balearic Sea (MBAL) and North-Balearic Sea (NBAL). **e** PCA diagram and **f** ordination categories of *O. patagonica* colony partial mortality and size-structure descriptors, and the roles of environmental parameters (n = 43 locations, or group of neighboring locations, with >25 measured colonies). *Mean size*: mean of the surface area of the colonies; *% <100 cm^2*: % colonies <100 cm^2 in surface area; *P90th-size*: percentile 90th colony-size; *Max. size*: maximum size; *g_1 SE^{-1}*: skewness coefficient; *g_2 SE^{-1}*: kurtosis coefficient.

Zonal variation in environmental parameters and *O. patagonica* demographics

Data from the range-expanding zone has been included in this section to provide an integrated view of the overall spatial variation in environmental parameters and *O. patagonica* demographics on studied natural locations along the whole Iberian coast (i.e., five zones, NALB to WLYO). The annual mean ST, P90th-ST, P10th-ST, PAR-3m and Chl-a varied significantly among zones (Kruskal-Wallis, $p < 0.0001$). The mean ST showed higher values at SBAL-MBAL (19.3-19.4ºC) when compared to NALB-NBAL (18.4-18.7ºC) and WLYO (17.1ºC; Table 4.5.1). The P90th-ST showed higher values at MBAL-NBAL (26.0-25.7ºC) when compared to SBAL (25.3ºC) and NALB-WLYO (23.6-23.0ºC; Table 4.5.1). The P10th-ST gradually decreased from southwest to northeast along the Iberian coastline length (~1300 Km) at -0.23ºC per 100 km ($r^2 = 0.93$, $p < 0.0001$), with higher values at NALB-SBAL (14.6-14.3ºC) when compared to MBAL (13.7ºC) and NBAL-WLYO (12.7-12.3ºC; Table 4.5.1). The maximum ST range showed lower values at NALB (10.6ºC) when compared to SBAL-WLYO (12.3-12.7ºC) and MBAL-NBAL (13.8-14.8ºC). The PAR-3m showed higher values at SBAL (31.6 mol photons m^{-2} day^{-1}) when compared to NALB-MBAL (28.3-29.0 mol photons m^{-2} day^{-1}) and NBAL-WLYO (24.8-26.2 mol photons m^{-2} day^{-1}; Table 4.5.1). The Chl-a showed higher values at NALB-NBAL (0.98-0.90 g m^{-3}) when compared to SBAL-MBAL-WLYO (0.45-0.48-0.61 g m^{-3}; Table 4.5.1). For detailed environmental data see SM 4.5.5.

Occurrence of *O. patagonica* in natural locations varied significantly exhibiting a bell-shaped pattern among the five zones (NALB to WLYO; $\chi^2 = 94.28$, df = 4, $p < 0.0001$; Fig. 4.5.3). The species was present on most of the natural locations at SBAL (97%) and a marked pattern of decrease in occurrence was found outside this zone, either going northeast: MBAL (83%), NBAL (39%) and WLYO (7%), and southwest: NALB (50%; Table 4.5.1). The proportion of coral populations (i.e., >0.05 colonies m^{-2}) in natural locations followed a pattern of variation among zones similar to that of occurrence (Fig. 4.5.3). In artificial locations, occurrence of the species exhibited a pattern of zonal variation ($\chi^2 = 72.73$, df = 4, $p < 0.0001$) similar to that observed in natural locations (Fig. 4.5.3). The observed occurrence of *O. patagonica* in artificial locations was higher than that in natural locations for each zone ($\chi^2 = 70.71$, df = 4, $p < 0.0001$), and also the proportion of coral populations ($\chi^2 = 159.00$, df = 4, $p < 0.0001$). The proportion of artificial locations in which coral populations were found (NALB to NBAL) increased between 27 and 200% (96 ± 41%, n = 4) from that in natural locations within each zone, and reached 100% at SBAL and MBAL (Fig. 4.5.3).

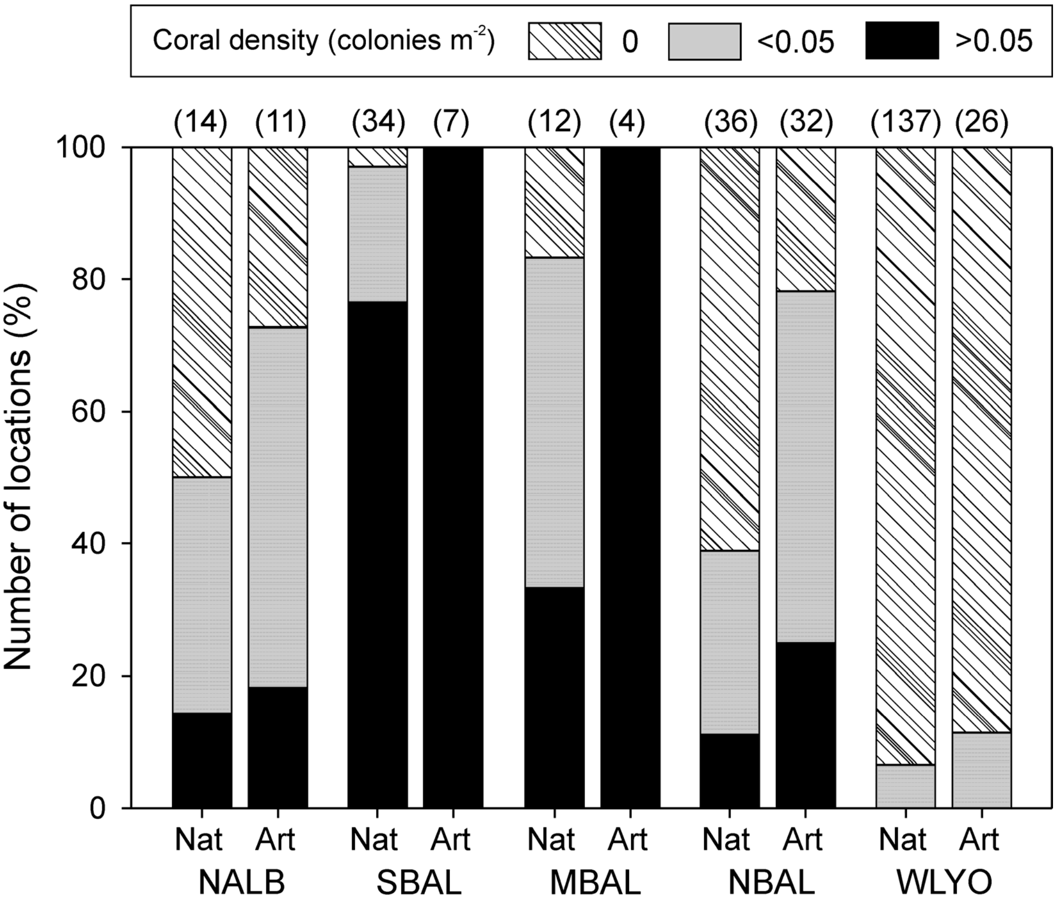

Fig. 4.5.3 Proportion of explored locations displaying the categories of abundance (i.e., density) of *Oculina patagonica* within the five zones distinguished along the whole Iberian coast (NALB to WLYO). Data is given distinguishing between location type (i.e., *Nat*: natural reefs and *Art*: artificial reefs). The number of locations surveyed for each zone and location type is indicated in brackets.

In the natural locations in which *O. patagonica* was found (n = 73), the mean coral density, total and living cover varied significantly among the five zones (Kruskal-Wallis, p <0.0001). The mean coral density at SBAL was 2.5-fold higher than at NBAL, and at least ~6-fold higher than those at NALB, MBAL and WLYO (Table 4.5.1). The mean total cover at SBAL was ~4-fold higher than at NBAL and at least 10-fold higher than those at NALB, MBAL and WLYO (Table 4.5.1). The zonal differences in coral cover exacerbated when the zonal variation in the proportion of colony partial mortality (i.e., recent and old, see below) was considered. Thus, the mean living coral cover at SBAL was 6-fold higher than at NBAL and at least 13-fold higher than those at NALB, MBAL and WLYO (Table 4.5.1). The mean maximum colony size also varied significantly among zones (one-way ANOVA, $F_{4,68} = 9.45$, p <0.0001 on log-transformed data), with values at SBAL being at least ~2-fold higher than those at NALB and NBAL, and 5-fold higher than at MBAL and WLYO (Table 4.5.1). Then, the demographics of *O. patagonica* in terms of occurrence, density, coverage and maximum colony size showed a similar pattern of variation among zones in which SBAL always displayed marked higher values than those at the other zones. For detailed coral abundance data see SM 4.5.6.

A total of 44 natural locations (or group of neighboring locations) were considered for *O. patagonica* colony data within the whole Iberian coast (NALB to WLYO). The mean colony old partial mortality ranged between 2 and 54% among locations (15.4 ± 1.6%; SM 4.5.7), and was characterized by parts of the skeleton overgrown by macroalgae (12.7 ± 1.5%), sessile invertebrates (0.3 ± 0.1%, such as sponges: *Crambe crambe*, *Phorbas* spp*.*, *Cliona* spp.; and bryozoans: *Schizoporella* spp.); and denuded skeletons with eroded calices and/or overgrown by barnacles and crustose coralline algae (2.2 ± 0.6%). The old colony partial mortality varied significantly among the five zones (one-way ANOVA, $F_{4,39} = 4.97$, $p = 0.0025$, on square root-transformed data) with values at NALB, MBAL, NBAL and WLYO (18 to 28%) being ~2-fold higher than those at SBAL (11%; Table 4.5.1). Similarly, the mean percentage of colonies with >40% of old partial mortality at NALB, MBAL, NBAL and WLYO (14 to 28%) were at least 2-fold higher than those at SBAL (6%; Table 4.5.1). The mean recent colony partial mortality (i.e., denuded skeleton with little to no filamentous algae colonization on non-eroded calices) ranged between 0 and 6% among locations (1.4 ± 0.2%; SM 4.5.7) and between 0.5 and 1.6% among zones (Table 4.5.1). Predation by corallivorous gastropods (i.e., *Babelomurex cariniferus*), abrasion by algae and/or sand, and sedimentation were among the main evident factors causing recent partial mortality. Although surveys were conducted during the warm period of the year (summer-autumn), no severe recent mortality episode was observed at any of the examined locations, nor any signs of a severe bleaching episode (i.e., the colonies generally had the brown-yellowish color given by the zooxanthellae).

The mean non-transformed colony size-frequency distributions for natural locations studied within the southern Iberian coast (NALB to NBAL) were unimodal and displayed significant positive skewness and kurtosis, indicating that the distributions were asymmetric: skewed to the right (with relatively fewer colonies in the larger size classes and a preponderance of smaller colonies) and more peaked than normal distributions for locations at NALB, SBAL, MBAL and NBAL, but not in the single studied population at WLYO (Fig. 4.5.4a). There were several other relevant differences among the five zones (Fig. 4.5.4a). The mean colony size at MBAL was at least 61% lower than those at the other zones (one-way ANOVA, $F_{4,39} = 4.09$, $p = 0.0073$; Table 4.5.1). The mean % colonies <100 cm^2 at MBAL was 29% higher than at NBAL and at least 50% higher than those at the other zones (one-way ANOVA, $F_{4,39} = 5.66$, $p = 0.0011$), and the colony $P90^{th}$-size at MBAL was at least 64% lower than those at the other zones (one-way ANOVA, $F_{4,39} = 4.78$, $p = 0.0031$; Table 4.5.1). The ln-transformed colony size-frequency distributions, which increased the resolution among the small size classes (Bak and Meesters 1998), were bell-shaped at the five zones and displayed negative skewness (Fig. 4.5.4b). However, the SBAL zone was the only one in which this skewness pattern was significant (g^1 SE^{-1} >2) and also the only one displaying positive kurtosis (Fig. 4.5.4b). For detailed colony size distributions see SM 4.5.8.

Table 4.5.1. Environmental parameters and *Oculina patagonica* demographics in the studied natural locations within the five zones distinguished along the whole Iberian coast (NALB to WLYO). *Mean-ST*: mean annual seawater temperature (ST), *P90*th*-ST*: percentile 90th ST, *P10*th*-ST*: percentile 10th ST, *Maximum ST range*: range between minimum P10th-ST and maximum P90th-ST over 2003-2010, *PAR-3m*: photosynthetically active radiation at 3 m depth, *Chl-a*: chlorophyll-a. N_1: all studied natural locations within each zone (n = 233). N_2: number of locations in which the species was found (n = 73). N_3: number of locations (or group of neighboring locations) with >25 measured colonies (n = 44). Mean percentage of the colony surface area with *recent* or *old mortality*. Percentage of colonies in each of 4 levels of severity based on the colony surface area affected by old partial mortality (*0-10*, *11-40*, *41-70* and *71-100%*). *Mean size*: mean of the surface area of the colonies; *% <100 cm*^{2}: % colonies <100 cm^2 in surface area; *P90*th*-size*: percentile 90th colony-size. Values are mean ± SE.

	NALB	SBAL	MBAL	NBAL	WLYO
Environmental parameters					
N_1	14	34	12	36	137
Mean-ST (ºC)	18.39 ± 0.07	19.29 ± 0.03	19.39 ± 0.04	18.67 ± 0.02	17.08 ± 0.03
P90th-ST (ºC)	23.56 ± 0.17	25.33 ± 0.06	26.00 ± 0.06	25.67 ± 0.03	23.00 ± 0.05
P10th-ST (ºC)	14.59 ± 0.02	14.34 ± 0.02	13.73 ± 0.03	12.71 ± 0.03	12.33 ± 0.03
Maximum ST range (ºC)	(14.12-24.69)	(13.71-26.02)	(13.09-26.88)	(12.17-26.94)	(11.67-24.39)
PAR-3m (mol photons m^{-2} day^{-1})	28.3 ± 0.5	31.6 ± 0.1	29.0 ± 0.4	24.8 ± 0.4	26.2 ± 0.2
Chl-a (g m^{-3})	0.98 ± 0.06	0.45 ± 0.02	0.48 ± 0.02	0.90 ± 0.05	0.61 ± 0.02
***O. patagonica* abundance**					
Occurrence (% locations)	50	97	83	39	7
N_2	7	33	10	14	9
Density (colonies m^{-2})	0.06 ± 0.04	1.07 ± 0.20	0.19 ± 0.10	0.43 ± 0.24	0.003 ± 0.001
Total cover (%)	0.40 ± 0.22	4.01 ± 0.78	0.30 ± 0.17	1.05 ± 0.54	0.01 ± 0.01
Live cover (%)	0.27 ± 0.17	3.44 ± 0.68	0.20 ± 0.11	0.55 ± 0.27	0.01 ± 0.00
Maximum colony size (cm^2)	1997 ± 494	3436 ± 623	473 ± 146	1403 ± 331	528 ± 150
Colony partial mortality and size					
N_3	4	27	6	6	1
Old mortality (%)	28.3 ± 9.8	10.8 ± 1.1	22.7 ± 4.1	19.9 ± 4.7	18.0
0-10% (%)	45.8 ± 14.5	73.6 ± 2.6	50.3 ± 8.4	60.2 ± 7.7	54.3
>10-40% (%)	26.1 ± 4.8	20.7 ± 1.9	30.8 ± 4.4	21.1 ± 1.6	31.4
>41-70% (%)	14.5 ± 6.4	4.4 ± 0.7	11.5 ± 2.9	11.1 ± 4.0	14.3
>71-100% (%)	13.6 ± 9.3	1.3 ± 0.4	7.4 ± 2.0	7.5 ± 2.3	0.0
Recent mortality (%)	0.5 ± 0.2	1.6 ± 0.3	1.4 ± 0.3	0.8 ± 0.1	0.5
Mean size (cm^2)	540 ± 106	369 ± 32	138 ± 40	357 ± 69	438
% <100 cm^2 (%)	20 ± 8	31 ± 3	63 ± 10	45 ± 8	31
P90th-size (cm^2)	1317 ± 289	838 ± 73	304 ± 92	1084 ± 197	908

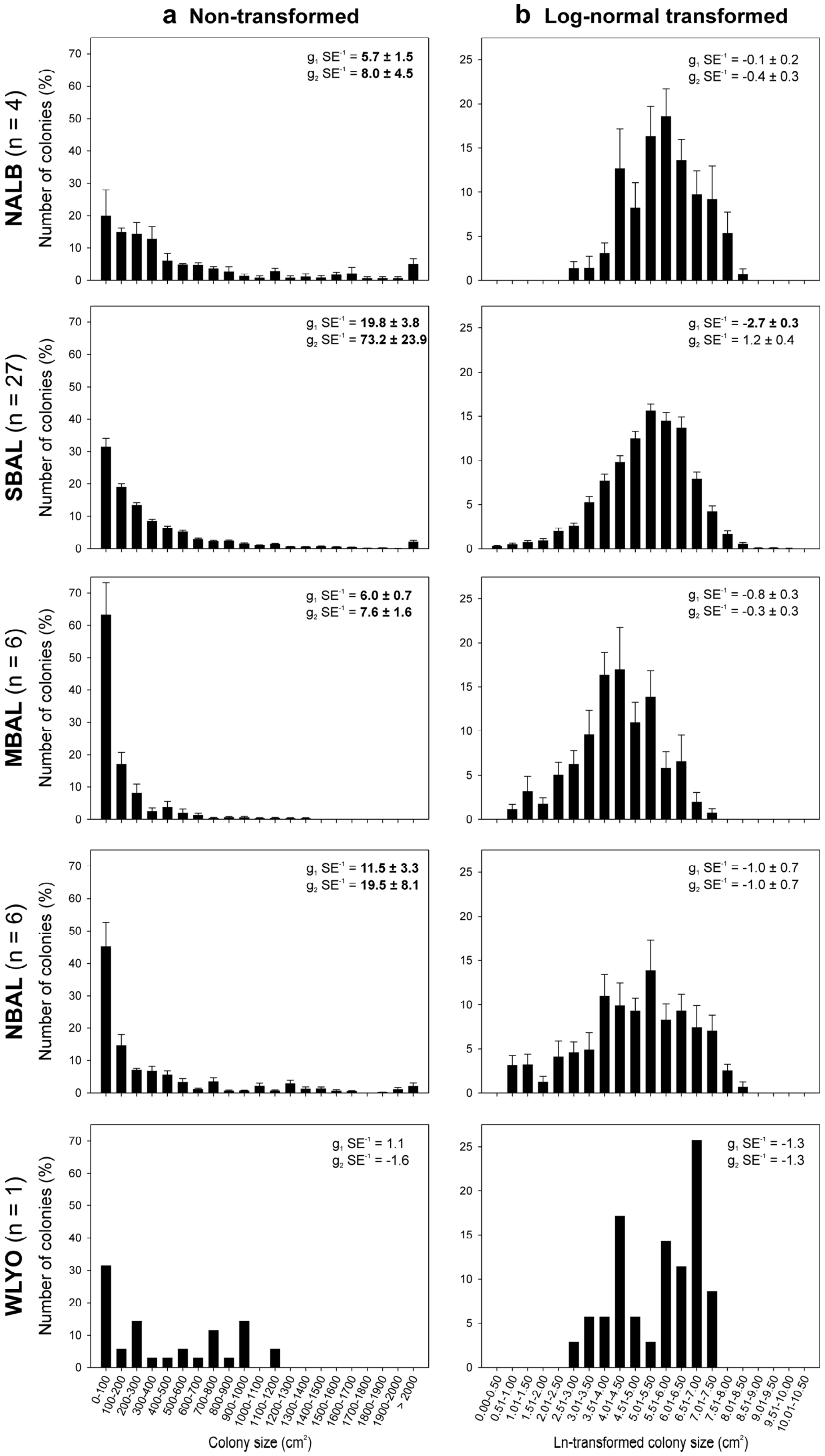

Fig. 4.5.4 Colony size-frequency distributions of *Oculina patagonica* within the five zones distinguished along the whole Iberian coast (NALB to WLYO). a Non-transformed and **b** ln-transformed estimates of colony surface area (cm^2). *n*: number of locations (or group of neighboring locations) with >25 measured colonies within each zone; g_1 SE^{-1}: skewness coefficient and g_2 SE^{-1}: kurtosis coefficient. Significant statistical values are highlighted in bold. Values are mean ± SE.

O. patagonica demographics in relation to environmental parameters

Spearman pairwise relationships among coral demographics and environmental parameters within the studied natural locations in the southern Iberian coast (NALB to NBAL) showed multicollinearity (Table 4.5.2). The mean coral density, total and living cover, maximum colony size, g_1 SE^{-1}and g_2 SE^{-1} were all positively correlated between them. The mean colony size was positively correlated with total and living coral cover. The mean size, maximum size and P90th-size were all positively correlated between them, and negatively correlated with % colonies <100 cm^2 (Table 4.5.2a). The mean ST was positively correlated with P90th-ST and PAR-3m, and negatively correlated with Chl-a. The P90th-ST was negatively correlated with P10th-ST and PAR-3m, and the P10th-ST was positively correlated with PAR-3m and negatively with Chl-a, and PAR-3m was negatively correlated with Chl-a (Table 4.5.2b).

Table 4.5.2 Spearman rank correlation coefficients (r) for associations among the demographics of *Oculina patagonica* and environmental parameters at studied natural locations in the southern Iberian coast (NALB to NBAL). a Coral density, total cover and living cover, colony partial mortality and size-structure descriptors. *Mean size*: mean of the surface area of the colonies; *% <100 cm^2*: % colonies <100 cm^2 in surface area; *P90th-size*: percentile 90th colony-size; *g_1 SE^{-1}*: skewness coefficient; and *g_2 SE^{-1}*: kurtosis coefficient. **b** Environmental parameters. *Mean-ST*: mean annual seawater temperature (ST), *P90th-ST*: percentile 90th ST, *P10th-ST*: percentile 10th ST, *PAR-3m*: photosynthetically active radiation at 3 m depth, *Chl-a*: chlorophyll-a. Correlations for coral density, total cover, living cover and environmental parameters correspond to all studied locations (n = 96). Correlations for colony partial mortality (*PM*) and size-structure descriptors correspond to the locations (or group of neighboring locations) with >25 measured colonies (n = 43). Significant statistical values are highlighted in bold: * P<0.05, ** P<0.01, *** P<0.001, ****P<0.0001.

a Coral parameters	Density	Total cover	Living cover	PM	Mean size	% <100 cm^2	P90th-size	Maximum size	g_1 SE^{-1}
Density									
Total cover	**0.99******								
Living cover	**0.98******	**1.00******							
Partial mortality	-0.09	-0.17	-0.24						
Mean size	0.00	**0.31***	**0.31***	-0.27					
% <100cm^2	0.07	-0.20	-0.21	0.26	**-0.86******				
P90th-size	-0.03	0.25	0.25	-0.27	**0.96******	**-0.78******			
Maximum size	**0.44****	**0.61******	**0.60******	-0.29	**0.64******	**-0.40****	**0.58******		
g_1 SE^{-1}	**0.73******	**0.67******	**0.67******	-0.18	-0.04	0.17	-0.10	**0.68******	
g_2 SE^{-1}	**0.61******	**0.53*****	**0.53*****	-0.19	-0.13	0.25	-0.19	**0.62******	**0.97******

b Environmental parameters	Mean ST	P90th-ST	P10th-ST	PAR-3m
Mean ST				
P90th-ST	**0.48******			
P10th-ST	0.10	**-0.68******		
PAR-3m	**0.62******	**-0.27****	**0.65******	
Chl-a	**-0.62******	0.03	**-0.27****	**-0.83******

Spearman pairwise correlations, which do not assume bivariate normality, showed several consistent relationships between the demographics of *O. patagonica* and environmental parameters along the southern Iberian coast (Table 4.5.3). The coral abundance (i.e., density, total and living cover) was positively correlated with mean ST, P10th-ST and PAR-3m, but negatively correlated with Chl-a. In all cases, the percentage of the variance in coral abundance explained by mean ST and PAR-3m (31-37%) was higher than that explained by Chl-a (19-21%) and P10th-ST (10-11%; Table 4.5.3). Spearman correlations using all locations (i.e., five zones, NALB to WLYO) yielded similar results, but coral abundance was also positively correlated with P90th-ST (37%; results not shown). The colony partial mortality was negatively correlated with mean ST (Table 4.5.3). The mean colony size and P90th-size were negatively correlated with mean ST and P90th-ST, and the % colonies <100 cm^2 was positively correlated with P90th-ST and negatively correlated with P10th-ST. The skewness and kurtosis coefficients were positively correlated with mean ST and negatively correlated with Chl-a (Table 4.5.3).

Table 4.5.3 Spearman rank correlation coefficients (r) for associations between the demographics of *Oculina patagonica* and environmental parameters at studied natural locations in the southern Iberian coast (NALB to NBAL). Correlations for coral density, total cover and living cover correspond to all studied locations (n = 96). Correlations for colony partial mortality and size-structure descriptors correspond to the locations (or group of neighboring locations) with >25 measured colonies (n = 43). *Mean size*: mean of the surface area of the colonies; *% <100 cm^2*: proportion of colonies <100 cm^2 in size; *P90th-size*: percentile 90th colony-size; *g_1 SE^{-1}*: skewness coefficient; *g_2 SE^{-1}*: kurtosis coefficient. *Mean-ST*: mean annual seawater temperature (ST); *P90th-ST*: percentile 90th ST; P10th-ST: percentile 10th ST; *PAR-3m*: photosynthetically active radiation at 3 m depth; *Chl-a*: chlorophyll-a. Significant statistical values are highlighted in bold: * P<0.05, ** P<0.01, *** P<0.001, ****P<0.0001.

	Mean-ST	P90th-ST	P10th-ST	PAR-3m	Chl-a
Density	**0.60******	0.05	**0.32****	**0.60******	**-0.46******
Total cover	**0.56******	0.00	**0.32****	**0.59******	**-0.44******
Living cover	**0.57******	-0.01	**0.34****	**0.61******	**-0.46******
Partial mortality	**-0.34***	0.08	-0.23	-0.29	0.22
Mean colony size	**-0.31***	**-0.42****	0.25	0.14	0.01
% <100 cm^2	0.24	**0.52*****	**-0.44****	-0.27	0.03
P90th-size	**-0.41****	**-0.39****	0.15	0.05	0.07
Maximum size	0.08	-0.16	0.17	0.19	-0.17
g_1 SE^{-1}	**0.44****	0.15	0.02	0.25	**-0.30***
g_2 SE^{-1}	**0.48****	0.17	0.04	0.21	**-0.31***

The five distinguished zones showed consistent relationships between the demographics of *O. patagonica* and environmental thresholds along the whole Iberian coast (Fig. 4.5.5). The living coral cover (i.e., an integrating measure of population growth) was maximum at locations from SBAL, characterized by a high mean ST (>19-20ºC) and a narrow seasonal amplitude (P90th-ST >25-26ºC and P10th-ST >14-15ºC; Fig. 4.5.5a-c). Although mean ST was similarly high between SBAL and

MBAL (>19-20ºC), the lower living coral cover at MBAL was related to higher P90th-ST and lower P10th-ST (>26-27ºC and <14-13ºC, respectively). The living coral cover was also lower at the lower-ST zones (mean ST <19-17ºC), either characterized by a low P90th-ST and high P10th-ST at NALB (<25-22ºC and >14-15ºC, respectively), by high P90th-ST and low P10th-ST at NBAL (>25-27ºC and <13-12ºC, respectively) and by both low P90th-ST and P10th-ST at WLYO (<24-22ºC and <13-12ºC, respectively; Fig. 4.5.5a-c). The highest living coral cover at SBAL was related to maximum PAR-3m (>32 mol photons m^{-2} d^{-1}) and minimum Chl-a values (<0.4 g m^{-3}) among the studied zones (Fig. 4.5.5d,e).

Artificial reefs (i.e., harbor dikes and breakwaters) were common features of the whole Iberian coast. The abundance of artificial reefs (i.e., cumulated length of artificial reefs per length coast) at SBAL and WLYO (0.05 and 0.04 km artificial reef km^{-1} coast, respectively) was at least 41% lower than those at NALB, MBAL and NBAL (0.09, 0.11 and 0.21 km artificial reef km^{-1} coast, respectively; SM 4.5.9). Within the studied coast, the living coral cover in natural locations was positively correlated with the distance (km) between natural locations and the nearest artificial reef ($b = 0.06$, $r^2 = 0.04$, $p = 0.0040$, $n = 233$; SM 4.5.10). A total of 38 natural locations with coral populations were examined for describing benthic community assemblages. The mean cover of benthic assemblages (standardized to that of space without *O. patagonica*) was characterized by erect algae (64 ± 3%), turf algae (23 ± 3%), crustose coralline algae and bare rock (10 ± 1%), and sessile invertebrates (3 ± 0%). The mean open space availability for *O. patagonica* to colonize (which includes turf algae, crustose coralline algae and bare rock) ranged between 3 and 80% among locations (33 ± 3%), and showed significant differences among zones (one-way ANOVA, $F_{4,33} = 3.41$, $p = 0.0192$), with values at WLYO (62%) being 2-fold higher than those at the other zones (NALB to NBAL, 26-32%). The mean sea urchin biomass ranged between 6 and 587 g m^{-2} among locations (154 ± 25 g wet weight m^{-2}; SM 4.5.11), with no significant differences among zones (one-way ANOVA, $F_{4,33} = 1.57$, $p = 0.21$, on log-transformed data). Within the studied coast, the living coral cover was significantly correlated with sea urchin biomass ($r^2 = 0.12$, $p = 0.0320$, $n = 38$) but was not correlated with open space availability, and the sea urchin biomass was not correlated with open space availability ($p > 0.05$).

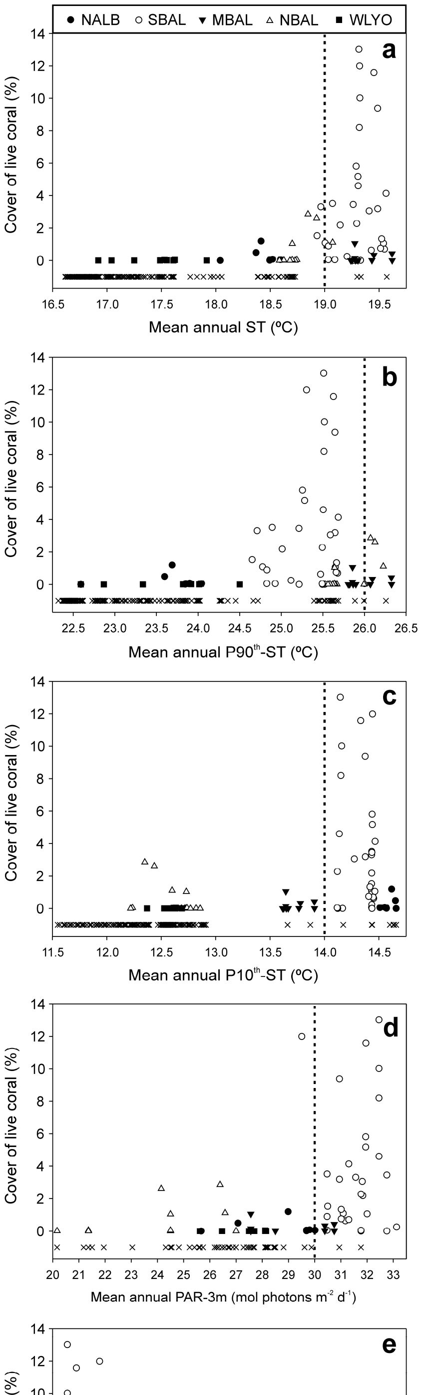

Fig. 4.5.5 Variation in percent cover of live coral *Oculina patagonica* with environmental parameters at studied natural locations (n = 233) within the five zones distinguished along the whole Iberian coast (NALB to WLYO). a Mean annual seawater temperature (*Mean ST*). **b** Mean annual percentile 90th ST (*P90th-ST*). **c** Mean annual percentile 10th ST (*P10th-ST*). **d** Mean annual photosynthetic active radiation at 3 m depth (*PAR-3m*). **e** Mean annual chlorophyll-a (*Chl-a*). *Crosses* below the zero line indicate locations in which *O. patagonica* was not found. *Vertical dashed lines* indicate thresholds of **a** >19ºC, **b** >26ºC, **c** <14ºC and **d** >30 mol photons m^{-2} d^{-1}.

Discussion

Since the first record of the zooxanthellate coral *O. patagonica* in 1966 at the Ligurian Sea (i.e., a single large colony ~135 cm in mean diameter; Zibrowius 1974), the species has been documented to be present in shallow-water rocky reefs (~0 to 8 m, up to ~15 m depth) from many distant regions throughout the Mediterra-nean Sea (e.g., Fine et al. 2001; Sartoretto et al. 2008; Salomidi et al. 2013; Rubio-Portillo et al. 2014a and references therein; Chapters 4.1, 4.2, this study). However, on the basis of mean linear extension rates documented in field studies conducted to date (~1-2 cm in diameter yr^{-1}; Fine et al. 2001; Rubio-Portillo et al. 2014b; Chapter 4.4), it can be estimated from the large colony sizes (i.e., >2000 cm^2, equivalent to >50 cm in diameter) observed in most of our examined zones (Table 4.5.1) and in most reported regions (SM 4.5.12) that the species may have been present before 1900 in the Mediterranean and that was established in most regions by ~1950s.

The results from our study in the framework of current knowledge (see above) on *O. patagonica* demographics across the Mediterranean indicate that the Iberian coast is the region with the highest abundance of the species, both in terms of the cumulated number of locations and extent of coastal length with records of the species. In this region, we found that colony size distributions of *O. patagonica* were unimodal and positively skewed, indicative of non-stable and growing populations. The demographics of this coral species (i.e., occurrence, density, cover, and colony partial mortality and size-structure) displayed significant correlations and showed a marked zonal pattern along the ~1300 km Iberian coast [being more successful at southeastern Iberia (SBAL) and decreasing success both northeastward (MBAL, NBAL and WLYO) and southwestward (NALB)]. This regional variation on the success of *O. patagonica* is in accordance with previous studies examining coral demographics at a local scale during 2010-2011 (concomitant to our study; Rubio-Portillo et al. 2014a; Terrón-Sigler et al. 2015; Chapters 4.1, 4.2, 4.3). The end result is that the demographics of *O. patagonica* within the Mediterranean Iberian coast appear to conform to the 'abundant-center' hypothesis (Sagarin et al. 2006), because it is most abundant at the center and declines in abundance toward the edges of this geographic range.

Potential causes of the 'abundant-center' pattern of *O. patagonica* in the Iberian coast

The distributional limits and geographic range structure of a species may be determined by the interacting influences of dispersal and history, and the clines in climate, resource availability and biotic factors (e.g., competition, facilitation, predation) that modulate species' success (survival, growth and reproduction; Brown et al. 1996; Sagarin et al. 2006; Gaston 2009; Guo 2014). The 'abundant-center' pattern of *O. patagonica* observed in this study within the Mediterranean Iberian coast could be interpreted as a result of an ongoing gradual expansion process with an initial focus at SBAL. This would be consistent with the strong gradients in coral demographics (i.e., occurrence, abundance and/or colony size-structure) previously documented along large-scale areas (~100-400 km coastal length) in the south-Aegean Sea (Salomidi et al. 2013), the Levant Sea (Fine et al. 2001) and in the expansion front along the northeastern Iberian coast (from NBAL to WLYO; Chapter 4.3). The fact that the species was first described in the 1970s as being already common along ~350 km coastal length at SBAL-MBAL (Zibrowius and Ramos 1983), and that current coral occurrences have been documented in this study to be higher at SBAL-MBAL than at the other zones, together with the documented northward expansion (Chapter 4.3), conform with an ongoing gradual expansion process. However, the coral demographics characterized in this study indicate that this is most probably not the only process occurring along the Iberian coast. Our current assessment on the occurrence and demographics of *O. patagonica* indicate relevant differences in population growth between the two zones where the species was already present in the 1970s (i.e., SBAL and MBAL). Current coral populations at MBAL have been less successful than at SBAL (e.g., 0.2% *versus* 3.4% in living cover). Moreover, the continuous distribution and large colony sizes (i.e., >50 cm in diameter) observed along the Iberian coast suggest that this species was widely established by ~1950s (Table 4.5.1, see above) and thus, the observed zonal differences in coral population growth appear to have contributed to zonal differences in coral demographics as much or more than differences in arrival.

Competition with macroalgae is a key limiting factor for zooxanthellate coral populations to grow, especially in shallow-water macroalgae-dominated temperate and subtropical areas, such as the Mediterranean (Zabala and Ballesteros 1989; Miller and Hay 1996; Miller 1998; McCook et al. 2001). The benthic assemblages in natural locations with *O. patagonica* populations were generally dominated by erect crowded algae (64%), and the mean open space availability for coral settlement and growth was 33% (which includes cover of bare rock, crustose coralline algae and sparse turf algae <1 cm in height). The availability of open space on algal-depleted reefs, either provided by the presence of natural- or human-related disturbances (e.g., overgrazing by sea urchins, wave-driven physical abrasion, artificial reefs, sea warming and pollution; e.g., Thibaut et al. 2017), has been identified as a primary factor fostering the growth of *O. patagonica* populations (Salomidi et al. 2013;

Rubio-Portillo et al. 2014a; Chapters 4.1, 4.2, 4.3). In accordance, the living coral cover within the Iberian coast was positively correlated with sea urchin biomass. However, the availability of open space did not vary among the studied zones and was not correlated with living coral cover. Therefore, the availability of open space did not contribute to explain the zonal variation in population growth of *O. patagonica* at the examined regional scale. This appears to be related to the fact that the mean open space availability within the Iberian coast was evenly higher than those reported to facilitate the population growth of zooxanthellate *Oculina* spp. (approximately >20%; Miller and Hay 1996; Chapter 4.2), which is consistent with the fact that algal-depleted reefs are common in the Iberian coast (e.g., Sala et al. 2012; Boada et al. 2017; Thibaut et al. 2017).

In this study, we showed that the occurrence of *O. patagonica* exhibited a concomitant zonal pattern of variation between natural and artificial locations along the Iberian coast, but exacerbated in the latter (e.g., occurrence of coral populations was 96% higher in artificial locations than in natural locations within each zone). This is in concordance with previous studies suggesting that the unique characteristics of artificial habitats enhance coral population growth (Perkol-Finkel and Benayahu 2009; Bulleri and Chapman 2010; Salomidi et al. 2013; Chapter 4.3). However, the zonal variation in *O. patagonica* population growth in natural locations within the Iberian coast cannot be attributed to a zonal variation in the abundance of artificial reefs. First, the lowest abundance of artificial reefs was found in the zone where the species was most abundant (SBAL). Second, the living coral cover on natural locations was positively correlated with the distance between natural locations and the nearest artificial reef. Finally, because despite the marked differences in abundance of artificial reefs among zones, the coral occurrence exhibited a concomitant zonal pattern of variation between natural and artificial locations along the Iberian coast.

The concomitant zonal pattern of higher coral abundance in artificial locations (i.e., the seaward side) than in nearby natural locations point to the relevant role of environmental parameters in determining occurrence and demographics of *O. patagonica* along the Mediterranean Iberian coast. In this sense, the coral demographics and the environmental parameters on natural locations showed a clear spatial pattern of 5 distinct regimes, and abrupt changes in coral demographics and environmental parameters were observed either side of SBAL. This is consistent with the fact that the SBAL zone is bordered by oceanographic fronts (Almeria-Oran at the southwest and Ibiza Channel at the northeast) that have documented to delimitate distinct water masses and constitute biogeographical barriers affecting the genetic distribution of marine species (e.g., Millot 2005; Pascual et al. 2017). Furthermore, the coral demographics (i.e., density, total and living cover, skewness and kurtosis coefficients) were positively correlated between them and correlated with environmental parameters (positively with annual mean ST, P10th-ST, P90th-ST and PAR-3m, and negatively with Chl-a). Hence, the occurrence of *O. patagonica* was scarce at the Alborán Sea (NALB zone) and in the zones influenced by the Northern Current originating in the Gulf of Lyons (NBAL and WLYO). This two peripheral water masses characterize by being upwelling areas, with low-ST regimes, increased nutrient enrichment and primary productivity (Chl-a), and reduced light conditions (PAR-3m). In contrast, the SBAL and MBAL zones, which host the largest coral occurrences within the Iberian coast, were characterized by reduced Chl-a, higher light conditions and a higher-ST regime (Estrada 1996; Millot 2005). These findings indicate that regional variation in environmental parameters play a major role in the 'abundant center' pattern of occurrence and demographics of *O. patagonica* observed along the Iberian coast. Low ST and light conditions (i.e., mean annual ST <19ºC and PAR-3m <30 mol photons m^{-2} d^{-1}) appear as relevant drivers constraining performance of *O. patagonica*, which is in accordance with previous studies on tropical zooxanthellate coral species (e.g., Kleypas et al. 1999; Muir et al. 2015).

The positive effect of light (PAR), and the negative effect of Chl-a (an estimate of plankton availability for heterotrophy), on *O. patagonica* population growth found within the Iberian coast suggests that autotrophic nutrition (photosynthesis from symbiotic algae) is the primary energy source for *O. patagonica*, while heterotrophy plays a secondary role. This result is consistent with previous studies on this and other shallow-water *Oculina* species before (Tremblay et al. 2011; Leal et al. 2014), and with the general pattern documented in tropical zooxanthellate corals (Houlbrèque and Ferrier-Pagès 2009; Muir et al. 2015). The observed positive effect of light on the growth of *O. patagonica* populations is also consistent with the annual growth cycle of *O. patagonica* colonies that has been documented to be positively correlated with PAR and enhanced with increasing light intensities at shallower depths (Rodolfo-Metalpa et al. 2008); and with the shallow bathymetric distribution of the species across the Mediterranean, being generally restricted to shallow waters and rare at depths of >10 m (SM 4.5.12) that, in general, are subjected to <10% of the surface irradiance (e.g., Estrada 1996). Even though *O. patagonica* colonies can thrive only by heterotrophic feeding in dark habitats (Fine et al. 2001), azooxanthellate colonies were rare in the study area, with the exception of the down-sides of concrete blocks in an artificial location at SBAL (authors' unpublished data), located in a man-made channel with enhanced currents that may enhance food availability and survival (e.g., Aichelman et al. 2016). Although the relative importance of autotrophy and heterotrophy in feeding of zooxanthellate corals in temperate areas can vary either seasonally and geographically in relation to the availability of food resources (Coma and Ribes 2003; Ferrier-Pagès et al. 2011; Leal et al. 2014), our results on natural habitats support autotrophic nutrition as a primary energy source for the growth of *O. patagonica* colonies and populations.

The variation in the thermal regime along the Iberian coast was also a relevant factor contributing to explain *O. patagonica* demographics (i.e., population growth and colony partial mortality and size-descriptors; Table 4.5.3). This is consistent with previous studies on the growth rate of coral colonies in the western Mediterranean, in which although the species behaved like a tropical coral with respect to colony growth enhancement with increasing ST and light, the relationships were stronger with the former (Rodolfo-Metalpa et al. 2008; Rubio-Portillo et al. 2014b; Chapter 4.4). The ST-growth response of *O. patagonica* at organismal (colony) level characterize by a minimum at 11-16ºC, enhancement up to a threshold of 24-26ºC, and a somewhat decline at >26-30ºC (e.g., Rodolfo-Metalpa et al. 2014; Chapter 4.4). Although the mean ST was similar between both southern Balearic Sea zones (SBAL and MBAL, >19-20ºC), coral success at MBAL was lower than at SBAL (e.g., 4-fold less living coral cover and flattered colony size-frequency distributions indicating less growing populations; Bak and Meesters 1998; Meesters et al. 2001). The thermal differences between both zones appear to be related to the wider amplitude of the thermal regime at MBAL (annual mean P10th-ST <14-12ºC and P90th-ST >26-27ºC) that regularly exceed both sub-lethal low-ST (<14ºC) and high-ST thresholds (>26ºC) that have been linked to reduced survival, growth and/or reproductive success in *O. patagonica* colonies (Shenkar et al. 2005; Rodolfo-Metalpa et al. 2008; Armoza-Zvuloni et al. 2011; Rubio-Portillo et al. 2014b, 2016; Chapter 4.4) and, therefore, may negatively affect coral population growth. Taking into account the positive relationship between ST and the growth of *O. patagonica* colonies described in the western Mediterranean, in which growth is 3-fold higher at 24-26ºC than at 18ºC (Rodolfo-Metalpa et al. 2008; Rubio-Portillo et al. 2014b; Chapter 4.4), the low-ST regime (annual mean ST <19-17ºC and the rarity of P90th-ST >25ºC) either with or without severe low-ST periods (P10th-ST <15-12ºC) found in NALB, NBAL and WLYO is conducive to a shorten growing season for the species than at SBAL. This may contribute to understand the lower coral population growth observed at these peripheral zones in contrast to that at SBAL (e.g., at least 18-fold lower living coral cover, and colony size-frequency distributions indicating more stable and aged populations).

Within the southern Iberian coast (NALB-NBAL), the absence of a correlation between *O. patagonica* abundance (density and cover) and P90th-ST, together with the negative correlation of P90th-ST with either mean colony size and P90th-size and the positive correlation of P90th-ST with the % colonies <100 cm^2 (Table 4.5.3), indicate that the severe high-ST period found at MBAL (P90th-ST >26-27ºC, which are the highest values observed within the study region; Table 4.5.1) may be negatively affecting coral colony growth. In accordance, the exceed of high-ST sub-lethal thresholds for *O. patagonica* (P90th-ST >26-27ºC) during summer have been related to mortality episodes of entire portions of the colonies (polyps and coenosarc) causing a shrinkage in size-structure at MBAL (Rubio-Portillo et al. 2014b, 2016) and in the Levant Sea (Shenkar et al. 2005). In contrast, the exceed of low-ST sub-lethal thresholds for *O. patagonica* (P10th-ST <14ºC) during winter have been related to a colony pattern of partial mortality that mainly affect the coenosarc (i.e., Dalmatian mortality pattern), which facilitates rapid recovery from injuries and steady colony growth without severe shrinkage (Chapter 4.4). The negative correlation between P10th-ST and the % colonies <100 cm^2

found within the Iberian coast is in accordance with low-ST periods allowing a steady colony growth of *O. patagonica* (Chapter 4.4).

The results on *O. patagonica* demographics (i.e., population growth and colony partial mortality and size-descriptors) within the Iberian coast are contributing to identify the most appropriate thermal regime for the successful growth of *O. patagonica* colonies and populations, which appear to be generally constrained by ST thresholds of annual mean ST <19ºC, P10th-ST <14ºC and P90th-ST <25ºC, but also a P90th-ST >26-27ºC. Our study represents a snapshot assessment in time and, therefore, cannot properly address the relative importance of negative effects of high- and low-ST thresholds on the population growth dynamics of *O. patagonica*. In this sense, it should be noted that the occurrence of single extremely low- or high-ST events are considered key drivers of population dynamics for long-lived species such as corals (e.g., Easterling et al. 2000; Takao et al. 2015; Tuckett et al. 2017) and both extreme summer and winters have episodically occurred in the study area (Coma et al. 2009; Vargas-Yáñez et al. 2012). Moreover, several field and laboratory experiments suggest regional and interannual differences in *O. patagonica* high-ST sub-lethal thresholds, ranging between P90th-ST >24 and >28ºC (e.g., Rodolfo-Metalpa et al. 2008, 2014; Rubio-Portillo et al. 2016), which may be related to a regional variation in the type of zooxanthellae symbionts and/or in the occurrence of pathogens (e.g., Rubio-Portillo et al. 2014c; Grupstra et al. 2017). Further broad-scale studies on seasonal and interannual dynamics on *O. patagonica* population growth would help to clarify this issue.

The results of the present study provide a baseline quantitative assessment of current *O. patagonica* occurrence and demographics along the Mediterranean Iberian coast. This detailed and large-scale data set has contributed to characterize that the Iberian coast is the region with the highest abundance of the species and that the pattern of variation in coral abundance within the study area conforms to the general pattern of the ‘abundant-center’ hypothesis (i.e., a most abundant center that declines toward the edges of a geographic range). However, the results on coral demographics indicate that this pattern is not only related to the time of establishment but points to the relevant role of differences in coral population growth that correlate with key environmental parameters. Nevertheless, it should be noted that our data provide correlational evidence, and that the cause-effect relationship between environmental parameters and the observed demographic pattern cannot be determined without additional experimental studies. The high occurrence of *O. patagonica* documented in the Iberian coast, and its invasive behavior (i.e., spreading geographically and experiencing populations outbreaks) that is leading to phase shifts from macroalgal to coral dominance in natural and artificial reefs from this and other Mediterranean regions (Blackburn et al. 2011; Salomidi et al. 2013; Chapters 4.1, 4.2, 4.3), is consistent with the ongoing process of coral-mediated tropicalization of shallow-water rocky ecosystems, such as those documented in other subtropical and temperate areas (reviewed in Vergés et al 2014a) under current sea warming.

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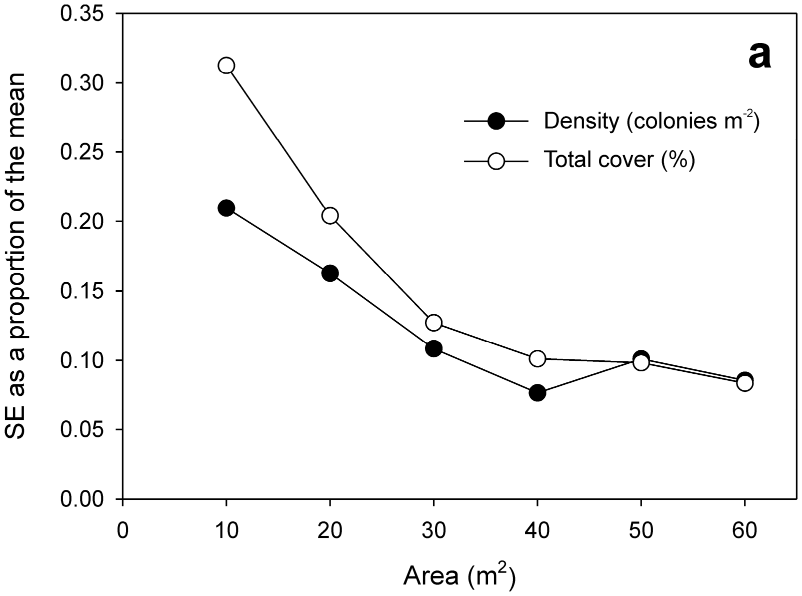
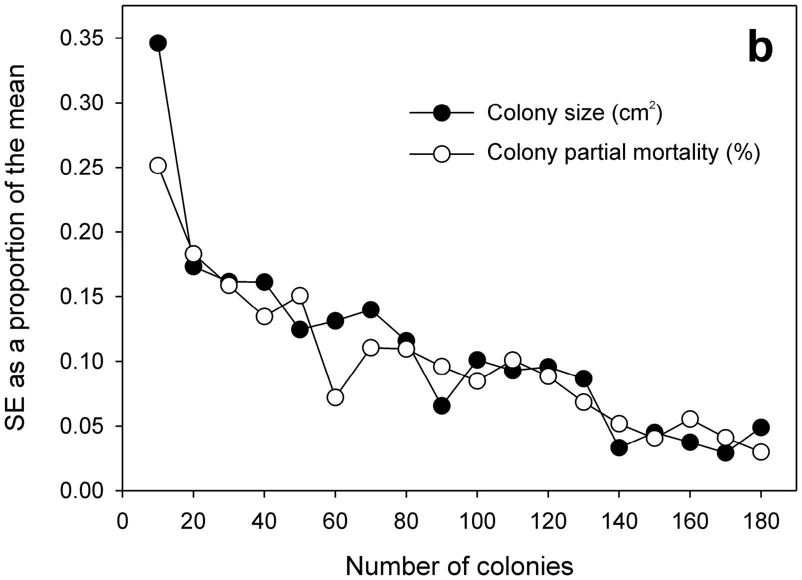
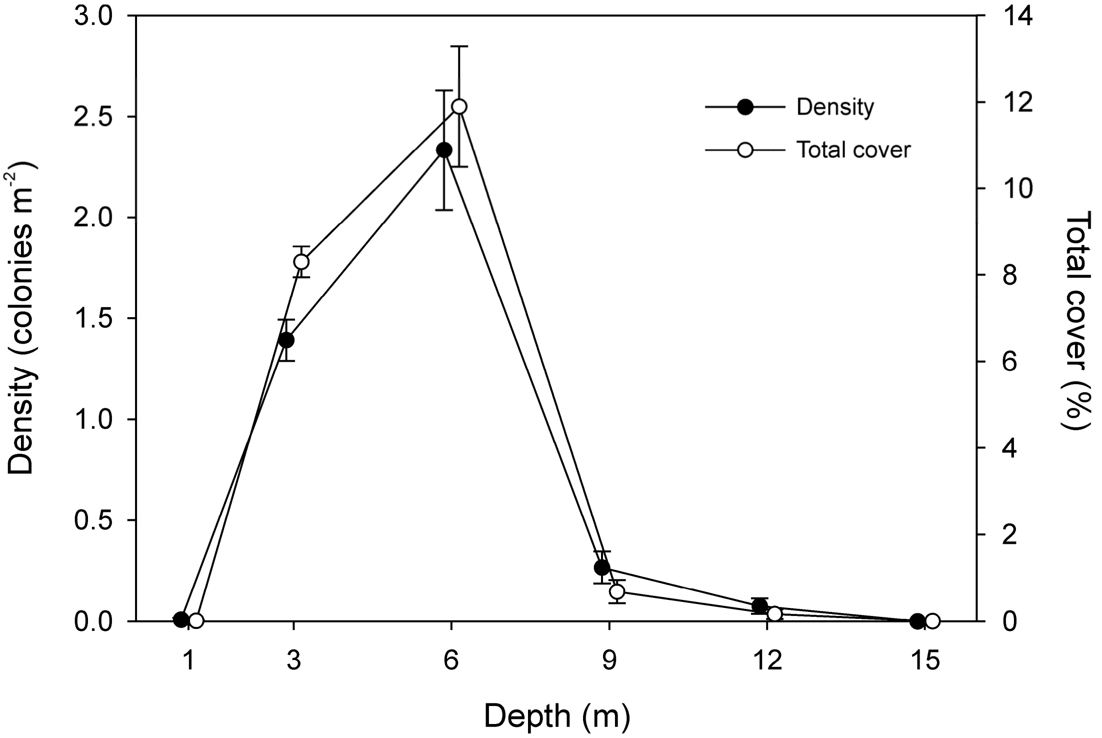
Supplementary Material (SM)

SM 4.5.1 Minimal sampling effort for estimates of *Oculina patagonica* demographics. The minimal sampling effort estimates were examined in 2007 at a natural location in the South-Balearic Sea, western Mediterranean (El Hormigón, 37°39'09"N–00°39'13"W), by examining an area of 200 m^2 using 10 m^2 belt-transects (10 x 1 m) set randomly on the rocky bottom at ~6 m depth. A total of 560 coral colonies were examined within the 20 transects. To determine the minimal sampling size, we utilized the function of the variation of the standard error (*SE*) as a proportion of the mean with sample size. **a** Minimal sample size (area in m^2) for coral density (colonies m^{-2}) and total cover (%) estimates. The SE as a proportion of the mean density and total cover decreased quickly with increasing sample area, remaining at a variance of <10% of the mean at a sample area of >40 m^2. **b** Minimal sample size (number of colonies) for colony size (surface area in cm^2) and partial mortality (%) estimates. The SE as a proportion of the mean of colony size and partial mortality decreased quickly with increasing sample size, remaining at a variance of <20% of the mean at a sample size of >20 colonies.





SM 4.5.2 Bathymetric distribution pattern of *Oculina patagonica*. The bathymetric distribution was examined in 2007 at a natural location in the South-Balearic Sea, western Mediterranean (El Hormigón, 37°39'09"N–00°39'13"W) by using three replicates of randomly positioned 40 m^2 transects (40 x 1 m) at 6 selected depth levels (1, 3, 6, 9, 12 and 15 m). The coral abundance data (number of colonies and colony surface area) was standardized based on the area surveyed, and the species density (colonies m^{-2}) and total cover (%) values were calculated for each depth.



SM 4.5.3 Studied sites for seawater temperature (ST) within the five zones distinguished along the ~1300 km of the Mediterranean Iberian coastline (NALB to WLYO). Surface ST time series over 2003-2010 were obtained from MODIS-Aqua sensor (Ocean Level-2) satellite-derived measurements performed by NASA's Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov/). The cumulative coastal length distances between the sites for which ST was examined, from southwest to northeast, are indicated. Length values were measured using Google Earth images at a scale of 1:1,000. *n*: number of valid daily ST measurements.

Zone	ST site	Coastal	Geographic coordinates		ST readings
		lenght (km)	Latitude	Longitude	N
North-Alborán Sea	Marbella	0	36°27'23"N	4°57'51"W	1167
(NALB)	Caleta Vélez	84	36°43'22"N	4°02'20"W	1127
	Motril	136	36°42'02"N	3°31'60"W	1177
	Almería	244	36°48'32"N	2°29'19"W	1144
South-Balearic Sea	Carboneras	319	36°58'53"N	1°52'21"W	1378
(SBAL)	Águilas	384	37°22'49"N	1°35'22"W	1256
	Cartagena	446	37°33'33"N	1°00'03"W	1108
	Cabo Palos	476	37°39'07"N	0°39'16"W	1539
Mid-Balearic Sea	Alacant	566	38°20'11"N	0°26'45"W	1169
(MBAL)	Dènia	667	38°50'20"N	0°10'22"E	1367
	València	755	39°29'56"N	0°17'37"W	1335
	Castelló	818	40°00'54"N	0°04'00"E	1174
North-Balearic Sea	Les Cases d'Alcanar	896	40°31'05"N	0°32'25"E	1089
(NBAL)	L'Ampolla	936	40°50'00"N	0°46'51"E	1202
	Vilanova i la Geltrú	1026	41°11'02"N	1°42'05"E	1454
	Premià de Mar	1096	41°29'28"N	2°25'28"E	1400
West Gulf Lyons	Platja d'Aro	1176	41°46'47"N	3°04'52"E	1385
(WLYO)	Medes Islands	1221	42°01'14"N	3°13'47"E	1397
	Cadaqués	1266	42°15'00"N	3°18'16"E	1410
	Port de la Selva	1300	42°21'52"N	3°12'19"E	1237

SM 4.5.4 Combination of analytical approaches used to identify regimes of *Oculina patagonica* demographics and the key environmental correlates of this variation at studied natural locations along the whole Mediterranean Iberian coast (NALB to WLYO).

Within the ~1300 km Iberian coast there was a positive autocorrelation (i.e., contagious distribution) of living coral cover at distance classes of <200 km, whereas a random distribution dominated at larger spatial scales (Moran's Index, $p < 0.0001$, $n = 233$ locations). We used principal component analysis (PCA) to provide insights into the spatial structure of the variation in species abundance (coral density and living cover) and underlying environmental parameters [mean annual seawater temperature (ST), percentiles 90th and 10th ST (P90th-ST and P10th-ST, respectively), photosynthetically active radiation at 3 m depth (PAR-3m) and chlorophyll-a (Chl-a) along two principal components (PC, $n = 233$ locations); Fig. SM 4.5.4]. PC1 accounted for 55% of total variance and explained the variation in *O. patagonica* abundance in relation to environmental parameters, with higher coral abundance at higher mean ST, P10th-ST, P90th-ST and PAR-3m, and lower Chl-a (at positive PC1 scores, loadings |0.70–0.88|). PC2 accounted for 19% of total variance and explained the variability of PAR-3m and Chl-a, with higher Chl-a and lower PAR-3m at positive PC2 scores (loadings |0.53–0.87|). PC3 accounted for 17% of total variance and explained the variation in coral abundance in relation to thermal regime, with higher coral abundance at lower mean ST, P10th-ST and P90th-ST (at positive PC3 scores, with low negative loadings: from -0.27 to -0.31). Based on the contagious distribution of living coral cover at distance classes of <200 km coastal length, the K-means partitional clustering process (Rai and Singh 2010) was used to categorize the locations with regards to their coral abundance and key environmental correlates of this variation. The K-means partitional clustering of the locations using coral abundance and the environmental parameters identified to be selective in PC2 (Chl-a and PAR-3m) did not yield any spatial grouping consistency in the study area (results not shown). In contrast, the K-means clustering using coral abundance and the two ST extremes identified to be selective in PC3 (P90th-ST and P10th-ST) yielded a map with ten clusters. The use of P90th-ST and P10th-ST in the analysis is consistent with both high- and low-ST extremes being related to sub-lethal effects in *O. patagonica* in the study area (e.g., Rubio-Portillo et al. 2014b, 2016; Chapter 4.4), and ST extremes rather than means are most often mediators of effects on marine organisms (e.g., Easterling et al. 2000). Therefore, only the combination of analytical approaches using PC1 and PC3 is shown in Fig. SM 4.5.4. The PCA diagram overlaid with the K-means clustering of the locations indicated that *O. patagonica* abundance and environmental correlates group into four clusters consistently separated in space (i.e., zones) along the southern Iberian coast (96 locations, ~1,000 km) that were named as: North-Alborán Sea (NALB), South-Balearic Sea (SBAL), Mid-Balearic Sea (MBAL) and North-Balearic Sea (NBAL); and a heterogeneous grouping into six clusters at the range-expanding area from the northeastern Iberian coast (137 locations, northernmost ~300 km; Chapter 4.3; Fig. SM 4.5.4). Given the spatial heterogeneity found in the northeastern Iberian coast (i.e., the species was scarce and the environmental correlates highly variable), the locations from the 6 northeastern clusters were grouped into a single zone: West-Gulf Lyons (WLYO). Therefore, the results highlighted the existence of five primary regimes of *O. patagonica* demographics and the key environmental correlates of this variation within the five zones (i.e., NALB to WLYO) distinguished along the whole Iberian coast. The combination of analytical approaches using only locations from the southern Iberian coast (i.e., 96 locations, ~1,000 km) showed a spatial aggregation that matched that obtained using the locations from the whole Iberian coast, and yielded similar results, with PC1 accounting for 50% of total variance and showing higher coral abundance at lower Chl-a, and higher mean ST, P10th-ST and PAR-3m (at positive PC1 scores, loadings |0.62–0.89|), except for the absence of a significant correlation with P90th-ST (loading +0.18).

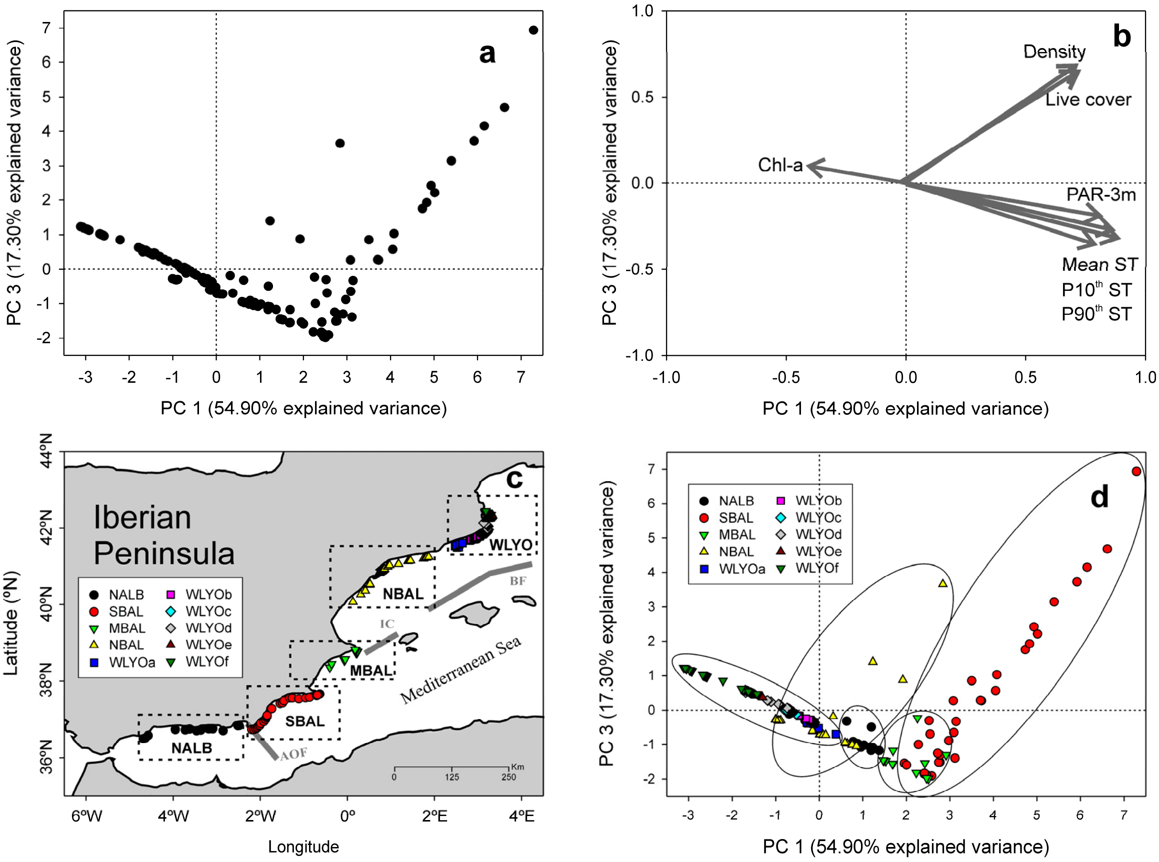
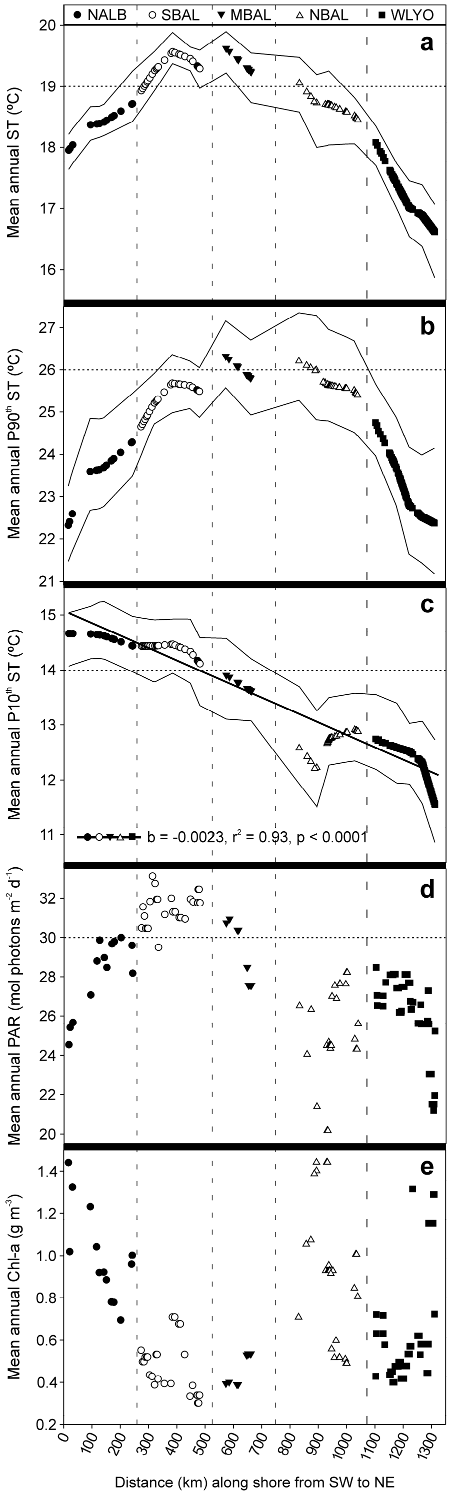
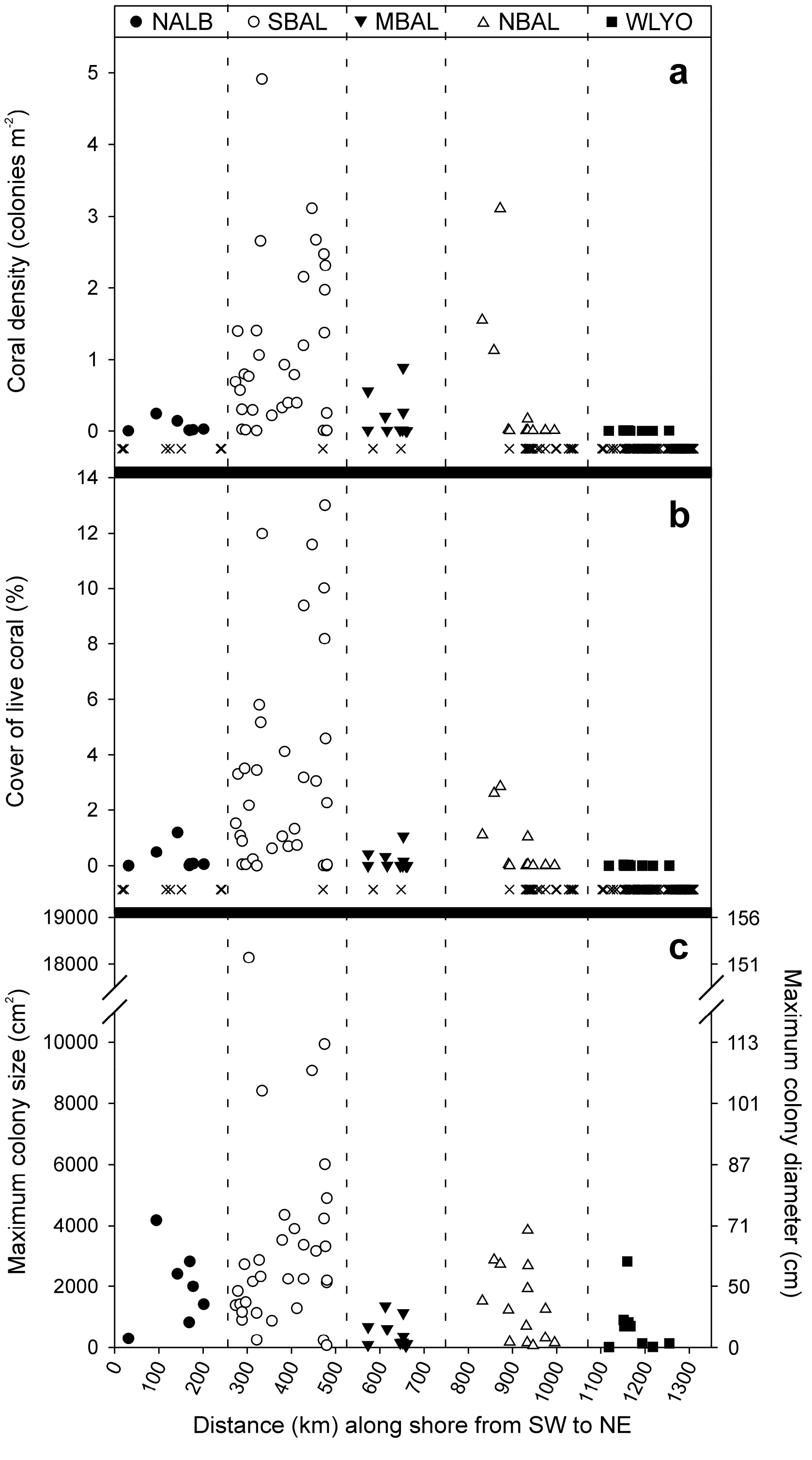


Fig. SM 4.5.4 a Principal component analysis (PCA) diagram showing the spatial variation in *O. patagonica* abundance and environmental parameters along the first and third principal components (PC). **b** Ordination categories of coral abundance and the roles of environmental variables. **c** Map of the study area with an overlaying K-means partitional clustering of the locations using coral abundance and the environmental parameters identified to be selective in PC3 (P90th-ST and P10th-ST). **d** PCA diagram with an overlaying K-means clustering of the locations. *Symbols* represent categorization of the locations matching the four well-defined groups by K-means clustering: NALB, SBAL, MBAL and NBAL; and the heterogeneous group of six clusters at WLYO (WLYOa–f). The *polygons* encompass 100% of the locations associated with each of five distinguished groups.

SM 4.5.5 Environmental parameters at studied natural locations within the five zones distinguished along the whole Mediterranean Iberian coast (NALB to WLYO). **a** Mean annual seawater temperature (ST). **b** Mean annual percentile 90th ST (*P90th-ST*). **c** Mean annual percentile 10th ST (*P10th-ST*). **d** Mean annual photosynthetic active radiation at 3 m depth (*PAR-3m*). **e** Mean annual chlorophyll-a (*Chl-a*). ST was obtained from satellite MODIS-Aqua over 2003-2010, and the minimum and maximum annual ST values are indicated with *grey solid lines*. The mean annual climatology over 2002-2009 of PAR and Chl-a was obtained from Bio-Oracle dataset. *Horizontal dashed lines* indicate thresholds of **a** >19ºC, **b** >26ºC, **c** <14ºC and **d** >30 mol photons m^{-2} d^{-1}.



SM 4.5.6 *Oculina patagonica* demographics at studied natural locations along the ~1300 km coastal length of the whole Mediterranean Iberian coast (NALB to WLYO, n = 233 locations). **a** Coral density. **b** Percent cover of live coral. **c** Maximum colony size. *Crosses* below the zero line (**a**,**b**) indicate locations in which *O. patagonica* was not encountered. *Symbols* represent categorization of the locations within the five zones distinguished in the studied coast: North-Alborán Sea (NALB), South-Balearic Sea (SBAL), Mid-Balearic Sea (MBAL), North-Balearic Sea (NBAL) and West-Gulf Lyons (WLYO). The boundaries of the five distinguished zones are indicated by *vertical dashed lines*.



SM 4.5.7 Colony partial mortality of *Oculina patagonica* at studied natural locations within the five zones distinguished along the whole Mediterranean Iberian coast (NALB to WLYO). Data correspond to the locations (or group of neighboring locations) with >25 measured colonies (n = 44). *n*: number of measured colonies. Mean (±SE) percentage of the colony surface area with recent (i.e., skeleton denuded of living tissue with very little turf algae colonization on non-eroded calices) and old (i.e., denuded skeleton with eroded calices or overgrown by thick turf or sessile organisms) partial mortality. Proportion of colonies in each of 4 levels of severity based on the proportion of colony surface area affected by old mortality (0-10, 11-40, 41-70 and 71-100%).

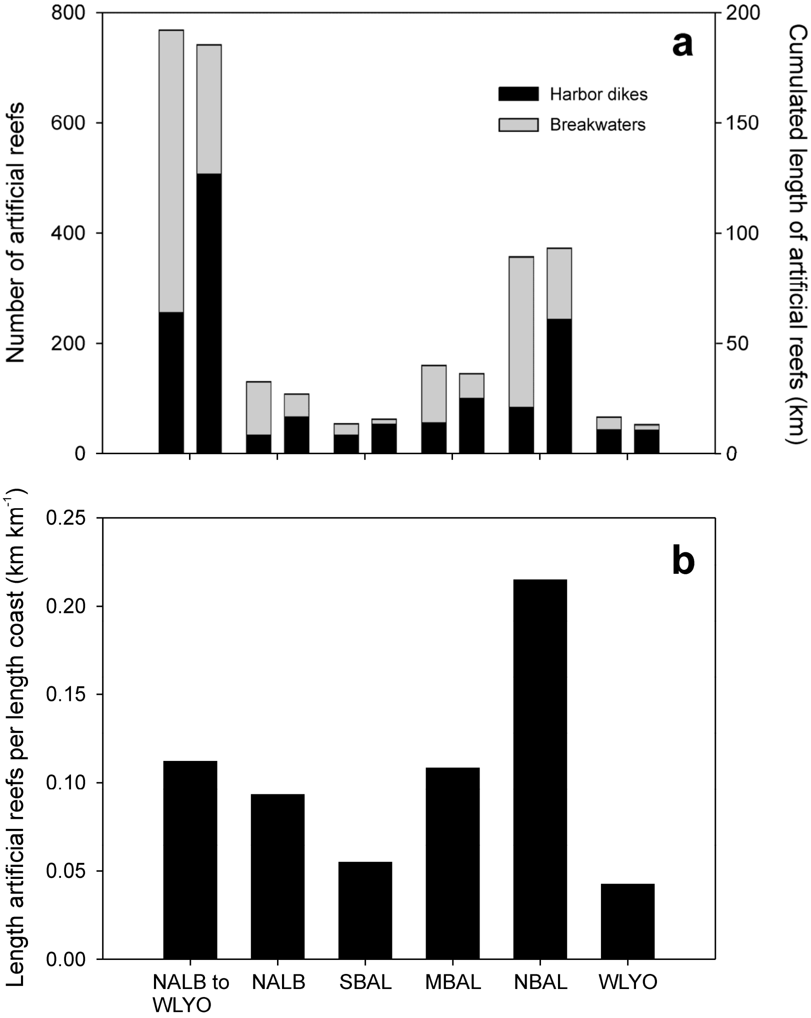
		% Partial mortality		Severity of old partial mortality (%)			
Zone-Location	n	Recent	Old	0-10%	11-40%	41-70%	71-100%
NALB-1	38	0.0 ± 0.0	54.0 ± 4.5	13.2	15.8	31.6	39.5
NALB-2	25	0.6 ± 0.4	13.2 ± 2.7	68.0	28.0	4.0	0.0
NALB-3	47	0.6 ± 0.3	33.2 ± 4.2	29.8	38.3	17.0	14.9
NALB-4	36	0.7 ± 0.5	12.9 ± 3.0	72.2	22.2	5.6	0.0
SBAL-1	93	2.1 ± 0.7	22.2 ± 2.5	49.5	33.3	11.8	5.4
SBAL-2	167	0.6 ± 0.2	13.1 ± 1.5	67.7	24.0	7.2	1.2
SBAL-3	84	1.0 ± 0.4	21.0 ± 2.7	52.4	31.0	9.5	7.1
SBAL-4	33	5.8 ± 2.3	5.0 ± 1.6	90.9	6.1	3.0	0.0
SBAL-5	50	2.2 ± 0.8	12.8 ± 2.3	72.0	24.0	4.0	0.0
SBAL-6	100	0.8 ± 0.3	6.6 ± 1.0	86.0	12.0	2.0	0.0
SBAL-7	25	4.8 ± 2.2	5.1 ± 2.0	88.0	12.0	0.0	0.0
SBAL-8	129	3.2 ± 1.3	11.7 ± 1.3	67.4	29.5	2.3	0.8
SBAL-9	53	5.9 ± 2.1	18.4 ± 3.1	54.7	32.1	9.4	3.8
SBAL-10	97	2.2 ± 0.6	12.3 ± 1.6	69.1	25.8	4.1	1.0
SBAL-11	144	2.3 ± 0.7	7.4 ± 1.0	81.3	16.7	1.4	0.7
SBAL-12	318	0.5 ± 0.2	3.0 ± 0.6	93.7	4.4	1.6	0.3
SBAL-13	589	2.0 ± 0.4	7.2 ± 0.6	83.5	12.6	3.2	0.7
SBAL-14	68	0.4 ± 0.2	5.9 ± 1.2	83.8	14.7	1.5	0.0
SBAL-15	119	0.1 ± 0.1	9.0 ± 1.2	76.5	20.2	3.4	0.0
SBAL-16	70	0.4 ± 0.2	11.3 ± 1.8	70.0	25.7	2.9	1.4
SBAL-17	115	0.5 ± 0.4	19.4 ± 1.9	53.0	33.0	13.0	0.9
SBAL-18	125	0.4 ± 0.1	10.9 ± 1.3	70.4	24.0	5.6	0.0
SBAL-19	86	0.2 ± 0.1	8.0 ± 1.4	80.2	16.3	3.5	0.0
SBAL-20	104	0.2 ± 0.1	1.8 ± 0.6	94.2	5.8	0.0	0.0
SBAL-21	416	0.3 ± 0.1	9.3 ± 0.7	75.5	20.9	3.4	0.2
SBAL-22	320	0.2 ± 0.1	16.5 ± 0.9	51.3	42.8	5.3	0.6
SBAL-23	47	0.2 ± 0.1	3.8 ± 0.8	95.7	4.3	0.0	0.0
SBAL-24	247	2.1 ± 0.5	16.4 ± 1.4	59.9	27.9	8.9	3.2
SBAL-25	140	2.7 ± 0.6	10.3 ± 1.3	73.6	22.9	1.4	2.1
SBAL-26	206	2.6 ± 0.6	9.1 ± 1.0	75.2	21.8	1.9	1.0
SBAL-27	231	0.9 ± 0.5	14.5 ± 1.6	70.6	14.7	9.5	5.2
MBAL-1	28	1.1 ± 0.8	16.3 ± 4.8	60.7	25.0	3.6	10.7
MBAL-2	66	2.5 ± 0.9	7.7 ± 1.6	80.3	16.7	3.0	0.0
MBAL-3	74	1.1 ± 0.3	30.5 ± 2.8	35.1	37.8	20.3	6.8
MBAL-4	27	0.7 ± 0.7	18.4 ± 4.4	63.0	22.2	11.1	3.7
MBAL-5	59	0.9 ± 0.4	30.6 ± 3.7	33.9	40.7	15.3	10.2
MBAL-6	38	1.8 ± 0.9	32.6 ± 4.7	28.9	42.1	15.8	13.2
NBAL-1	186	1.2 ± 0.6	33.2 ± 2.3	38.7	24.7	22.0	14.5
NBAL-2	156	0.8 ± 0.4	32.4 ± 2.5	41.0	25.6	19.2	14.1
NBAL-3	341	0.2 ± 0.1	24.4 ± 1.5	51.0	22.6	18.2	8.2
NBAL-4	29	0.8 ± 0.7	11.7 ± 3.4	72.4	20.7	3.4	3.4
NBAL-5	79	1.0 ± 0.4	9.4 ± 1.7	79.7	15.2	3.8	1.3
NBAL-6	28	0.6 ± 0.3	8.5 ± 3.0	78.6	17.9	0.0	3.6
WLYO-1	35	0.5 ± 0.2	18.0 ± 3.4	54.3	31.4	14.3	0.0

SM 4.5.8 Colony size-structure descriptors for *Oculina patagonica* at studied natural locations within the five zones distinguished along the whole Mediterranean Iberian coast (NALB to WLYO).

Data correspond to the locations (or group of neighboring locations) with >25 measured colonies (n = 44). *n*: number of measured colonies; *Mean size*: mean of the surface area of the colonies; *Min-Max*: minimum and maximum sizes; *% <100 cm^2*: proportion of colonies <100 cm^2 in size; *P90th-size*: percentile 90th colony-size; g_1: skewness and g_2: kurtosis; *SE*: standard error. Significant statistical values are highlighted in bold.

		Non-transformed data								Ln-transformed data			
Zone-Location	N	Mean size (cm^2)	Min-Max (cm^2)	% <100 cm^2	P90th (cm^2)	g_1 ± SE	g_1 SE^{-1}	g_2 ± SE	g_2 SE^{-1}	g_1 ± SE	g_1 SE^{-1}	g_2 ± SE	g_2 SE^{-1}
NALB-1	38	492 ± 123	12.6–4185	21	1046	3.7 ± 0.4	**9.6**	15.7 ± 0.7	**20.9**	0.0 ± 0.4	0.1	0.2 ± 0.7	0.3
NALB-2	25	748 ± 133	70.9–2419	4	1698	1.2 ± 0.5	**2.6**	0.4 ± 0.9	0.4	0.0 ± 0.5	0.0	-0.6 ± 0.9	-0.7
NALB-3	47	654 ± 101	33.2–2827	13	1886	1.6 ± 0.3	**4.8**	2.1 ± 0.7	**3.1**	-0.2 ± 0.3	-0.6	-0.6 ± 0.7	-0.8
NALB-4	36	265 ±52	15.9–1419	42	638	2.3 ± 0.4	**6.0**	5.9 ± 0.8	**7.7**	0.1 ± 0.4	0.2	-0.3 ± 0.8	-0.4
SBAL-1	93	311 ± 31	4.9–1385	26	707	1.5 ± 0.3	**6.0**	2.3 ± 0.5	**4.7**	-0.7 ± 0.3	**-3.0**	0.2 ± 0.5	0.4
SBAL-2	167	292 ±26	0.4–1847	35	755	2.0 ± 0.2	**10.9**	5.1 ± 0.4	**13.7**	-0.8 ± 0.2	**-4.5**	0.5 ± 0.4	1.3
SBAL-3	84	274 ± 30	7.1–1419	32	552	1.8 ± 0.3	**7.0**	4.2 ± 0.5	**8.1**	-0.5 ± 0.3	-1.9	-0.2 ± 0.5	-0.4
SBAL-4	33	262 ±39	26.0–908	15	616	1.5 ± 0.4	**3.7**	1.8 ± 0.8	**2.2**	-0.4 ± 0.4	-1.0	0.0 ± 0.8	0.1
SBAL-5	50	341 ±41	15.9–1164	28	698	1.2 ± 0.3	**3.6**	1.3 ± 0.7	**2.0**	-0.5 ± 0.3	-1.6	-0.5 ± 0.7	-0.8
SBAL-6	100	498 ±48	12.6–2734	13	1257	1.9 ± 0.2	**7.8**	4.4 ± 0.5	**9.2**	-0.7 ± 0.2	**-2.7**	0.5 ± 0.5	1.0
SBAL-7	25	361 ±77	12.6–1486	24	990	1.6 ± 0.5	**3.6**	2.2 ± 0.9	**2.5**	-0.4 ± 0.5	-0.8	-0.5 ± 0.9	-0.5
SBAL-8	129	458 ±141	0.8–18146	29	707	10.7 ± 0.2	**50.0**	118.1 ± 0.4	**278.9**	-0.4 ± 0.2	-1.8	1.8 ± 0.4	**4.3**
SBAL-9	53	191 ± 46	0.4–2165	57	491	4.3 ± 0.3	**13.2**	22.7 ± 0.6	**35.2**	-0.1 ± 0.3	-0.4	1.3 ± 0.6	**2.0**
SBAL-10	97	306 ± 27	7.1–1419	20	638	1.7 ± 0.2	**6.9**	3.6 ± 0.5	**7.5**	-0.9 ± 0.2	**-3.8**	1.0 ± 0.5	**2.1**
SBAL-11	144	615 ±51	0.8–2875	15	1521	1.6 ± 0.2	**8.1**	2.5 ± 0.4	**6.2**	-1.4 ± 0.2	**-7.1**	2.8 ± 0.4	**7.0**
SBAL-12	318	209 ±16	0.1–2333	51	552	2.9 ± 0.1	**20.9**	12.8 ± 0.3	**46.8**	-0.7 ± 0.1	**-5.0**	0.0 ± 0.3	-0.1
SBAL-13	589	278 ±24	0.1–8413	39	594	9.6 ± 0.1	**94.9**	118.8 ± 0.2	**591.0**	-0.5 ± 0.1	**-4.6**	0.7 ± 0.2	**3.6**
SBAL-14	68	352 ±56	1.8–3526	24	755	5.0 ± 0.3	**17.4**	33.5 ± 0.6	**58.4**	-1.0 ± 0.3	**-3.5**	2.1 ± 0.6	**3.7**
SBAL-15	119	528 ±51	4.9–4359	13	1164	3.3 ± 0.2	**15.1**	18.2 ± 0.4	**41.4**	-0.9 ± 0.2	**-4.0**	1.1 ± 0.4	**2.5**
SBAL-16	70	185 ±34	3.1–2248	44	346	5.7 ± 0.3	**19.8**	39.9 ± 0.6	**70.5**	-0.5 ± 0.3	-1.6	0.2 ± 0.6	0.3
SBAL-17	115	222 ±43	0.4–3904	52	531	5.5 ± 0.2	**24.3**	37.5 ± 0.4	**83.8**	-0.3 ± 0.2	-1.2	0.1 ± 0.4	0.2
SBAL-18	125	162 ±18	0.8–1288	51	346	3.3 ± 0.2	**15.0**	14.2 ± 0.4	**33.0**	-0.5 ± 0.2	**-2.4**	0.4 ± 0.4	0.9
SBAL-19	86	296 ±38	4.9–2248	35	661	2.7 ± 0.3	**10.5**	10.8 ± 0.5	**21.0**	-0.4 ± 0.3	-1.5	-0.3 ± 0.5	-0.6
SBAL-20	104	439 ±58	4.9–3370	27	962	2.7 ± 0.2	**11.5**	8.3 ± 0.5	**17.7**	-0.3 ± 0.2	-1.3	-0.1 ± 0.5	-0.3
SBAL-21	416	424 ±34	1.8–9076	38	1134	5.7 ± 0.1	**48.0**	57.5 ± 0.2	**240.7**	-0.3 ± 0.1	**-2.5**	-0.6 ± 0.2	**-2.4**
SBAL-22	320	154 ±17	0.8–3167	65	389	5.1 ± 0.1	**37.1**	37.3 ± 0.3	**137.3**	0.0 ± 0.1	0.0	-0.5 ± 0.3	-1.9
SBAL-23	47	586 ±126	12.6–4902	19	1320	3.2 ± 0.3	**9.3**	13.4 ± 0.7	**19.7**	0.1 ± 0.3	0.3	-0.3 ± 0.7	-0.5
SBAL-24	247	515 ±43	0.8–4243	24	1385	2.5 ± 0.2	**16.2**	7.5 ± 0.3	**24.3**	-0.7 ± 0.2	**-4.6**	1.1 ± 0.3	**3.6**
SBAL-25	140	705 ±100	0.8–9940	18	1257	5.7 ± 0.2	**27.8**	39.1 ± 0.4	**96.2**	-0.9 ± 0.2	**-4.5**	1.8 ± 0.4	**4.4**
SBAL-26	206	747 ±75	0.8–6720	17	1698	2.9 ± 0.2	**16.9**	9.4 ± 0.3	**28.0**	-0.4 ± 0.2	**-2.6**	0.4 ± 0.3	1.3
SBAL-27	231	258 ±25	0.2–3318	35	594	4.8 ± 0.2	**30.0**	30.9 ± 0.3	**96.9**	-0.6 ± 0.2	**-4.0**	0.7 ± 0.3	**2.1**
MBAL-1	28	39 ±7	0.8–154	93	87	1.4 ± 0.4	**3.1**	2.0 ± 0.9	**2.3**	-0.6 ± 0.4	-1.3	-0.5 ± 0.9	-0.6
MBAL-2	66	98 ±16	0.8–683	70	227	2.3 ± 0.3	**7.8**	6.1 ± 0.6	**10.4**	-0.1 ± 0.3	-0.3	-0.7 ± 0.6	-1.2
MBAL-3	74	300 ±33	23.8–1353	20	638	1.9 ± 0.3	**6.7**	3.5 ± 0.6	**6.3**	0.0 ± 0.3	0.1	-0.4 ± 0.6	-0.8
MBAL-4	27	95 ±24	3.1–616	67	189	3.1 ± 0.4	**6.8**	11.7 ± 0.9	**13.4**	-0.2 ± 0.4	-0.4	-0.2 ± 0.9	-0.2
MBAL-5	59	210 ±31	0.8–1134	53	531	1.8 ± 0.3	**5.9**	3.7 ± 0.6	**6.0**	-0.6 ± 0.3	-1.8	0.3 ± 0.6	0.6
MBAL-6	38	85 ±12	9.6–363	76	154	2.1 ± 0.4	**5.4**	5.5 ± 0.7	**7.4**	-0.4 ± 0.4	-1.1	0.2 ± 0.7	0.2
NBAL-1	186	143 ±16	0.8–1521	66	398	3.2 ± 0.2	**17.7**	13.1 ± 0.4	**36.9**	-0.2 ± 0.2	-1.1	-0.5 ± 0.4	-1.3
NBAL-2	156	471 ±44	0.8–2875	34	1288	1.5 ± 0.2	**7.6**	2.1 ±0.4	**5.5**	-0.8 ± 0.2	**-3.9**	-0.4 ± 0.4	-0.9
NBAL-3	341	191 ±19	0.8–2734	65	594	3.3 ± 0.1	**24.8**	13.6 ±0.3	**51.6**	0.1 ± 0.1	0.7	-1.0 ± 0.3	**-3.7**
NBAL-4	29	383 ± 86	3.1–1924	28	1225	1.9 ± 0.4	**4.4**	3.5 ±0.8	**4.2**	-0.7 ± 0.4	-1.5	1.0 ± 0.8	1.1
NBAL-5	79	598 ± 87	28.3–3848	22	1644	2.3 ± 0.3	**8.4**	5.5 ±0.5	**10.3**	0.1 ± 0.3	0.3	-0.8 ± 0.5	-1.6
NBAL-6	28	356 ± 116	0.8–2688	54	1353	2.7 ± 0.4	**6.0**	7.5 ±0.9	**8.7**	-0.2 ± 0.4	-0.4	0.2 ± 0.9	0.2
WLYO-1	35	438 ± 63	15.9–1164	31	908	0.5 ± 0.4	1.1	-1.2 ±0.8	-1.6	-0.5 ± 0.4	-1.3	-1.0 ± 0.8	-1.3

SM 4.5.9 Man-made coastal structures (i.e., artificial reefs) within the five zones distinguished along the whole Mediterranean Iberian coast (NALB to WLYO). a Number (*left*) and cumulated length (*right*) of artificial reefs, distinguishing between the dikes of harbors and breakwaters. **b** Length of artificial reefs per length of coast. Length values were measured using Google Earth images between 2003 and 2004 at a scale of 1:1,000.



SM 4.5.10 Pearson product moment correlation (r^2) between the live cover of *Oculina patagonica* at sutudied natural locations and the distance between natural locations and the nearest artificial reef. Data correspond to surveyed natural locations along the whole Mediterranean Iberian coast (NALB to WLYO, n = 233). Correlations are given separately for each zone, and for all possible combinations of groups of neighboring zones. *n*: number of locations within each group. The minimum length of artificial reefs used for estimates of the distance between natural locations and the nearest artificial reef was >500 m (mean of 1.16 ± 0.14 km, n = 47). Distance and length values were measured using Google Earth images between 2003 and 2004 at a scale of 1:1,000. The distance between natural locations and the nearest artificial reef correspond to the linear distance through the sea. Significant statistical values are highlighted in bold.

Zone (or group of neighboring zones)	N	b	r^2	p-value
NALB	14	0.00	0.00	0.94
SBAL	34	+0.15	0.05	0.22
MBAL	12	0.00	0.00	0.89
NBAL	36	-0.06	0.04	0.27
WLYO	137	0.00	0.01	0.17
NALB+SBAL	48	+0.16	0.06	0.10
SBAL+MBAL	46	**+0.21**	**0.09**	**0.0374**
MBAL+NBAL	48	-0.03	0.02	0.34
NBAL+WLYO	173	-0.01	0.01	0.16
NALB+SBAL+MBAL	60	**+0.19**	**0.08**	**0.0265**
SBAL+MBAL+NBAL	82	**+0.26**	**0.18**	**<0.0001**
MBAL+NBAL+WLYO	185	-0.01	0.01	0.17
NALB+SBAL+MBAL+NBAL	96	**+0.21**	**0.14**	**0.0002**
SBAL+MBAL+NBAL+WLYO	219	**+0.07**	**0.04**	**0.0037**
NALB+SBAL+MBAL+NBAL+WLYO	233	**+0.06**	**0.04**	**0.0040**

SM 4.5.11 Benthic community composition and sea urchin wet-weight biomass (*Paracentrotus lividus* and *Arbacia lixula*) at studied natural locations within the five zones distinguished along the whole Mediterranean Iberian coast (NALB to WLYO). Data correspond to the studied locations with coral populations (i.e., >0.05 colonies m^{-2}, n = 38). Four large categories were distinguished: *erect algae* (i.e., crowded algae with a canopy height of >1 cm), *turf algae* (i.e., sparse algae with a canopy height of <1 cm), crustose coralline algae and bare rock (*CCA-bare rock*) and *sessile invertebrates* (e.g., sponges, bryozoans and tunicates). *Open space availability* corresponds to the sum of turf algae and CCA-bare rock.

Zone	Sea urchins wet weight biomass (g m^{-2})	Benthic composition (%)				
		Erect algae	Turf algae	CCA-Bare rock	Sessile Invertebrates	Open space availability
NALB-1	7.2	62	26	10	1	36
NALB-2	47.2	82	15	2	1	17
SBAL-1	6.8	58	24	16	3	40
SBAL-2	26.2	66	19	14	1	34
SBAL-3	148.0	62	20	13	5	33
SBAL-4	9.5	56	22	18	3	40
SBAL-5	310.5	60	29	7	4	36
SBAL-6	105.2	60	25	11	4	36
SBAL-7	499.8	75	14	4	6	19
SBAL-8	586.8	69	23	7	1	30
SBAL-9	140.5	66	25	4	4	30
SBAL-10	6.0	30	63	4	3	68
SBAL-11	157.6	65	26	2	6	29
SBAL-12	50.6	80	13	5	2	19
SBAL-13	54.5	75	8	12	4	20
SBAL-14	132.3	72	10	13	5	23
SBAL-15	424.1	77	9	10	4	19
SBAL-16	173.8	94	3	1	2	3
SBAL-17	74.5	92	3	2	3	6
SBAL-18	274.2	81	11	6	3	17
SBAL-19	163.3	55	35	4	6	39
SBAL-20	321.0	72	16	12	1	28
SBAL-21	438.2	45	26	27	2	53
SBAL-22	431.7	73	5	18	3	24
SBAL-23	287.9	76	7	13	4	20
MBAL-1	61.6	20	74	4	2	78
MBAL-2	61.2	73	16	8	3	24
MBAL-3	106.2	75	15	6	4	20
MBAL-4	106.0	81	13	3	4	16
MBAL-5	8,2	85	11	3	1	15
NBAL-1	81.0	93	3	3	0	6
NBAL-2	50.9	74	24	1	1	25
NBAL-3	45.2	30	61	1	8	62
NBAL-4	56.9	63	32	4	1	36
WLYO-1	55.4	42	29	23	6	52
WLYO-2	197.2	15	38	42	5	80
WLYO-3	74.8	35	34	21	10	56
WLYO-4	82.9	32	32	30	7	62

SM 4.5.12 Historical and current demographics of *Oculina patagonica* in the Mediterranean Sea. Data is given separately for each recorded region with the species, ordered in an anti-clockwise gyre starting in the Ligurian Sea. *Year first*: year of first record. *Max. diam.*: colony maximum mean diameter. *Year max. diam*: year of record of maximum colony diameter. *Establishment period:* approximate estimate of the time period of establishment based on maximum colony diameter and year of record, and mean linear extension rates documented in previous field studies (i.e., 1-2 cm in diameter yr^{-1}; Fine et al. 2001; Rubio-Portillo et al. 2014b; Chapter 4.4).

Region	Depth (m)	Year first	Max. diam.	Year Max. diam.	Establishment period	References
Ligurian Sea	0.5-5	1966	135 cm	1966	1831-1898	Zibrowius 1974
Gulf of Lyons	0-15	2000	60 cm	2010	1950-1980	Chapter 4.3; This study
North-Balearic Sea	0-28	1992	70 cm	2011	1941-1976	Chapter 4.3; This study
Mid-Balearic Sea	0-15	1972	50 cm	2010	1910-1960	Zibrowius and Ramos 1983; Rubio-Portillo et al. 2014a; This study
Balearic Islands	0.5-15	1995	85 cm	2009	1924-1966	Ballesteros 1998; authors' unpubl. data
South-Balearic Sea	0-15	1975	152 cm	2011	1859-1935	Zibrowius and Ramos 1983; This study
Alborán Sea	0-15	2006	73 cm	2011	1938-1974	Templado et al. 2006; This study
Algerian and Tunissian waters	0.5-4	2006	38 cm	2008	1932-1970	Sartoretto et al. 2008
Levant Sea	0-10	1981	150 cm	2005	1855-1930	Çinar et al. 2006; Sartoretto et al. 2008; Bitar and Zibrowius 1997
Aegean Sea	0.5-11	2005	no data			Salomidi et al. 2013
Adriatic Sea	3	2011	16 cm	2011	1995-2003	Cvitković et al. 2013

4.6. Synthesis of Results

Synthesis of Results

The main results that arise from the manuscripts of this **PhD Thesis** are described below:

- **Chapter 1. A phase shift from macroalgal to coral dominance in the Mediterranean**

- The zooxanthellate coral *Oculina patagonica* was the dominant species at shallow-water rocky reefs (~0–3 m depth) from Torre Pirulico in the South-Balearic Sea in 2009, with a mean density of 24 colonies m^{-2} and a mean cover of 55% of the 750 m^{2} study area.
- The colonies of *O. patagonica* ranged from 0.07 to 3,578 cm^{2} in surface area, and the colony size-frequency distribution was positively skewed, with 37% of colonies with <100 cm^{2} in surface area.
- Other components of the benthic community included sparse turf algae <1 cm in height (37%), erect algae (7%) and sponges (1%).
- Sea urchins were absent and physical disturbance from sand scouring was the main source of open space (i.e., algal-depleted rocky reefs) for *O. patagonica* to colonize.

- **Chapter 2. Sea urchins predation facilitates coral invasion in a marine reserve**

- Over the ~8-yr study period (2002–2010) at the marine reserve of Cabo de Palos-Islas Hormigas in the South-Balearic Sea, the density of *O. patagonica* populations increased at a rate of 0.09–0.18 colonies m^{-2} and the cover at a rate of 0.9–1.4% yr^{-1}, a consistent pattern documented in the two annually studied locations (La Hormiga and El Hormigón).
- The mean colony size of *O. patagonica* and the coefficient of variation (SD/mean) did not vary over time, and the colony size-frequency distributions were positively skewed over time, with a prevalence of small size classes at both locations (17–36% of colonies were <100 cm^{2} in surface area). The colony size-frequency distributions were leptokurtic, which indicated that the increase in coral abundance was a rather recent process at both studied locations.
- The mean density of sea urchins increased over time (from ~2–3 individuals m^{-2} in 2003–2005 to ~4–7 individuals m^{-2} in 2007–2010), a pattern mainly driven by a high recruitment of *Paracentrotus lividus* occurring in 2006–2007; and there was a sustained increase in the mean size of individuals and biomass of *P. lividus*, a consistent pattern at both studied locations.
- The increase in density and cover of *O. patagonica* over the study period at the two locations was strongly correlated with the increase in density and biomass of sea urchins.

- The increase in density and cover of *O. patagonica* documented in the two annually studied locations over 2002–2010 was similar to that documented in two additional locations from the marine reserve (Bajo de Dentro and Bajo de Fuera) examined in 2002 and 2010, also the increase in density of sea urchins. Thus, there was a local-scale pattern of increase in the abundance of *O. patagonica* and sea urchins in shallow-water rocky reefs (~6 m depth) at four nearby islands and pinnacles, disconnected by >50 m deep channels and separated in space by ~4 km.
- The open space for *O. patagonica* to colonize (i.e., rocky reefs with encrusting coralline algae and barren grounds) was a common feature at La Hormiga and El Hormigón, with a mean cover of 16% and a mean size of 0.8 m^2 in 2010, and did not differ between both locations. The number of open spaces associated with small colonies of *O. patagonica* (<100 cm^2 in surface area) did not differ between the two locations or over time (four sampling occasions: 2005, 2006, 2007 and 2010). The mean observed proportion of small coral colonies associated with open spaces over time was 68% larger than that expected according to random distribution.

- **Chapter 3. Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean**

- Over the 19-yr study period (1992–2010) at the north-eastern Iberian coast, the coral *O. patagonica* experienced a northward distributional range shift along ~361 km of coastline at a mean rate of 22 km yr^{-1}, based on the annual/biannual monitoring of 223 locations (i.e., natural and artificial reefs) regularly distributed along the ~400 km studied coast. The coral spread underwent some long-distance dispersal events ranging between 76 and 182 km that created new proliferation foci.
- The occurrence of *O. patagonica* increased from being present in one location in 1992 to occur on 19% of the locations in 2010 (i.e., 43 of the 223 explored locations), at a rate of ~1% yr^{-1}. The species did not disappear from any of the locations where it has been recorded over 1992–2010.
- The spread curve of *O. patagonica* over 1992–2010 (i.e., the cumulated number of locations with the species) exhibited a lag phase of 9-yr followed by an exponential growth phase. The number of locations at which the species was present at the end of the lag phase was low (4%), indicating that the exponential phase began short after the species established some foci in a particular area.
- After the lag phase, the mean square displacement between the locations at which *O. patagonica* was present over time showed a scaling exponent of ~2, indicating an acceleration of spreading over time mainly driven by a few intermittent long-distance dispersal events. Within the southernmost 150 km of the studied coastline, where the species was already recorded in 1993, the mean square displacement after the lag phase showed a scaling exponent of ~0.4, indicating a declining of spreading over time at local scales.

- The pattern of the spread curves of *O. patagonica* diverged between artificial and natural locations, with a half-reduced duration of the lag phase and a 56% higher slope for the exponential phase in the former. Between 2001 and 2006, the slope of the exponential phase for the overall spread curve was reduced because the natural locations were still in the lag phase.
- In 2010, the occurrence, abundance and maximum colony size of *O. patagonica* showed a concomitant pattern of decrease from south to north along the studied coast. Significant coral populations (i.e., >0.05 colonies m^{-2}) were recorded in five locations from the southernmost area, whereas at all other locations the species occurred at densities <0.05 colonies m^{-2}.
- In 2010, the occurrence of *O. patagonica* was recorded in 44% of the explored artificial locations and only in 11% of the natural locations. In artificial locations, the proportion of locations where the species was recorded decreased steadily from 94% in the southernmost 100 km coastal length to 11% in the northernmost 100 km coast, while in natural habitats decreased steadily from 38 to 2%. The occurrence of significant coral populations, and their coral density and cover, were at least 2-fold higher in artificial than in natural locations. The 80% of total number of colonies was recorded in the artificial locations, while only 20% was recorded in the natural locations (mean of 22 and 7 colonies per location, respectively).
- The mean annual thermal regime of seawater over 2003–2010 along the ~400 km studied coastline characterized by a northward latitudinal decrease in mean seawater temperature (ST; from 18.7 to 16.7ºC), in percentile 95th-ST (from 26.8 to 23.2ºC, at a rate of -0.9ºC for each 100 km north), and in percentile 5th-ST (from 12.4 to 11.3ºC, at -0.26ºC for each 100 km north; excluding the value of 11.7ºC from the southernmost 50 km coastal length, subjected to particular local conditions such as discharge from Ebro River and shallow coastal waters). The number of days on which the ST was >18ºC (i.e., a ST indicator of warm conditions that enhance *O. patagonica* growth), and >24ºC and 26ºC (i.e., indicators of high-ST conditions that have been documented to cause coral colony damage after a certain period of exposure) also exhibited a decreasing latitudinal pattern from south to north (at 12, 22 and 7 d yr^{-1} for each 100 km in coastal length, respectively).

- **Chapter 4. Recurrent partial mortality events in winter shape the dynamics of the zooxanthellate coral *Oculina patagonica* at high latitude in the Mediterranean**

- The mean annual photosynthetically active radiation at 5 m depth (PAR-5m) at L'Ampolla (41ºN, North-Balearic Sea) over 2009–2011 was 19.5 mol photons m^{-2} d^{-1}, and characterized by a high-radiation period from April to September (27.3 mol photons m^{-2} d^{-1}) and a low-radiation period from October to March (12.1 mol photons m^{-2} d^{-1}). The mean annual seawater temperature at 5 m depth (ST-5m) was 18.5ºC, and characterized by a low-ST period from December to April (13.5ºC) with a warming shift in May (18.1ºC), and a high-ST period from June to October (23.6ºC) with a cooling shift in November (17.4ºC). The light and thermal regimes exhibited similar seasonal trends but with a time delay (i.e., the maximum correlations were between the ST and the PAR measured 1–2 months earlier).

- Each year throughout the four annual cycles examined (2008–2012; at an average sampling interval of 87 d), the 29 colonies of *O. patagonica* transplanted onto plates (i.e., excluded from space competition) at 5 m depth in L'Ampolla exhibited a strong seasonal cycle that includes partial mortality and cessation of linear extension during winter (December to April), tissue regeneration starting in late spring (May) and linear extension during summer and fall (June to November).

- During the low-ST periods (December to April), the mean partial mortality rate of *O. patagonica* colonies was 0.32% d^{-1} (equivalent to 10.0 mm^2 d^{-1}). The April peak in colony partial mortality affected a mean of 70% of the colonies with 49% of affected surface area. The mean partial mortality rate during the period of lesion regeneration (May to July) was -0.35% d^{-1} (equivalent to -10.3 mm^2 d^{-1}). After this rapid recovery phase, tissue regeneration of the remaining areas with partial mortality continued at a slower pace from August to November (-0.05% d^{-1}), leading to the lowest values of colony partial mortality in November (<8%).

- The colony partial mortality of *O. patagonica* during low-ST periods resulted from the dissociation of polyps from their connective coenosarc (i.e., loss of coloniality, termed as 'Dalmatian mortality pattern').

- The mean size of *O. patagonica* colonies increased from 10 to 60 cm^2 over 2008–2012, at a mean linear extension rate of 13.27 cm^2 yr^{-1} (equivalent to 1.3 cm diameter yr^{-1}), and a maximum value of an individual colony of 2.5 cm diameter yr^{-1}.

- During the ~4-yr study period, the mean linear extension rate of *O. patagonica* colonies reached a minimum from December to May (0.0016 cm diameter d^{-1}, concomitant with the low-ST periods and the occurrence of partial mortality). Colony linear extension resumed in June following the rapid tissue regeneration that started in May, and reached a maximum from June to November (0.0058 cm diameter d^{-1})

- The partial mortality rate of *O. patagonica* colonies was negatively correlated with ST-5m but not with PAR-5m. The proportion of colony partial mortality and ST exhibited opposite trends but with a time delay (i.e., the maximum correlations were between the partial mortality and the ST measured 2–3 months earlier), indicating that the April peak in partial mortality was related to the lowest STs of January-February. The partial mortality rate and ST exhibited opposite trends with no time delay, with positive mortality rates related to the <14ºC ST-threshold that occurred from December to April.

- The linear extension rate of *O. patagonica* colonies was positively correlated with ST-5m but not with PAR-5m. The linear extension rate and ST exhibited similar trends with no time delay, with higher linear extension rates related to the >16ºC ST-threshold that occurred from May to November.

- The rates of linear extension and partial mortality of *O. patagonica* colonies exhibited opposite trends but with a time delay (i.e., the maximum correlations were between the linear extension rate and the partial mortality rate measured 1–2 months earlier), indicating that the high mortality rate from the previous 1–2 months negatively affected linear extension rate.

- The April peak in partial mortality of *O. patagonica* colonies over 2009–2012 was always associated with similarly low values of partial mortality in previous November (<8%), despite that mortality in 2009 (26%) was less severe than in 2010–2012 (48, 57 and 66%, respectively). The annual peak in partial mortality rate was also lower in 2009 (0.18% d^{-1}) than in 2010–2012 (0.54% d^{-1}). The mean annual linear extension rate of coral colonies was 2-fold higher in 2009 (1.9 cm diameter yr^{-1}) than in 2010 and 2011 (0.9–1 cm diameter yr^{-1}).

- The extent of partial mortality on *O. patagonica* colonies was lower during the less severe low-ST period of 2008–2009 (26% and 0 d <12ºC, respectively) than during the other three more severe low-ST periods (from 2009–2010 to 2011–2012; 48–66% and 15–29 d <12ºC). The annual peak in partial mortality rate during the period of lesion regeneration was similar among the studied years (-0.35% d^{-1}). As a result, the lower extent of partial mortality in 2009 resulted in resumption of growth in May and complete regeneration by June, but as the extent of partial mortality increased in 2010 and 2011, the regeneration time was longer and growth resumed later. During the high-ST periods, there was no episode of colony partial mortality or bleaching, and the high-ST period was more severe in 2009 (e.g., 90 d >24ºC and 22 d >27ºC) than in 2010 and 2011 (66-69 d >24ºC and 0 d >27ºC).

- **Chapter 5. Variation in demographics of the zooxanthellate coral *Oculina patagonica* along the Mediterranean Iberian coast in relation to environmental parameters**

- We provide a baseline quantitative assessment of the demographics of *O. patagonica* (i.e., occurrence, density, cover, and colony partial mortality and size-structure) by examining 233 locations (i.e., natural and artificial reefs) along ~1,300 km Mediterranean coast of the Iberian Peninsula (Alborán Sea, Balearic Sea and Gulf of Lyons).

- On natural locations within the Iberian coast there was a positive autocorrelation (i.e., contagious distribution) of living cover of *O. patagonica* at distance classes of <200 km, whereas random distribution dominated at larger spatial scales. The combination of analytical approaches (i.e., principal component analysis and an overlaying K-means partitional clustering of the locations) using coral abundance (i.e., density and living cover) and environmental parameters [annual mean surface ST, percentiles 90^{th}-ST and 10^{th}-ST, PAR at 3 m depth (PAR-3m) and chlorophyll-a] showed a consistent spatial pattern of five primary regimes (i.e., zones) along the whole Iberian coast that conforms to the general pattern of the 'abundant-center' hypothesis (i.e., a most abundant center that declines toward the edges of a geographic range). The combination of analytical approaches using the southern Iberian coast (96 locations, ~1,000 km) yielded similar results (i.e., four primary regimes), but coral abundance was not correlated with percentile 90^{th}-ST. The spatial grouping of the locations from the southern Iberian coast, based on coral colony partial mortality and size data (mean size, percentile 90^{th}-size, % colonies <100 cm^2, maximum size, and skewness and kurtosis coefficients) and environmental parameters, generally matched that obtained using coral abundance.

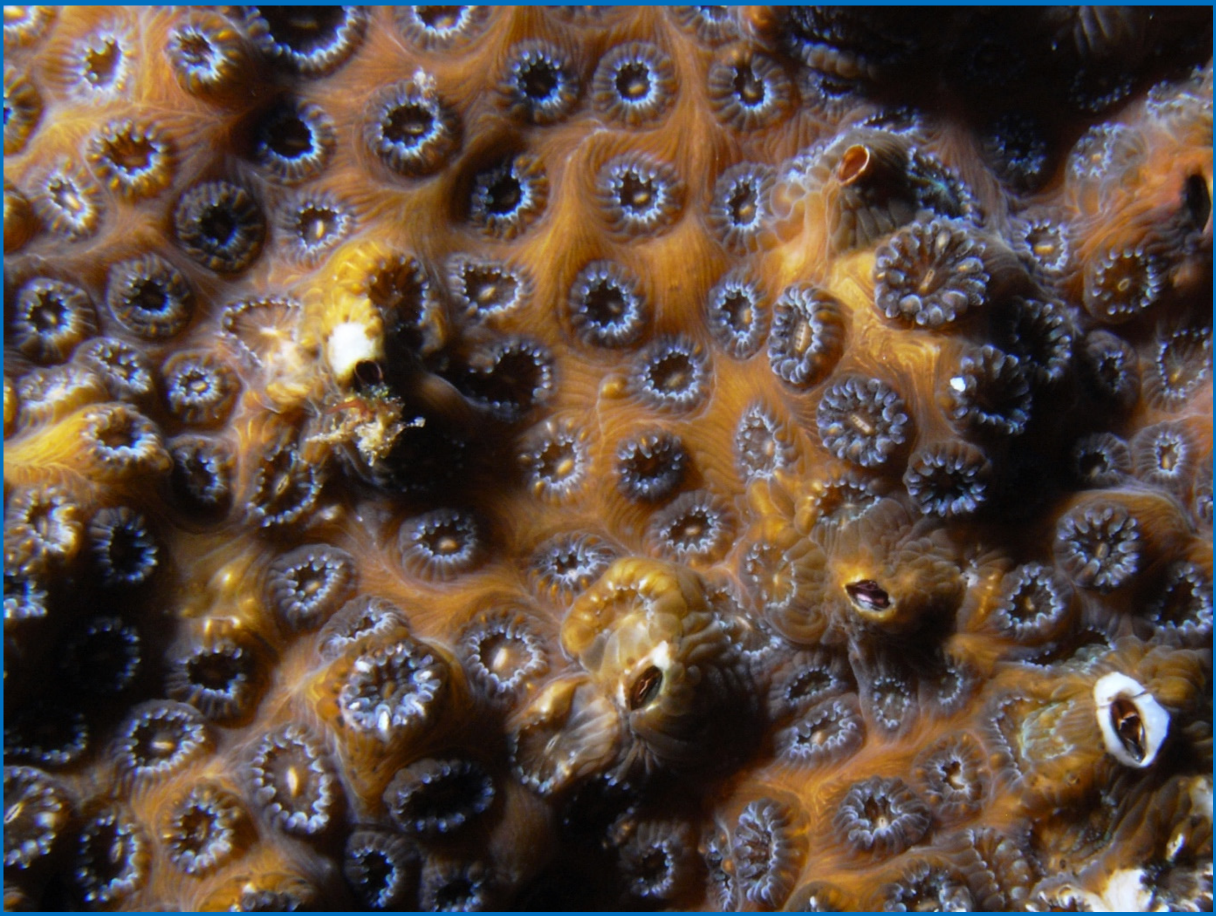
- The demographics of *O. patagonica* showed a similar pattern of variation among zones in which the zone from the south-eastern Iberian coast (South-Balearic Sea, SBAL) always displayed marked more successful values than those at the other zones (e.g., up to 6-fold higher mean liver cover, 3.4%, up to 13%). Abrupt changes in coral demographics and environmental parameters were observed either side of SBAL, with demographic success decreasing both north-eastward: Mid-Balearic Sea (MBAL), North-Balearic Sea (NBAL) and West-Gulf of Lyons (WLYO); and south-westward: North-Alboran Sea (NALB).

- The mean old partial mortality of *O. patagonica* colonies (i.e., overgrown by sessile organisms) ranged between 2 and 54% among studied coral populations (15%), with higher values at NALB, MBAL, NBAL and WLYO (18–28%) than that at SBAL (11%). The mean recent colony partial mortality (i.e., denuded skeleton) ranged between 0.5 and 1.6% among zones.

- The colony size-frequency distributions of *O. patagonica* populations within the southern Iberian coast (NALB to NBAL) were unimodal and displayed positive skewness and kurtosis, but not in the single studied population at WLYO. The mean colony size at MBAL was at least 61% lower than those at the other zones. The mean % colonies <100 cm^2 at MBAL was 29% higher than at NBAL and at least 50% higher than those at the other zones, and the percentile 90th-size at MBAL was at least 64% lower than those at the other zones. The ln-transformed colony size-frequency distributions, which increased the resolution among the small size classes, displayed negative skewness at the five zones, although the SBAL zone was the only one in which the skewness pattern was significant, and also the only displaying positive kurtosis.
- The living cover of *O. patagonica* (i.e., an integrating measure of population growth) was maximum at locations from SBAL, characterized by a high mean ST (>19–20ºC) and a narrow seasonal amplitude (percentiles 90th-ST >25–26ºC and 10th-ST >14–15ºC). Although mean ST was similarly high between SBAL and MBAL (>19–20ºC), the lower cover at MBAL was related to higher percentile 90th-ST and lower percentile 10th-ST (>26–27ºC and <14–13ºC, respectively). The living coral cover was also lower at the lower-ST zones (mean ST <19–17ºC), either characterized by a low percentile 90th-ST and high percentile 10th-ST at NALB (<25–22ºC and >14–15ºC, respectively), by high percentile 90th-ST and low percentile 10th-ST at NBAL (>25–27ºC and <13–12ºC) and by both low percentiles 90th-ST and 10th-ST at WLYO (<24–22ºC and <13–12ºC). The highest living coral cover at SBAL was related to maximum PAR-3m (>32 mol photons m^{-2} d^{-1}) and minimum chlorophyll-a (<0.4 g m^{-3}) values among the studied zones.
- The results on *O. patagonica* demographics showed that the coral 'abundant-center' pattern within the Iberian coast is not only related to the timing of establishment but points to the relevant role of differences in coral population growth that correlate with key environmental variables. The continuous distribution and large colony sizes (i.e., >50 cm in diameter) observed along the Iberian coast suggest that this species was widely established by ~1950s and thus, the observed zonal differences in coral population growth appear to have contributed to zonal differences in coral demographics as much or more than differences in arrival.

- The demographics of *O. patagonica* (mean density, total and living cover, maximum colony size, and skewness and kurtosis coefficients) within the studied natural locations in the whole Iberian coast were all positively correlated between them and correlated with environmental parameters (positively with mean ST, percentiles 10th-ST and 90th-ST, and PAR-3m, and negatively with chlorophyll-a). The correlations using the southern Iberian coast (NALB to NBAL) yielded similar results, but coral abundance (i.e., density, total and living coral cover), and skewness and kurtosis coefficients were not correlated with percentile 90th-ST. In all cases, the percentage of the variance in coral abundance explained by mean ST and PAR-3m (31–37%) was higher than that explained by chlorophyll-a (19–21%) and percentile 10th-ST (10–11%). The mean colony size and percentile 90th-size were negatively correlated with mean ST and percentile 90th-ST, and the % colonies <100 cm^2 was positively correlated with percentile 90th-ST and negatively correlated with percentile 10th-ST. The identified thresholds that limit the growth of *O. patagonica* colonies and populations on natural locations within the Iberian coast include annual mean PAR-3m <30 mol photons m^{-2} d^{-1}, mean ST <19ºC, percentile 10th-ST <14ºC and percentile 90th-ST <25ºC, but without severe high-ST periods (percentile 90th-ST >27ºC).
- Variation in the pattern of occurrence of *O. patagonica*, and in the occurrence of coral populations, was concomitant between natural and artificial locations within each zone of the Iberian coast. In artificial locations, the coral occurrence was higher than in natural locations within each zone (mean of 72% and 55%, respectively; NALB to WLYO), also the occurrence of coral populations (mean of 49% and 27%; NALB to NBAL).
- The abundance of artificial reefs at SBAL and WLYO (~0.05 km artificial reef km^{-1} coast) was at least 41% lower than those at NALB, MBAL and NBAL (0.09–0.21 km artificial reef km^{-1} coast). The living coral cover in natural locations was positively correlated with the distance (km) between natural locations and the nearest artificial reef.
- The benthic community assemblages in natural locations with *O. patagonica* populations (standardized to that of space without *O. patagonica*) within the Iberian coast were dominated by erect algae (mean cover of 64%), and the mean open space availability for *O. patagonica* to colonize (i.e., 33% cover of bare rock, encrusting coralline algae and sparse turf algae <1 cm in height) did not vary among zones from the southern Iberian coast (NALB to NBAL). The mean wet weight biomass of sea urchins was 154 g m^{-2}, with no differences among zones. The mean living coral cover was significantly correlated with mean sea urchin biomass, but was not correlated with mean open space availability, and the sea urchin biomass was not correlated with open space availability.

5. GENERAL DISCUSSION



Chapter 5

5. GENERAL DISCUSSION

5.1. Geographic distribution and demographics of *Oculina patagonica* in the Mediterranean Sea

In this **PhD Thesis**, we searched a total of 314 locations along ~1300 km of the Mediterranean Iberian coast for the occurrence of *Oculina patagonica*, and examined quantitative demographics of the species in the 121 locations where it was found (**Chapters 4.1**, **4.2**, **4.3**, **4.5**). Examination of the existing literature (peer-reviewed manuscripts, grey literature and authors' unpublished data) on which *O. patagonica* has previously been recorded within the Iberian coast and other Mediterranean regions (n = 279 additional locations, updated at July 2017) provides a framework about the current geographic distribution and some demographics aspects of *O. patagonica* across its whole distribution range (Table 5.1 and references therein; Fig. 5.1).

The global dataset compilation on reported locations with the presence of *O. patagonica* show that its current distribution range span from 6º50'W to 35º04'E in longitude, and 31º01'N to 44º20'N in latitude, including most biogeographic regions from both western and eastern Mediterranean basins: Balearic Sea, Gulf of Lyons, Ligurian Sea, Adriatic Sea, Aegean Sea, Levant Sea, Algerian and Tunissian waters and Alborán Sea; and adjacent eastern Atlantic coast (Table 5.1; Fig. 5.1). The maximum linear distance among locations in which *O. patagonica* has been recorded was ~4,000 km (i.e., from west to east), and the cumulated coastal length was ~2,331 km (i.e., the sum of distances of coast for each zone, estimated as the distance between the two most distant locations with the species within each zone; Table 5.1; Fig. 5.1). It seems plausible that the locations discovered up to the present, and compiled in this dataset, are not the only ones in the respective regions, and that the species may be already present in some other regions (e.g., in the unexplored Mediterranean African coast).

Table 5.1 Historical and current demographics of *Oculina patagonica* in the Mediterranean Sea. Based on available data in previously published records of the species in peer-reviewed manuscripts, grey literature, and from this **PhD Thesis** and authors' unpublished data (updated at July 2017). Data is given separately for each studied region (see Fig. 5.1). Data from regions studied in the present **PhD Thesis** is detailed separately to data obtained from the literature review on previous studies, and is highlighted in bold. *Depth*: bathymetric range of distribution in meters. *Year first*: year of first record and *N Loc.*: number of locations with the species. *Max. Diam. (year)*: maximum mean diameter and year of record. Establishment period: approximate estimate of the time period of establishment based on maximum mean diameter and year of record, and mean linear extension rates documented in previous field studies (i.e., 1-2 cm in diameter $year^{-1}$; Fine et al. 2001; Rubio-Portillo et al. 2014b; **Chapter 4.4**). *Year max.*: year in which maximum demographics have been recorded, and *N Cum. Loc.*: cumulated number of locations, and *Cum. coastal length*: cumulated coastal length (i.e., the sum of distances of coast for each zone, estimated as the distance between the two most distant locations with the species within each zone). Within each region, the sections of coast of >50 km in length without the species were not considered for the sum of distances, and the isolated locations along the coast were considered as 1 km in coastal length. Length values were measured using Google Earth images at a scale of 1:10,000. The pattern of distribution was classified in two categories: fragmented (i.e., <1 location with the species per 10 km coastal length) or continuous (i.e., ≥1 location with the species per 10 km coastal length). The coral abundance was classified in three categories based on the number of colonies commonly found per location: isolated (<10 colonies), tens of colonies (10-100 colonies), hundreds of colonies (>100 colonies). Note that for regions studied in this **PhD Thesis**, the total number of cumulated locations corresponds to the sum of our locations plus those recorded in previous studies, whereas the cumulated coastal length corresponds to the maximum value for each region. The references (*Ref.*) of *O. patagonica* records are indicated below, separated by regions and ordered on an increasing species' performance (i.e., the pattern of distribution followed by the number of colonies per location and the cumulated number of locations).

Region	Depth (m)	Year First	N Loc.	Max. Diam. (year)	Establishment period	Year max.	N Cum. Loc.	Cum. coastal length	Pattern of distribution	No. colonies per location	Ref.
South-Balearic Sea	**0-15**	1975	1	55 cm (1996) **152 cm (2011)**	1941-1968 1859-1935	2015 **2011**	34 **41**	230 km **210 km**	**Continuous**	**Hundreds**	*1*
Mid-Balearic Sea	**0-15**	1972	1	50 cm (2010) **42 cm (2011)**	1910-1960 1927-1969	2015 **2011**	62 **14**	150 km **100 km**	**Continuous**	**Tens to hundreds**	*2*
Aegean Sea	0.5-11	2005	1	no data	no data	2016	52	145 km	Continuous	Tens to hundreds	*3*
Levant Sea	0-10	1981	1	150 cm (2005)	1855-1930	2015	28	325 km	Continuous	Tens to hundreds	*4*
North-Balearic Sea	**0-28**	1992	1	~50 cm (2010) **70 cm (2011)**	1910-1960 1941-1976	2014 **2011**	27 **39**	230 km **260 km**	**Continuous**	**Isolated to tens**	*5*
North-Alborán Sea	**0-15**	2004	1	49 cm (2007) **73 cm (2011)**	1958-1982 1938-1974	2015 **2010**	30 **15**	300 km **215 km**	**Continuous**	**Isolated to tens**	*6*
Algerian and Tunissian waters	0.5-12	2006	1	157 cm (2010)	1853-1931	2015	12	215 km	Continuous	Isolated to tens	*7*
Balearic Islands	0.5-15	1995	2	85 cm (2009)	1924-1966	2016	17	125 km	Continuous	Isolated	*8*
West-Gulf of Lyons	**0-15**	2000	1	**60 cm (2010)**	1950-1980	**2010**	**12**	**135 km**	**Fragmented**	**Isolated**	*9*
Ligurian Sea	0.5-5	1966	1	135 cm (1966)	1831-1898	2008	7	75 km	Fragmented	Isolated	*10*
South-Alborán Sea	1-13	2005	1	45 cm (2005)	1960-1982	2012	5	~4 km	Fragmented	Isolated	*11*
Eastern Atlantic	0-8	2005	1	no data	no data	2010	2	~2 km	Fragmented	Isolated	*12*
East-Gulf of Lyons	no data	1972	2	no data	transplant	1992	2	15 km	Fragmented	Isolated	*13*
Adriatic Sea	3	2011	1	16 cm (2011)	1995-2003	2011	1	~1 km	Fragmented	Isolated	*14*

1 Zibrowius and Ramos (1983); Fine et al. (2001); Junta de Andalucía (2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, personal communication); Moreno (2010); Casado-Amezúa et al. (2014); Rodolfo-Metalpa et al. (2014); Leydet and Hellberg (2015, 2016); Terrón-Sigler et al. (2015, 2016, personal communication); **Chapters 4.1**, **4.2**, **4.5**.

2 Zibrowius and Ramos (1983); Ramos-Esplá (1985); Fine et al. (2001); Izquierdo et al. (2007); Rubio-Portillo et al. (2014a, 2014b, 2016); Rodolfo Metalpa et al. (2014); Ferrero-Vicente et al. (2016); **Chapter 4.5**.

3 Salomidi et al. (2006, 2013); Leydet and Hellberg (2015, 2016); Dailianis et al. (2016).

4 Fine and Loya (1995); Bitar and Zibrowius (1997); Kushmaro et al. (1997); Fine et al. (2001); Israely et al. (2001); Fine and Loya (2003); Shenkar et al. (2005, 2006); Çinar et al. (2006); Ainsworth et al. (2008); Sartoretto et al. (2008); Armoza-Zvuloni et al. (2011, 2012); Leydet and Hellberg (2015, 2016).

5 Casado-Amezúa et al. (2011, 2014); Rubio-Portillo et al. (2014a); **Chapters 4.3**, **4.5**.

6 Junta de Andalucía (2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, personal communication); Moreno (2010); Terrón-Sigler et al. (2015, 2016, personal communication); **Chapter 4.5**.

7 Sartoretto et al. (2008); Lamouti and Bachari (2010, 2011); Lamouti et al. (2011); Rebzani-Zahaf et al. (2013); Bachetarzi et al. (2016).

8 Ballesteros (1998); authors' unpublished data.

9 **Chapters 4.3**, **4.5**.

10 Zibrowius (1974); Zibrowius and Ramos (1983); Fine et al. (2001); Sartoretto et al. (2008); Rodolfo-Metalpa et al. (2006a, 2006b, 2008, 2014); Rodolfo-Metalpa (2007).

11 Templado et al. (2006); Sartoretto et al. (2008); authors' unpublished data.

12 Junta de Andalucía (2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, personal communication); Terrón-Sigler et al. (2016).

13 Zibrowius (1974, 1992); Zibrowius and Ramos (1983); Sartoretto et al. (2008).

14 Cvitković et al. (2013).

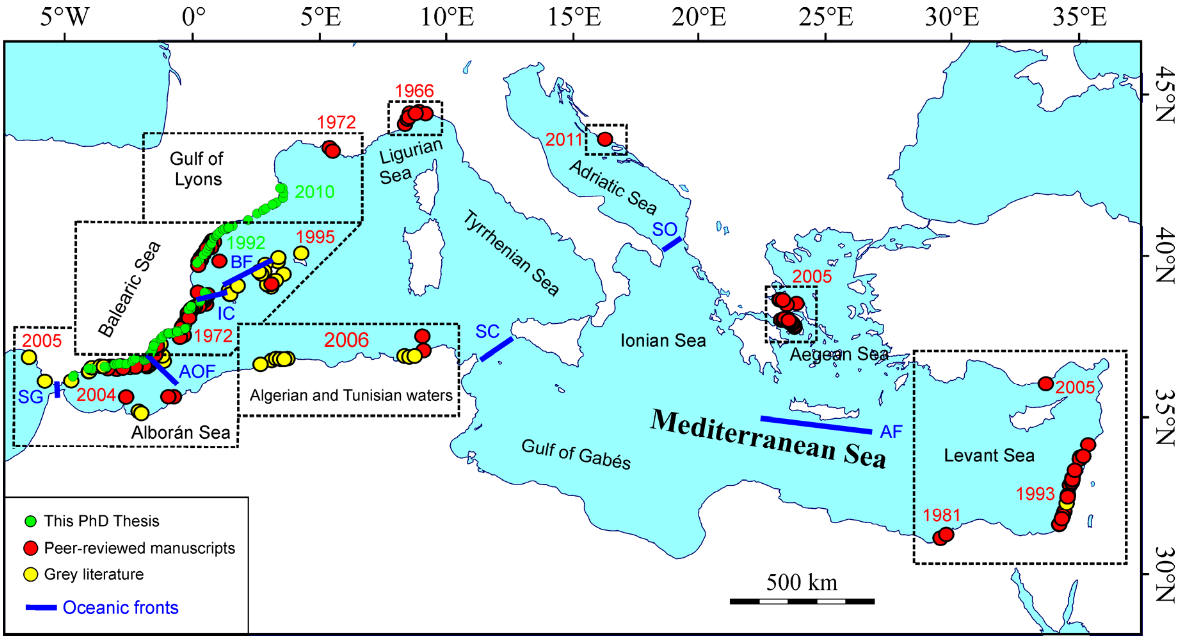


Fig. 5.1 Map of the Mediterranean Sea showing the current geographical distribution range of *Oculina patagonica*. The positions of the 400 locations in which the species has been recorded are indicated, distinguishing between records from this **PhD Thesis** (*green circles*), peer-reviewed manuscripts (*red circles*), and grey literature and authors' unpublished data (*yellow circles*; updated at July 2017). The year of first record of *O. patagonica* is indicated for each biogeographic region. The positions of the oceanic fronts (SG: Strait of Gibraltar, *AOF*: Almeria-Oran front, *IC*: Ibiza Channel *BF*: Balearic front, *SC*: Sicily Channel, *SO*: Strait of Otranto, *AF*: Aegean Front) are indicated (adapted from Millot 2005; Pascual et al. 2017). The *dashed polygons* indicate the eight biogeographic regions detailed in Fig. 5.2. Data is based on the global data set compilation of the number of locations with species' records (see Table 5.1).

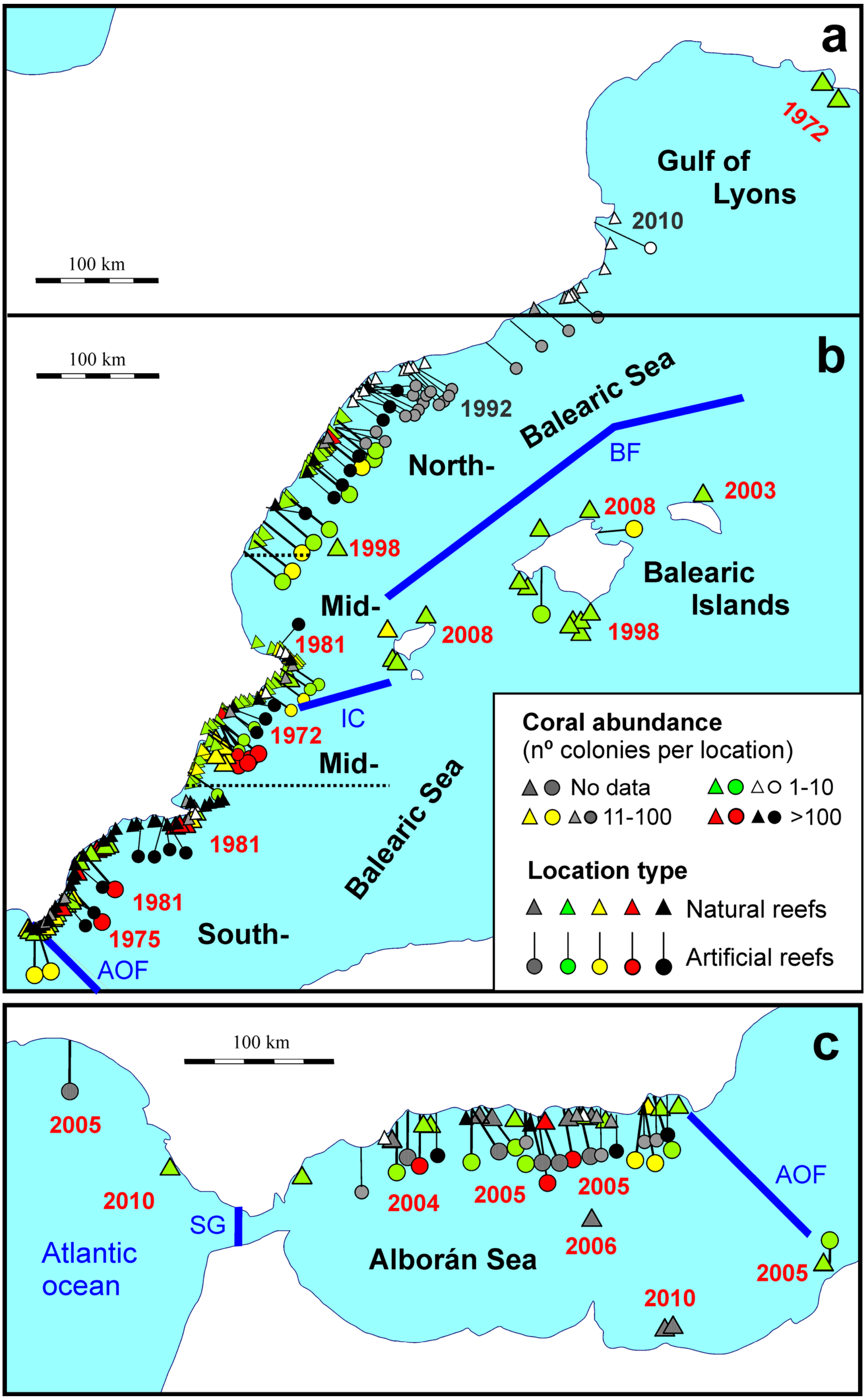
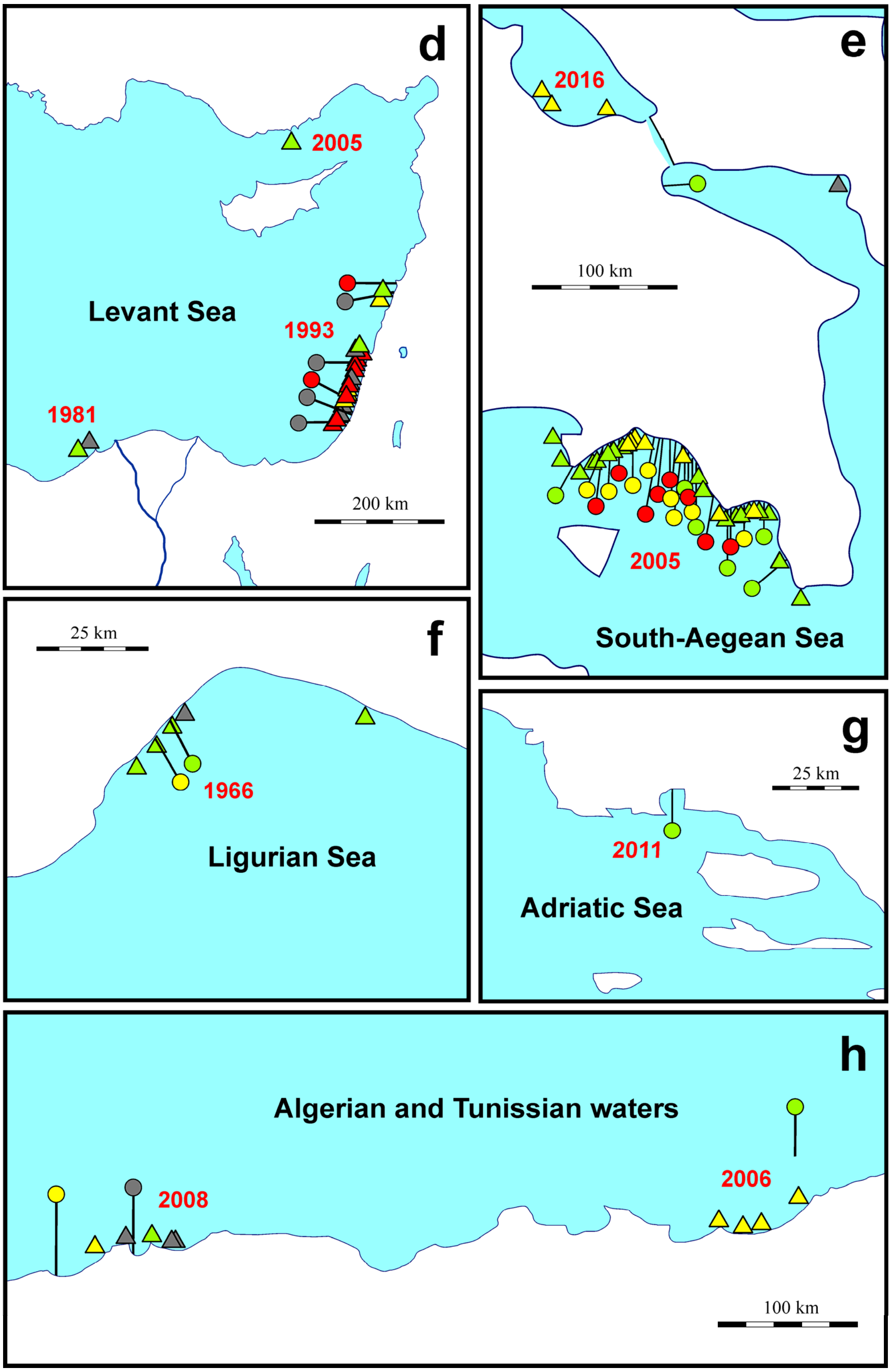


Fig. 5.2 Detailed maps of the Mediterranean biogeographic regions showing the current geographical distribution range and abundances of *Oculina patagonica*. The eight biogeographic regions (**a-h**) in which the species has been recorded (**a-h**) correspond to the dashed polygons drawn on the map of the Mediterranean from Fig. 5.1. **a** Gulf of Lyons and **b** Balearic Sea. **c** Alborán Sea and adjacent eastern Atlantic coast. **d** Levant Sea. **e** South-Aegean Sea. **f** Ligurian Sea. **g** Adriatic Sea. **h** Algerian and Tunissian waters.

The positions of the 400 locations in which the species has been recorded are indicated, distinguishing between location types (i.e., natural reefs: *triangles*, and artificial reefs: *circles*), and distinguishing between records from this **PhD Thesis** (small symbols and grey scale: white-grey-black) and previous studies (large symbols and color scale: green-yellow-red; large grey symbols indicate locations without data on coral abundance). The coral abundance was classified in three categories based on the number of colonies recorded per location: isolated (1-10 colonies), tens of colonies (11-100) and hundreds (>100). The year of first record for each sub-region is indicated. The positions of the oceanic fronts (*SG*: Strait of Gibraltar, *AOF*: Almeria-Oran front, *IC*: Ibiza Channel *BF*: Balearic front) are indicated (adapted from Millot 2005; Pascual et al. 2017).



A solitary colony of *O. patagonica* was discovered for the first time in a rocky reef from the Ligurian Sea in 1966 (Zibrowius 1974). Over the last ~50 years (i.e., from 1966 to 2017), the number of locations in which *O. patagonica* has been recorded across the Mediterranean has increased exponentially (Fig. 5.3). On the basis of mean linear extension rates documented in field studies conducted to date (i.e., ~1-2 cm in diameter yr^{-1}; Fine et al. 2001; Sartoretto et al. 2008; Rubio-Portillo et al. 2014b; **Chapter 4.4**) and maximum coral colony sizes, we estimated the time period of establishment at each region (Table 5.1). However, it should be kept in mind that it is not possible to determine with exactitude the establishment period of the colonies of *O. patagonica* because i) colonial corals have a modular growth and may suffer partial mortalities, fissions and fusions; ii) the highly variable growth form of *O. patagonica* colonies (i.e., 2D *versus* 3D; see Box 1.2); and iii) the local and regional variation in coral growth due to differences in environmental parameters; which can decouple the relationship between colony size and age (Hughes and Jackson 1985; Fine et al. 2001). Anyway, the large colony sizes (i.e., >50-157 cm in diameter) observed in most regions suggest that *O. patagonica* may have been present before 1900 in the Mediterranean Sea and that was established in most regions by ~1950s (Table 5.1). However, the spread curve over 1966-2017 show that it was not until the 2000s when *O. patagonica* has been exponentially recorded in additional locations throughout the Mediterranean, with significant coral populations in several regions (i.e., tens to hundreds of colonies per location; Fig. 5.3; Table 5.1), suggesting a rather recent invasive behavior according to the definition of Blackburn et al. (2011; see Box 1.4). In accordance, the conspicuous coral *O. patagonica (*i.e., big colonies thriving in shallow-water rocky reefs) was not recorded in previous benthic surveys on sessile invertebrates in none of these regions, and it is not present in local museum collections or in fossil records, even though other species of corals (i.e., including scarce, solitary and deep-water coral species), were collected decades ago, suggesting that during earlier surveys *O. patagonica* was either absent or rare (Zibrowius 1974; Fine et al. 2001; Sartoretto et al. 2008; Salomidi et al. 2013; Cvitović et al. 2014; and references therein). Moreover, when *O. patagonica* was first recorded (or few years after) in the southern Balearic Sea during the 1980s, in the Levant Sea during the 1990s, and in the Aegean Sea during the 2000s, the coral colonies were already abundant in several locations distributed along wide areas (i.e., ~100-300 km in coastal length; Zibrowius and Ramos 1983; Fine et al. 2001; Salomidi et al. 2013). Finally, the populations of *O. patagonica* across the western and eastern Mediterranean basins are genetically similar to each other, and did not show a genetic signal of expansion (Leydet and Hellberg et al. 2015). Overall, these evidences support the hypothesis of a rather recent and rapid spread of *O. patagonica* throughout the Mediterranean, and that its spread has followed over decades in a slow undetectable motion (Hughes et al. 2013) until the 2000s, when accelerated being exponentially recorded until reaching its current geographical distribution range.

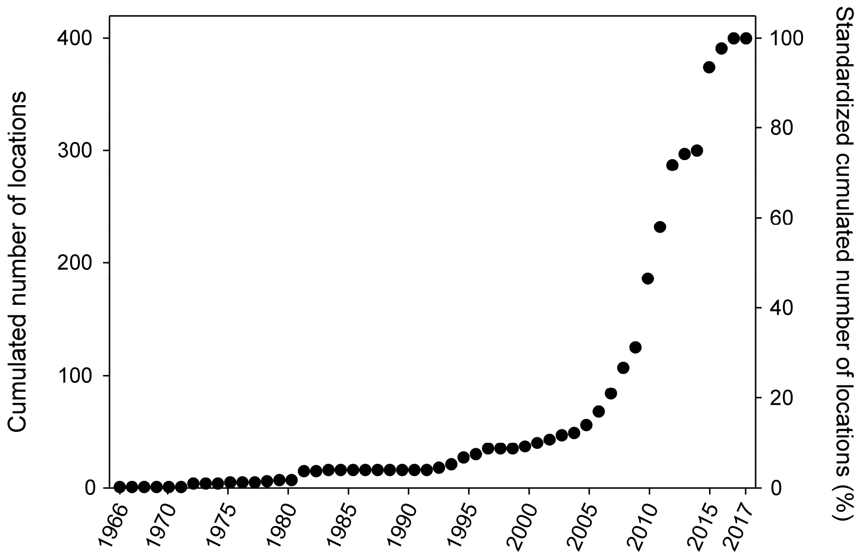


Fig. 5.3 Spread curves of *Oculina patagonica* based on the cumulative number of locations with species' records in the literature over the last 50 years (1966 to 2017). Data is based on the global data set compilation of the number of locations with species' records (see Table 5.1).

Noteworthy, this global dataset corresponds to cumulated records of the species, and the reported data may be regionally biased depending on the historical species-specific sampling and publishing effort within each region (Coll et al. 2010), which might have biased the conclusions obtained from this literature review. It should be also kept in mind that the sequence of discovered sites does not necessarily illustrate the advancing front of the invader, and that the estimated establishment period of the species indicate that the species has an old presence in most regions before its first record. Moreover, most studies are punctual descriptive records, and long-term and species-specific monitoring studies are needed to demonstrate the distributional range shift of a species (i.e., the presence in a location where it was not present before) and the population outbreak of a species (i.e., the increase in population size over time). Therefore, the pattern of recent spread of *O. patagonica* suggested by the total cumulative number of locations with species' occurrence across its distribution range (i.e., spread curve; Fig. 5.3) must be interpreted with caution. In this sense, this **PhD Thesis** contains the only detailed studies allowing the demonstration of a distributional range shift of *O. patagonica* (i.e., a species-specific yearly monitoring of 233 locations over 1992-2010, documenting its northward distributional range shift along ~400 km of the north-eastern Iberian coast, from the North-Balearic Sea to the Gulf of Lyons; **Chapter 4.3**) and populations outbreaks of *O. patagonica* (i.e., a yearly monitoring of four populations over 2002-2010 in the south-eastern Iberian coast, showing a 3-fold increase in species' abundance; **Chapter 4.2**). These evidences demonstrate the hypothesis of a rather recent and rapid spread of *O. patagonica* in the Iberian coast (western Mediterranean), but further data on coral demographics and population growth dynamics from other areas of the Mediterranean would be necessary to contribute understanding if the spread of *O. patagonica* is a general process occurring throughout the Mediterranean Sea and adjacent Atlantic coast.

The presence of man-made structures (i.e., artificial reefs) appear as an important factor enhancing the spread of *O. patagonica*. The number of locations in which *O. patagonica* has been recorded across its distribution range was higher for natural reefs than for artificial reefs (68 and 32% of total number of locations, respectively), which appear to be related to distinct sampling effort between location types. Interestingly, the occurrence and abundance of *O. patagonica* (i.e., percentage of explored locations with the species and number of colonies per location, respectively) was higher in artificial locations (i.e., the seaward side) than in natural locations within the same zone (i.e., at a detailed local scale; Fig. 5.2). In this **PhD Thesis** we showed that in the 5 zones studied within the Alborán Sea, Balearic Sea and Gulf of Lyons, the coral occurrence was higher in artificial locations than in nearby natural locations (mean of 72% and 55%, respectively), also the occurrence of coral populations (i.e., >0.05 colonies m^{-2}; **Chapter 4.5**). In addition, within the range-expanding area in the north-eastern Iberian coast (North-Balearic Sea and Gulf of Lyons), 80% of total number of colonies was recorded in the artificial locations, while only 20% was recorded in natural locations (mean of 22 and 7 colonies per location, respectively; **Chapter 4.3**). Moreover, a study in the Aegean Sea showed that although the occurrence of *O. patagonica* in artificial locations was only slightly higher than in adjacent natural locations (88% and 80%, respectively), the 96% of total number of coral colonies was recorded in artificial locations whilst only the 4% in natural locations (mean of 228 and 8 colonies per location, respectively; Salomidi et al. 2013). Overall, these results showed a consistent pattern of higher occurrence and abundance of *O. patagonica* in artificial locations than in nearby natural locations, indicating that man-made structures foster the demographics of this range-expanding coral in the Mediterranean Sea. In **Chapter 4.3**, we showed that the pattern of the spread curves of *O. patagonica* (i.e., the cumulated number of locations with the species) diverged between artificial and natural locations, with a half-reduced duration of the lag phase and 2-fold higher slope for the exponential phase in the former (based on 233 locations monitored over 1992-2010 along the range-expanding area in the north-eastern Iberian coast). Therefore, we discovered new evidence regarding the crucial role of artificial reefs for *O. patagonica* by showing that artificial reefs facilitate the distributional range shift of this range-expanding coral.

The current geographical distribution pattern of *O. patagonica* is continuous (i.e., ≥1 location with the species per 10 km coastal length) and coral abundance is high (i.e., from tens to hundreds of colonies per location) in the south-western Mediterranean (Algerian and Tunissian waters, Alborán Sea and Balearic Sea) and in the eastern Mediterranean (Aegean Sea and Levant Sea; Table 5.1; Fig. 5.1; Fig. 5.2). In contrast, the species' distribution pattern is fragmented and the coral abundance is low (i.e., <10 colonies per location) in the north-western areas (Balearic Islands, Gulf of Lyons, Ligurian Sea and Adriatic Sea). The synthesis of reported data on *O. patagonica* demographics across the Mediterranean Sea revealed that the Iberian coast is the most invaded region by the species, in terms of both the cumulated number of locations and invaded coastal length (Table 5.1). In addition, we showed that *O. patagonica* has been able to form dense colony aggregations and drive a regime shift from macroalgal- to coral-dominated states (i.e., 55% coral cover) in a natural shallow-water rocky reef from the South-Balearic Sea (**Chapter 4.1**). At present, this is the only record of a phase shift mediated by *O. patagonica* in a natural habitat, but previous studies have documented *O. patagonica*-mediated phase shifts in two artificial locations, one from the Mid-Balearic Sea (Alacant harbor; Izquierdo et al. 2007; Rodolfo-Metalpa et al. 2014) and the other from the Aegean Sea (i.e., Piraeus harbor; Salomidi et al. 2013). Overall, these evidences contribute to highlight the Iberian coast as a hot-spot for the range-expanding coral *O. patagonica*, with the largest and spreading coral populations recorded in the central Iberian coast of the South-Balearic Sea (i.e., mean of one reported location with the species each ~4 km in coastal length, and hundreds of colonies per location; Table 5.1).

The spatial variation in the demographics of zooxanthellate corals may reveal important differences in environmental parameters that affect the establishment, survival, growth and reproduction of corals as individuals, and becomes integrated in the abundance and size-frequency distribution of their populations (Bak and Meesters 1998; Meesters et al. 2001; Goffredo et al. 2008; Kružić et al. 2012; Airi et al. 2014). The global dataset compilation on reported locations with *O. patagonica* suggests that the range-expanding process (i.e., the coral establishment, survival, increase in size as individuals and populations, and dispersion to nearby locations; Blackburn et al. 2011) has apparently shown distinct patterns among the invaded regions within the Mediterranean Sea. For instance, the year of first record and/or the estimated time period of establishment was earlier in regions that nowadays have low coral abundance, such as the Ligurian Sea; while in other regions where the species established later, the current coral abundances are higher, such as the North-Balearic Sea (Table 5.1; Fig. 5.2). In addition, there is a concomitant zonal pattern of higher coral occurrence and abundance in artificial locations (i.e., the seaward side) than in nearby natural locations (Salomidi et al. 2013; **Chapter 4.3, 4.5**). These evidences suggest that the spatial variation in the spread of *O. patagonica* appear to be determined by the interacting influences of invasion history and the acclimatization of its biological traits to the spatial variation of key environmental conditions and habitat types (i.e., natural and artificial reefs), modulating its population growth dynamics (i.e., establishment, growth, reproduction and dispersal) across the Mediterranean.

Although the global dataset compilation provides insights into the spread dynamics, there is a lack of large-scale standardized monitoring required to understand the key underlying factors and ecological processes underlying the demographics of *O. patagonica* populations across the Mediterranean. In this sense, the dataset obtained within the Iberian coast in this **PhD Thesis**, which represents 30% of total reported locations with the species (121 locations out of total recorded 400 locations), is unique because contains quantitative data over a large-scale (~1300 km) using standardized methods, and differs from previous studies that describe the distribution and qualitative abundance of *O. patagonica* at local scales. In this sense, the detailed large-scale (i.e., 314 locations along ~1300 km coastline) and quantitative dataset on *O. patagonica* demographics (i.e., coral density, cover, colony partial mortality and size descriptors; for the 121 locations where it was found) obtained in this **PhD Thesis** within the Iberian coast (the most invaded region by the species) showed that the species abundance conforms to the general pattern of the 'abundant-center' hypothesis (i.e., a most abundant center that declines toward the edges of a geographic range; **Chapter 4.5**). However, the results on coral demographics showed that this pattern is not only related to the timing of arrival but points to the relevant role of differences in coral population growth that correlate with key environmental parameters. Therefore, our unique large-scale and quantitative dataset of *O. patagonica* demographics within the Iberian coast is of key significance to explore the role of environmental conditions in determining the species' demographics and identify potential shifting trends, while providing a baseline quantitative assessment in which to detect potential spread and impacts in the near future. Understanding of processes driving the *O. patagonica*-mediated tropicalization of Mediterranean temperate ecosystems is crucial to develop management strategies in the context of global environmental change.

5.2. Key factors modulating population growth dynamics of *Oculina patagonica*

A fundamental issue in marine ecology is explaining the patterns of species' distribution and abundance, together with the biotic and abiotic processes that drive these patterns (Gaston 2000; Gage 2004; Magurran et al. 2011). Geographical distribution ranges are determined by an alignment of different contributory mechanisms, so that range boundaries and population abundances can be set by multiple factors that interact in complex ways across ranges and through time, even with singular environmental conditions at every site (Sagarin 2006; Gaston 2003). In this sense, data on actual distribution and demographics of a species across a broad geographic scale, coupled with basic population demographics and biophysical parameters, is necessary to narrow the range of viable hypothesis to explain its distribution range boundaries and regional variation in population growth dynamics. These broad perspective studies have highlighted the roles that differential acclimatization of biological traits of a species, heterogeneous abiotic factors, biotic interactions affecting keystone species, biogeographic differences within range boundaries and variation in the strength of human-related impacts, play in driving population demographics, range distribution boundaries and species responses to global change.

Shallow-water coastal species such as *O. patagonica* are considered ideal systems to test large-scale hypothesis owing their distribution range, due to the unique geometry of their geographical ranges along the coast (i.e., ranges of thousands of kilometers long, but generally <0.1 km wide at all points; Sagarin et al. 2006). In a broad perspective, the scarcity of zooxanthellate corals in temperate areas such as the Mediterranean (Cairns 2000; Veron 2000; Veron et al. 2015) has been related to the synergistic and/or antagonistic interactions among (i) biological traits of zooxanthellate corals, (ii) biotic interactions (i.e., competition, facilitation, predation) and (iii) abiotic factors (i.e., seawater temperature, ST; solar radiation, nutrients and the saturation state of seawater aragonite) that modulate species' establishment and success (i.e., survival, growth, reproduction and dispersal; Kleypas et al. 1999; Miller and Hay 1996; Miller 1998; Hoegh-Guldberg et al. 2009; Muir et al. 2015). In this context, here we explore the underlying factors modulating the demographics and population ecology of the range-expanding zooxanthellate coral *O. patagonica* in the temperate Mediterranean Sea.

5.2.1. Exploring the biological traits of *O. patagonica* to understand its successful spread

The successful proliferation of the range-expanding coral *O. patagonica* throughout the Mediterranean may be first related to its life-history traits. In particular, (i) its capacity to disperse and reproduce both sexually *via* broadcast spawning and asexually *via* polyp expulsion; (ii) its broad trophic capacities; and (iii) its ability to survive, grow and reproduce under a wide range of environmental conditions.

On one hand, the dispersal and population growth of *O. patagonica* is based on sexual and asexual propagules, which provide alternatives for its spread. Regarding sexual reproduction, it is a gonochoric coral species (i.e., 'dioecious', separate sexes) that produce only male or female gametes within each colony during its lifetime, with a broadcast spawning mode of development (gamete release on the water column followed by external fertilization; Fine et al. 2001; Armoza-Zvuloni et al. 2011, 2012). *O. patagonica* is iteroparous and reproduce annually (Fine et al. 2001; Armoza-Zvuloni et al. 2011, 2012). Sexual maturity in *O. patagonica* is attained at a colony size of >2 cm, with an age of first reproduction of 1-2 years (Fine et al. 2001; authors' unpublished data). The mean size of oocytes at maturation is ~100 µm and female fecundity ranges between ~300 and 3,000 oocytes polyp^{-1} (Zibrowius 1992; Fine et al. 2001; Correa 2013). Oocytes are released singly and are negatively buoyant, whereas sperm is released in clouds. Shortly after spawning, the fecundation of oocytes occurs and free-living planulae larvae develop (mean size of ~150 µm), and ~8 h after spawning, larvae already contain zooxanthellae acquired from free-living zooxanthellae found in the water column (horizontal acquisition; Trench 1987; Fine et al. 2001). Marine currents disperse the larvae until its settlement in a rocky substrate, where it transforms into a primary polyp that can lead to the foundation of a new colony through budding. In addition to sexual reproduction, *O. patagonica* can also reproduce and disperse asexually *via* 'polyp expulsion', in which individual polyps, including their calices, lift on elongated calcareous stalks before detaching and settling elsewhere near the 'mother' colony, and form a new colony through budding (Kramarsky-Winter et al. 1997).

Currents likely contribute to local- and large-scale dispersal of sexually produced planulae larvae (i.e., autotrophic coral larvae, such as those of *O. patagonica*, can survive weeks or months on the water column; Fine et al. 2001; Harrison 2011), while the asexual reproduction *via* the expulsion of calcified polyps (Kramarsky-Winter et al. 1997) likely enhances dispersal and population growth at local scales. In addition, transoceanic transport of *O. patagonica* as a fouling organism on the hull of ships was considered as the most probable vector for its first introduction in the Mediterranean (Zibrowius 1974), while the intense intra-Mediterranean traffic may have assisted in its large-scale dispersal across Mediterranean regions, either as a fouling organism and/or *via* larvae dispersion in ballast waters. The observation of several colonies of *O. patagonica* fouling the hull of a recreational ship supports this hypothesis (authors' unpublished data). In **Chapter 4.3** we describe the distributional range shift of *O. patagonica* along the north-eastern Iberian coast over a 19-yr period (1992-2010), showing that the species shifted northward at a rate of 22 km yr^{-1} at 2 spatial scales of dispersal: neighborhood and long-distance. The velocity of spread documented in *O. patagonica* is among the highest reported values of poleward range shifting of marine species (i.e., mean of 7 km yr^{-1}; Sorte et al. 2010) and zooxanthellate corals (i.e., up to 14 km yr^{-1}; Yamano et al. 2011). The reproductive and dispersal traits of *O. patagonica* explained above are considered among the most efficient and successful strategies within zooxanthellate corals (Harrison 2011), and likely may have contributed to its successful proliferation throughout the Mediterranean.

On the other hand, the feeding strategy of the coral *O. patagonica* is autotrophic passive suspension, so acquires the nutrients required for its biological functions (e.g., build coral tissues, gametes, skeleton) *via* both autotrophic and heterotrophic pathways. In zooxanthellate corals, the autotrophic pathway is mainly provided by the symbiotic microalgae *Symbiodinium* spp. living in the coral tissue, which transfer most (~95%) of the photo-assimilates to the host (Muscatine et al. 1981; Muscatine 1990). The endolithic filamentous algae harbored in the skeleton of *O. patagonica* colonies also produce photo-assimilates which are translocated to the coral soft tissue, representing an alternative photosynthetic source of energy (Fine and Loya 2002). The part of the solar radiation spectrum that drives the autotrophic production (i.e., absorbed by the photosynthetic systems of the symbiotic algae) is referred to as photosynthetically active radiation (PAR, wave lengths 400–700 nm). Coral species that acquire zooxanthellate from the water column during the free-living planula larvae and/or the benthic stages (horizontal transmission), such as *O. patagonica* (Fine et al. 2001), generally form associations with a broad range of symbiotic genotypes, when compared to coral species that acquire zooxanthellate from the parents (during the oocytes or brooded larvae stages; vertical transmission; Douglas 1998; Karako-Lampert et al. 2004; Harii et al. 2009). The capacity of *O. patagonica* to associate with different *Symbiodinium* types (Leydet and Hellberg et al. 2016; Grupstra et al. 2017), and even its ability to switch between them, may contribute to the acclimatization of the coral holobiont to different environmental conditions, because unique *Symbiodinium* types exhibit variable tolerance to different environmental regimes (e.g., Silverstein et al. 2015; Hume et al. 2016). Plankton capture and uptake of dissolved and particulate organic matter, and microorganisms, constitute the heterotrophic pathway of acquisition of energy (Houlbrèque et al. 2004; Houlbrèque and Ferrier-Pagès 2009; Fabricius 2005; Tremblay et al. 2011). The coral *O. patagonica* is also capable of ingesting fish pellets and gelatinous plankton (authors' unpublished data), which suggests that it has a varied diet. The coral *O. patagonica* is a facultative zooxanthellate species, so the coral colonies present in dark habitats are able to thrive uniquely through heterotrophy, but are restricted to caves or overhangs with high hydrodynamic energy and thus, with enhanced nutrient availability (Fine et al. 2001; Aichelman et al. 2016; **Chapter 4.5**). The heterogeneous nutrition pathways of *O. patagonica* suggest a broad trophic ability that likely enables its survival and spread under broadly variable environmental conditions.

Finally, the ability of *O. patagonica* to survive, grow and reproduce under the wide range of environmental conditions found within its distribution range across the Mediterranean Sea may have contributed to its successful proliferation (e.g., Fine et al. 2001; Sartoretto et al. 2008; Armoza-Zvuloni et al. 2011, 2012). For instance, it is able to thrive in tide pools at STs ranging between 10–40ºC and at salinities of 28-50‰, in dark light conditions, in polluted areas and artificial reefs, as well as on canopy-forming algal-dominated rocky reefs (Fine et al. 2001; **Chapters 4.2, 4.5**). In **Chapter 4.4** we showed that during low-ST stress, the colony partial mortality resulted from the dissociation of polyps from their connective coenosarc (i.e., loss of coloniality, termed as 'Dalmatian mortality pattern'). The similar isolation of polyps within their calices has been documented under low-pH experimental conditions, and this process was mediated by programmed cell-death mechanisms (i.e., apoptosis), representing an essential mechanism to withstand stress (Kvitt et al. 2015). In fact, the Dalmatian mortality pattern of coral colonies under low-ST stress during winter at high-latitudes, which left the polyps alive and isolated within their calices, also appeared as a crucial mechanism beyond the rapid start of lesion recovery after low-ST stress, the capacity to nearly fully recover from lesions, and the subsequent survival and resumption of coral colony growth during the favorable season in summer (**Chapter 4.4**). Besides its capacity to survive harsh environmental conditions, normal gametogenesis in *O. patagonica* has been described in most Mediterranean regions (i.e., Ligurian Sea, Gulf of Lyons, Balearic Sea and Levant Sea), including both pristine and highly polluted locations, and dark habitats (Fine et al. 2001; Armoza-Zvuloni et al. 2012). Indeed, the reproduction of *O. patagonica* colonies can acclimatize to chronic disturbances, such as recurrent bleaching episodes and metal pollution (i.e., despite the first year of disturbance can significantly affect reproduction success, the species is capable to acclimate and reproduce the second year of repeated disturbance; Armoza-Zvuloni et al. 2011, 2012). In conclusion, the life-history traits of *O. patagonica*, such as high reproductive and dispersal capabilities, ecological generalization and broad tolerance to environmental parameters; which are characteristic of opportunistic colonizer species (Shigesada et al. 1995; Alpert et al. 2000; Harrison 2011; Darling et al. 2012; Cardeccia et al. 2016), likely have contributed to its successful proliferation throughout the Mediterranean Sea.

5.2.2. Exploring biotic interactions modulating population growth dynamics of *O. patagonica*

The proliferation of *O. patagonica* throughout the Mediterranean may also be related to the successful outcomes of biotic interactions (i.e., competition, facilitation and predation) with other organisms. In particular, (i) its ability to outcompete other organisms for space occupancy; (ii) the positive biotic interactions such as enhanced coral growth in algal-depleted reefs; and (iii) the scarcity of corallivorous predators.

Among biotic interactions, competition for space occupancy is the main limiting factor for species establishment and growth in benthic, shallow-water rocky communities (Dayton 1971). The colonies of *O. patagonica* have an encrusting growth form and compete for space occupancy at their growing edges, contacting with the surrounding benthic organisms, such as macroalgae (Fig. 5.4a) and sessile invertebrates (e.g., sponges, tunicates, bryozoans, vermetid gastropods, and azooxanthellate and zooxanthellate scleractinians; Fig. 5.4b-g). The outcome of contacts between the colonies of *O. patagonica* and surrounding benthic organisms relies on the interaction of several abiotic and biotic factors affecting the success of contacting species, and can vary seasonally (Ballesteros 1989, 1991; Zabala and Ballesteros 1989; Fine and Loya 2003). Nevertheless, given that *O. patagonica* is a long-lived species capable to develop permanent calcareous bioconstructions formed by the aggregation of contacting colonies (**Chapter 4.1**; Fig. 5.4e), together with its great aptitudes for adapting to disturbances and environmental stress, it seems likely that it is a good competitor for space and opportunistic species that may threat the native biodiversity of shallow-water rocky communities.

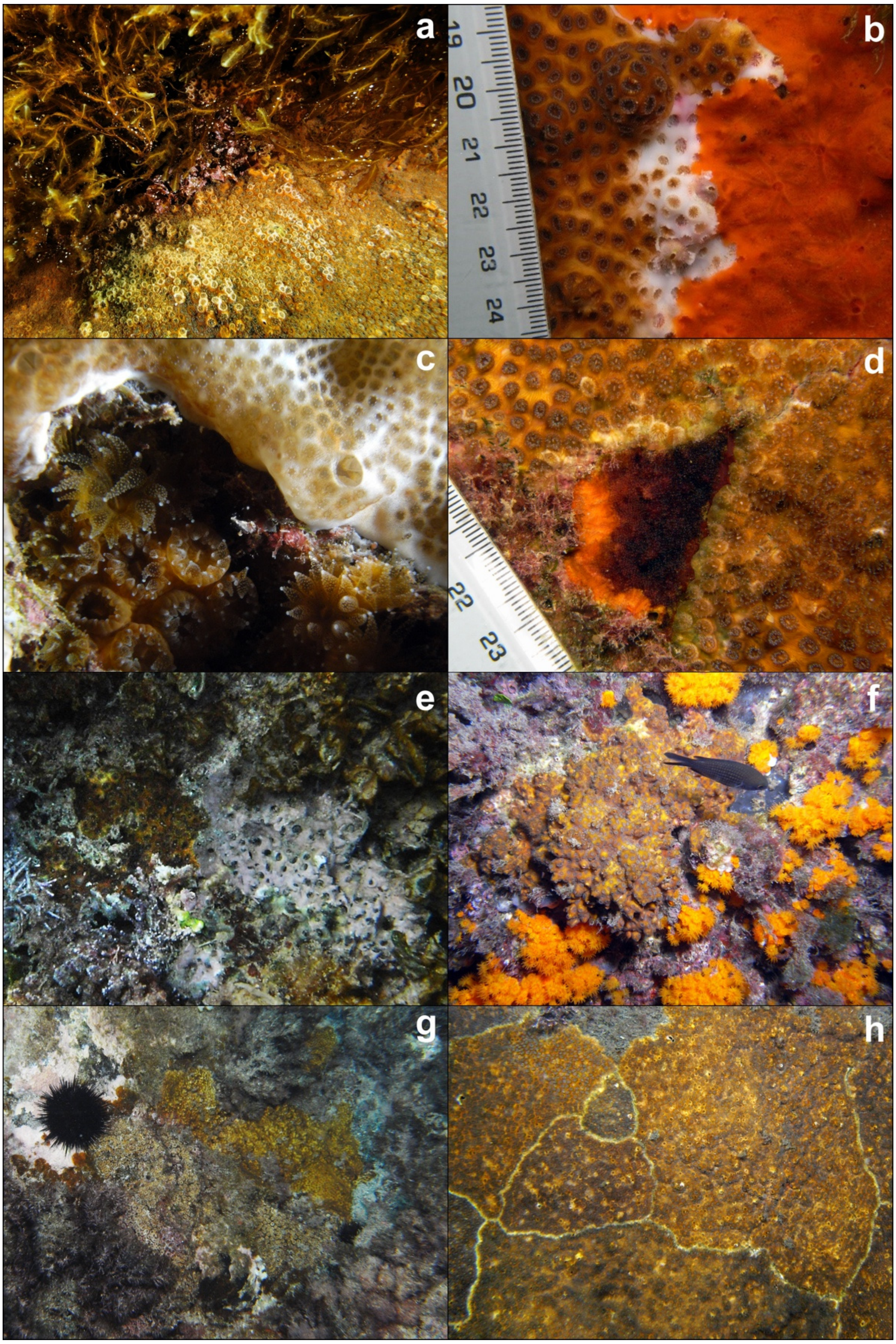


Fig. 5.4 Competition for space between the encrusting colonies of the zooxanthellate scleractinian *Oculina patagonica* and surrounding benthic organisms. a The canopy-forming macroalgae *Dictyopteris polyploides* and underneath algae. Photograph by Juan Carlos Calvín. **b** The sponge *Crambe crambe*. Note the band of coral skeleton without living coral tissue and the coral skeleton underneath of the sponge tissue. **c** A didemnid ascidian, likely *Lissoclinum perforatum* (*sensu* Xavier Turon). **d** The bryozoan *Schizoporella* spp. **e** The vermetid gastropod *Dendropoma lebeche*. **f** The azooxanthellate scleractinian *Astroides calycularis*. **g** The zooxanthellate scleractinian *Cladocora caespitosa*. **h** Contact fronts between eight distinct colonies of *O. patagonica* developing permanent calcareous bioconstructions.

Competition with macroalgae is a key limiting factor for zooxanthellate coral populations to grow, especially in macroalgae-dominated temperate and subtropical areas, such as the Mediterranean (Zabala and Ballesteros 1989; Miller and Hay 1996; Miller 1998; McCook et al. 2001). Shallow-water rocky reefs dominated by canopy-forming macroalgae likely contribute to suppressing the growth of coral colonies and populations by shading and abrasion, superior resource utilization (e.g., light and space), and through diminishing the recruitment and survival of coral larvae (e.g., McCook et al. 2001; Diaz-Pulido et al. 2010). In the Mediterranean, healthy rocky ecosystems in shallow-waters are generally dominated by canopy-forming macroalgae (Phaeophyceae), but a variety of natural- and human-related impacts (e.g., storms, overgrazing and pollution) can result in benthic communities dominated by turf algae and barren grounds (i.e., algal-depleted reefs; see Box 5.1 and references therein). Therefore, the hypothesis is that the increased availability of open space on algal-depleted reefs is a primary factor fostering the population growth of the zooxanthellate coral *O. patagonica* in the Mediterranean. The results obtained in this **PhD Thesis** within the Iberian coast support the hypothesis that algal-depleted reefs enhance the population growth of *O. patagonica*. First, the most abundant coral population in natural habitats (i.e., 55% total coral cover) was found dwelling in a vertical cliff with algal-depleted benthic assemblages (i.e., the remaining 37% cover was sparse algae with a canopy height of <1 cm), likely related to severe sand scouring conditions (**Chapter 4.1**). Second, in benthic assemblages from Cabo de Palos-Islas Hormigas, dominated by canopy-forming algal species, small coral colonies (i.e., <10 cm in mean diameter) were observed preferentially on barren grounds (**Chapter 4.2**; Fig. 5.6a-b). Third, the mean open space availability (i.e., cover of bare rock, encrusting calcareous algae and sparse turf algae <1 cm in height) within studied natural locations along the Iberian coast was 33% (**Chapter 4.5**), which is evenly higher than thresholds previously reported to facilitate the population growth of shallow-water *Oculina* spp., particularly in *O. patagonica* (20-24%; **Chapters 4.2**, **4.5**) and *O. arbuscula* (20-30%; Miller and Hay 1996). In accordance, Rubio-Portillo et al. (2014a) found a positive correlation between algal-depleted reefs (i.e., turf algae) and the qualitative abundance of *O. patagonica* along ~400 km coastal length in the Mid- and North-Balearic Sea. Overall, these correlational results indicate that the population growth of the zooxanthellate coral *O. patagonica*, which spatially competes with macroalgae, is facilitated by the availability of open space on disturbed, algal-depleted reefs (i.e., turf-forming algae and barren grounds). Further experimental studies are required to demonstrate the cause-effect of distinct composition of benthic assemblages and its seasonal changes in biomass (Ballesteros 1989, 1991, 1992) on *O. patagonica* population growth dynamics.

Box 5.1. Dynamics of macroalgae assemblages in the shallow-water Mediterranean rocky reefs

The distribution and abundance of macroalgae species is controlled by both top-down and bottom-up processes. Light availability, which diminish with increasing depth and the verticality of the substrate, is the main abiotic factor determining the dominance of macroalgae in shallow-water rocky reefs from the temperate Mediterranean Sea (Ballesteros 1989, 1991; Zabala and Ballesteros 1989). Fucoid species are the main canopy-forming macroalgae (i.e., algal forests) on healthy ecosystems (Fig. 5.5a). The removal of canopy-forming macroalgae assemblages can occur either naturally (e.g., under severe storms and grazing pressures) or caused by the interaction of human-related impacts such as sea warming, habitat degradation, eutrophication, pollution and population outbreak of herbivores (e.g., Sala et al. 1998a; Hereu et al. 2008; Sales and Ballesteros 2009; Coll et al. 2010; Pagès et al. 2013; Thibaut et al. 2005, 2017).

The sea urchins *Paracentrotus lividus* and *Arbacia lixula* are the main native herbivores feeding on both adult macroalgae and on the epilithic algal turf (Fig. 5.5b), and the outbreak of their populations can drive an ecosystem shift from macroalgae- to barren-dominated landscapes (Boudouresque and Verlaque 2007; Hereu et al. 2012; Boada et al. 2017; Fig. 5.5c). The outbreak of sea urchins populations can occur naturally due to episodic high recruitment events, or due to impacts such as predator release *via* overfishing. The native herbivorous fish species in the Mediterranean (e.g., *Sarpa salpa*) fed exclusively on adult macroalgae (i.e., browsers) and thus are not capable to cause barrens (Hereu et al. 2008; Fig. 5.5d). In contrast, two alien tropical herbivorous fish species (i.e., the rabbit fishes *Siganus luridus* and *Siganus rivulatus*) are spreading throughout the Mediterranean and fed complementarily on both adult macroalgae and on the epilithic algal turf (i.e., browsers and grazers/scrapers, respectively), which typically contain algal recruits, preventing the establishment and growth of macroalgae (Sala et al. 2011; Vergés et al. 2014a, 2014b). In eastern Mediterranean regions with abundant rabbit fish populations, these functionally diverse tropical herbivorous can severely reduce the algal biomass and recruitment, and cause a shift from macroalgal dominance to barrens (Sala et al. 2011; Fig. 5.5e,f). The phase shift from canopy algal assemblages to barren states implies a relevant decline in habitat complexity, biomass, biodiversity and function of the shallow-water rocky ecosystems (e.g., Ballesteros 1989; Sala et al. 2011; Cheminée et al. 2013).

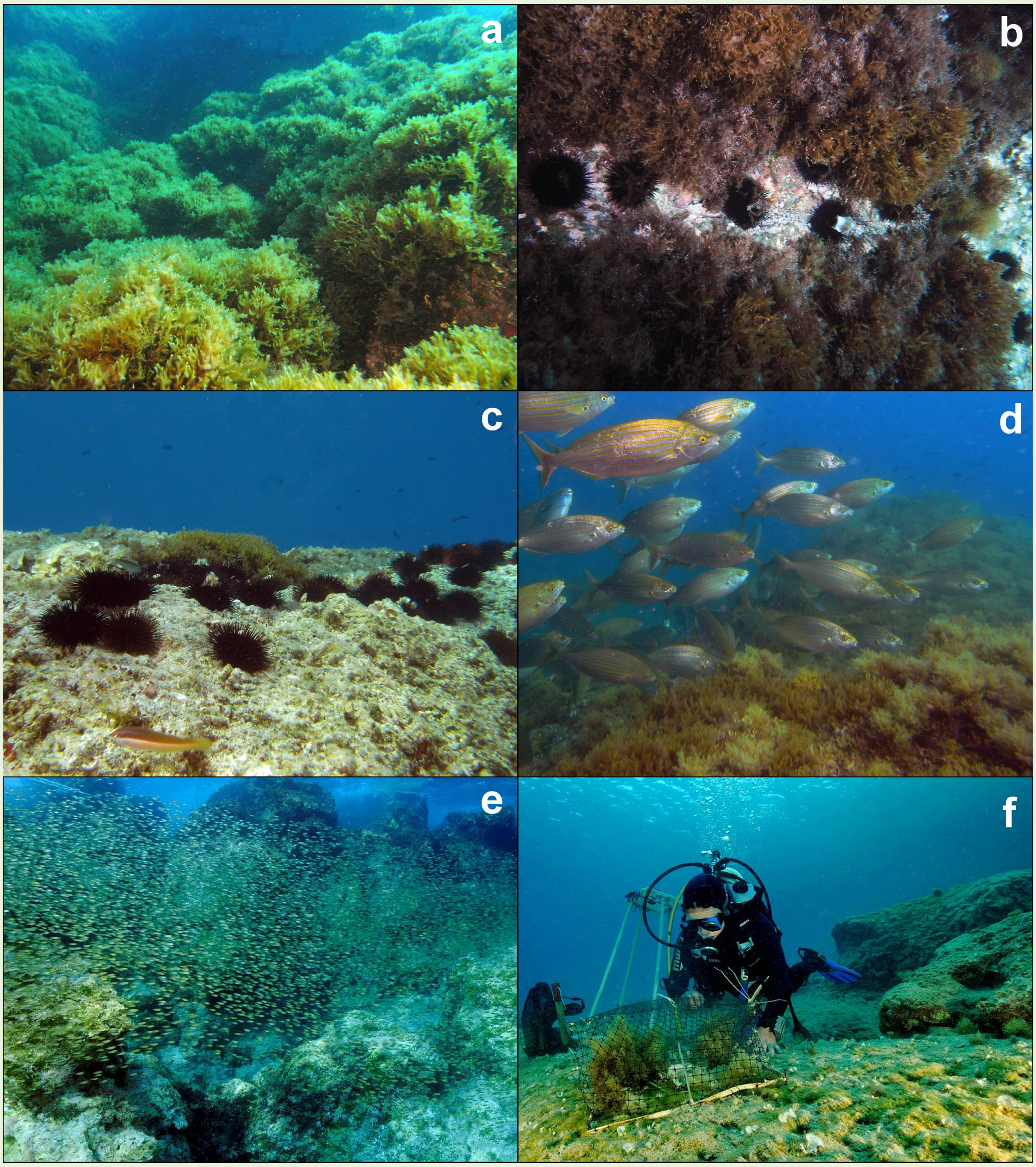


Fig. 5.5 Dynamics of macroalgae-dominated ecosystems in shallow-water rocky reefs from the Mediterranean Sea. a Healthy ecosystem dominated by canopy-forming fucoid macroalgae at the marine protected area of Cabo de Palos-Islas Hormigas, and **b** the sea urchin *Paracentrotus lividus* grazing the canopy-forming macroalgal assemblages. **c** The outbreak of sea-urchins populations overgraze macroalgal assemblages, causing an ecosystem shift to less structured algal-depleted reefs and barren grounds. Note the remaining algae stain on the back of the photo. **d** The native herbivorous fish *Sarpa salpa* feeding on adult macroalgal assemblages. **e** School of invasive juvenile rabbit fish (*Siganus luridus*) in the Levant Sea**. f** A fish-exclusion cage with a canopy-forming algal assemblage, in contrast to the surrounding algal-depleted assemblages in a location with abundant tropical herbivorous rabbit fish (e,f: note the absence of sea urchins; adapted from Sala et al. 2011).

In shallow-water rocky reefs from the Mediterranean, grazing by sea urchins (i.e., *Paracentrotus lividus* and *Arbacia lixula*) is the main mechanism creating barren grounds and subsequent algal-depleted reefs (Boudouresque and Verlaque 2001; Hereu et al. 2012; Boada et al. 2017; Box 5.1). As mentioned above, the growth of *O. patagonica* appear to be enhanced in algal-depleted reefs, and thus, the hypothesis is that the coral demographics and population dynamics may benefit from the barren grounds (i.e., open space) created by sea urchin species on the benthic-dominant species of macroalgae (i.e., facilitative interactions between species; Fig. 5.6c). In this **PhD Thesis**, we tested this hypothesis in the marine reserve of Cabo de Palos-Islas Hormigas (South-Balearic Sea; **Chapter 4.2**), where the shallow-water benthic assemblages are dominated by canopy-forming algal species of >10 cm in height such as *Dictyopteris polyploides* and *Sargassum vulgare* (i.e., mean cover of 73-76%; **Chapters 4.2**, **4.5**; Fig. 5.5a-c in Box 5.1). We found that grazing by sea urchins was the main mechanism creating barrens in otherwise spatially-limited assemblages, and that small coral colonies settled preferentially on areas cleared by sea urchins (**Chapter 4.2**). In addition, the large-scale study along the whole Mediterranean Iberian coast showed that the living cover of coral populations was positively correlated with sea urchin biomass (**Chapter 4.5**). These results indicate that the population growth of *O. patagonica* is facilitated by the barrens created by sea urchin grazing. Similarly, the relevant role of sea urchins in promoting population growth of zooxanthellate scleractinian corals has also been documented in coral reefs from the Caribbean. In the 1980s, the occurrence of wide-scale phase shifts from coral- to macroalgal-dominance was exacerbated by the mass mortality of the main sea urchin *Diadema antillarum*, which remained rare until the late 1990s, when reappeared in large numbers; and by 2000, the high densities of *D. antillarum* were correlated with significantly reduced macroalgal cover and increased abundance of small coral recruits (Carpenter 1990; Edmunds and Carpenter 2001; Carpenter and Edmunds 2006).

Man-made coastal structures (i.e., artificial reefs) are common and widespread features of the Mediterranean, either as part of commercial/fishing ports and recreational marinas (e.g. seawalls and jetties), or as various types of coastal defenses (e.g. breakwaters, groynes and ripraps). Comparative studies on *O. patagonica* occurrence and abundance between natural and artificial locations at a local scale indicate a higher success of *O. patagonica* in artificial reefs (see Chapter 5.1). This pattern was consistent among the examined Mediterranean biogeographic regions, including the range-expanding area in the north-eastern Iberian coast (Alborán Sea, Balearic Sea, Gulf of Lyons and Aegean Sea; Salomidi et al. 2013; **Chapters 4.3**, **4.5**). Therefore, artificial reefs appear to play a key role in the spread of *O. patagonica* at both population growth and distributional range levels, likely acting as a focus for coral population growth, reproduction and geographical dispersal by means of increased propagule pressure. The reasons beyond the higher success of *O. patagonica* in artificial locations than in nearby natural locations are probably related to distinct abiotic and biotic conditions that shape key ecological processes such as recruitment and biotic interactions among species (i.e., artificial reefs do not function as surrogates of natural reefs; Glasby and Connell 1999; Bulleri 2006; Bulleri and Chapman 2010). Although further experimental studies are required to understand the causes underlying the enhanced growth of *O. patagonica* in artificial reefs, the higher open space availability in recently-constructed artificial reefs (i.e., the main initial difference with natural reefs), appear to enhance the recruitment and population growth of the opportunistic coral *O. patagonica* (authors' unpublished data; Fig. 5.6d). For instance, the largest coral population in the range-expanding area in the north-eastern Iberian Peninsula (i.e., 1.1 colonies m^{-2} and 5.5% total cover; **Chapter 4.3**) was recorded in 2010 at L'Ampolla breakwater, a 16-yr old artificial reef at that time (i.e., boulders were deployed in 1994; authors' unpublished data), which highlights the role of 'new' rocky reefs (i.e., open space availability) in enhancing the growth of the opportunistic coral *O. patagonica*. In fact, the benthic assemblages in natural and artificial reefs do not usually resemble each other, with artificial reefs generally characterized by higher space availability and lower biodiversity (Bulleri and Chapman 2010), which are factors that increase habitat susceptibility to invasion by alien species and opportunistic colonizers (Glasby et al. 2007; Stachowicz et al. 1999, 2002; Zhang et al. 2006; Perkol-Finkel and Benayahu 2009). In many instances, however, the factors underlying susceptibility to invasion appear to be multiple and largely interactive (e.g., Elton 1958; Alpert et al. 2000; Klein et al. 2005; Catford et al. 2011).

The corallivorous polychaete *Hermodice carunculata* is the main described predator of the coral *O. patagonica* in the eastern Mediterranean, causing scars with a dotted pattern on coral skeleton (Fine et al. 2002). However, *H. carunculata* is a warm-water species scarce in the western Mediterranean, and we only observed this species in very few occasions within the Iberian coast. On the other hand, predation by corallivorous gastropods (i.e., *Babelomurex cariniferus*) was an evident factor causing recent partial mortality on coral colonies within the Iberian coast (i.e., denuded skeleton; **Chapter 4.5**; Fig. 5.6e). Although the episodic outbreak of corallivorous gastropods has been reported to cause considerable damage on Mediterranean coral species (e.g., 5% recent partial mortality on colonies of *C. caespitosa*; Kružić et al. 2013), no population outbreak of gastropods was observed at any of the examined locations within the Iberian coast, so their effect on *O. patagonica* was recorded in very few occasions, with a low impact on coral colonies (<0.1% of colony surface area with predation-related recent partial mortality). The sea urchins *P. lividus* and *A. lixula* were observed in a few occasions above the *O. patagonica* colonies, but we were not able to discern if they were feeding on epilithic algae overgrowing the denuded coral skeleton and/or predating on coral tissues (Fig. 5.6f). In contrast, the sea urchins were observed many times feeding on the algal assemblages surrounding the coral colonies, without feeding on coral soft tissues, which supports the hypothesis of facilitative interactions between coral and sea urchin species (Fig. 5.6g-h). Overall, these results suggest that predation does not appear to be a relevant factor impacting the demographics of *O. patagonica*, but further studies may elucidate the importance of sea urchin predation on living coral tissues and small coral recruits (e.g., Bak and van Eys 1975).

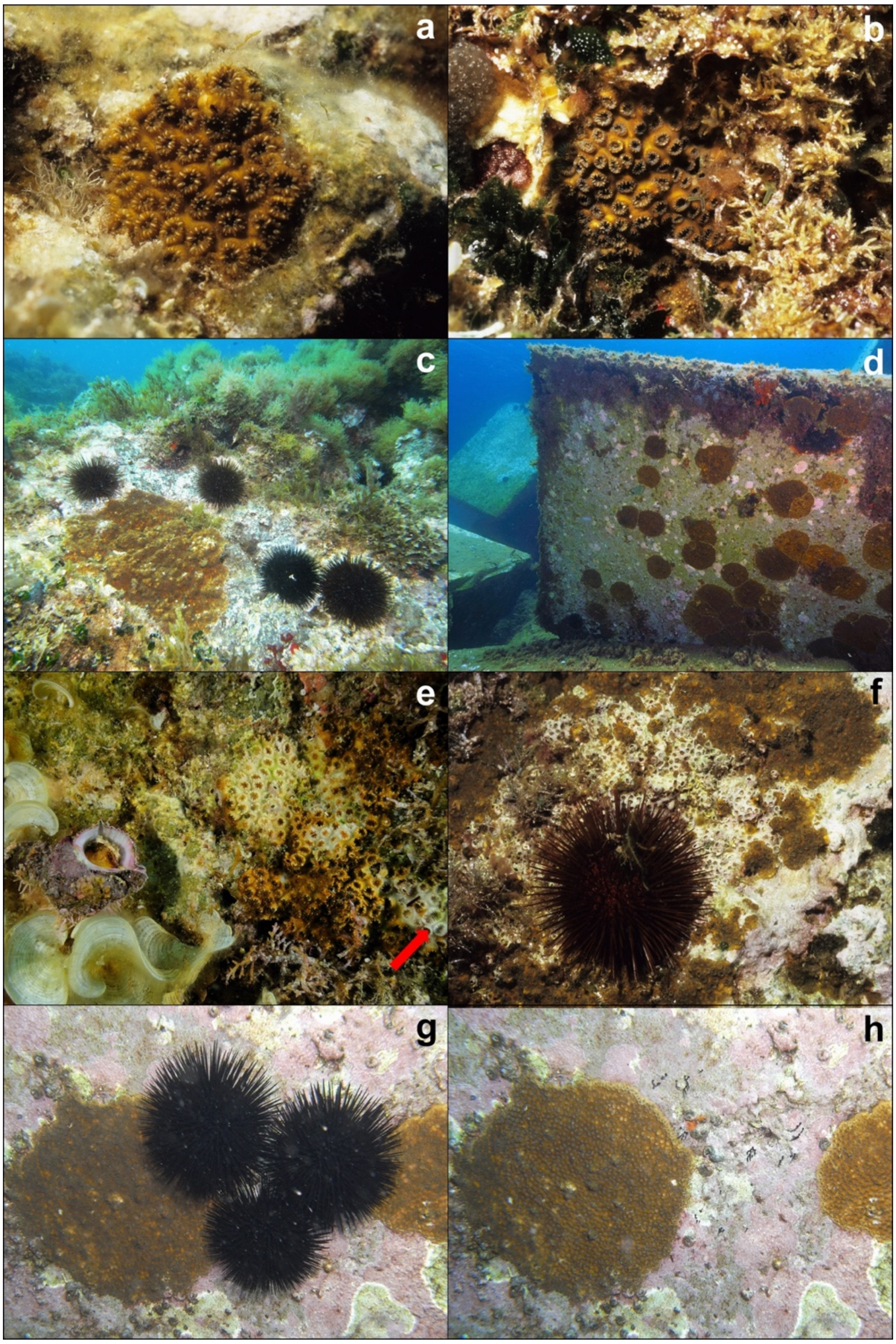


Fig. 5.6 Biological interactions of *Oculina patagonica* in shallow-water Mediterranean rocky reefs. Small coral colony settled on **a** barren ground with sparse turf algae, and **b** canopy-forming fucoid algal assemblages. **c** Coral colony edges growing in a barren ground created *via* grazing by the sea urchins *Paracentrotus lividus* and *Arbacia lixula*. **d** Abundant coral colonies colonizing the vertical wall of a recently-constructed artificial reef (i.e., concrete boulders deployed in 2003, photograph in 2008). **e** Predation by corallivorous gastropod *Babelomurex cariniferus*, the *red arrow* indicates the lesions inflicted on the coral colony. **f** An individual of *P. lividus* above a dead portion of a coral colony with denuded skeleton overgrown by turf algae. **g** Several individuals of *A. lixula* grazing on benthic assemblages surrounding two coral colonies, and **h** the same photograph after removing sea urchins. Photographs (a, f) by Enric Ballesteros, and (d, e) by Juan Carlos Calvín.

5.2.3. Exploring abiotic factors modulating population growth dynamics of *O.patagonica*

The reason why zooxanthellate scleractinian corals dominate shallow-water tropical ecosystems, but are rare on temperate ecosystems where biogenic structure is provided by macroalgae, is a global-scale question in marine biogeography (e.g., Zabala and Ballesteros 1989; Kleypas et al. 1999; Veron 2000). The latitudinal clines in abiotic factors (e.g., ST, solar radiation and nutrients) are the primary drivers modulating coral *versus* macroalgal biogeography. The growth of zooxanthellate corals is mainly constrained by the lower limits of ST and light, which decrease with increasing latitude and limit the global distribution of most coral reefs at latitudes between ~35ºN and 35ºS of the equator and that of zooxanthellate scleractinians between ~40ºN and 40ºS (Kleypas et al. 1999; Veron 2000; Muir et al. 2015). The present distribution range of *O. patagonica* in the temperate Mediterranean Sea, which encompass from 35 to 44ºN in latitude (Fig. 5.1), falls within the high-latitude limit of distribution for zooxanthellate scleractinians. The Mediterranean Sea is a miniature ocean with a high regional variability of key abiotic factors for zooxanthellate corals such as *O. patagonica*, which allow the co-occurrence of both temperate and subtropical climates (Fig. 5.7). The annual mean ST in the Mediterranean ranges from 17 to 24ºC and increases from north to south and from west to east, distinguishing two regions based on the ~20ºC mean ST divide: the west and north-east low-ST areas (i.e., temperate), and the south-east high-ST area (i.e., subtropical; Coll et al. 2010; Fig. 5.7a). It has a strong seasonality in ST, characterized by warm summers ranging from 21 to 32ºC (Fig. 5.7b) and cold winters ranging from 9 to 19ºC in mean monthly ST (Fig. 5.7c). The higher STs are found in the Levant Sea and the lowest in the north-Aegean Sea, Adriatic Sea, Gulf of Lyons and Alborán Sea. The annual mean PAR at sea surface decrease with increasing latitude due to shorter days and lower sun angles (Fig. 5.7d). The basin is generally oligotrophic with a gradient on biological production inversely related to that of ST, although regional features enrich coastal areas (Fig. 5.7e) and diminish irradiance at shallow-water rocky reefs by increasing light-depth attenuation coefficient (Estrada 1996).

In this context, the proliferation of *O. patagonica* throughout the Mediterranean may also be related to the acclimatization of its biological traits to the spatial variation of key environmental conditions (i.e., abiotic factors) modulating the population growth dynamics of zooxanthellate coral species. In particular, the role of (i) light (PAR; autotrophy) and nutrient (e.g., chlorophyll-a as an estimate of plankton availability for heterotrophy) conditions; ii) the thermal regime (annual mean ST and seasonal ST extremes); and iii) the seawater acidification (i.e., saturation state of seawater aragonite) on the growth of *O. patagonica* colonies and populations (i.e., establishment, growth, reproduction and dispersal).

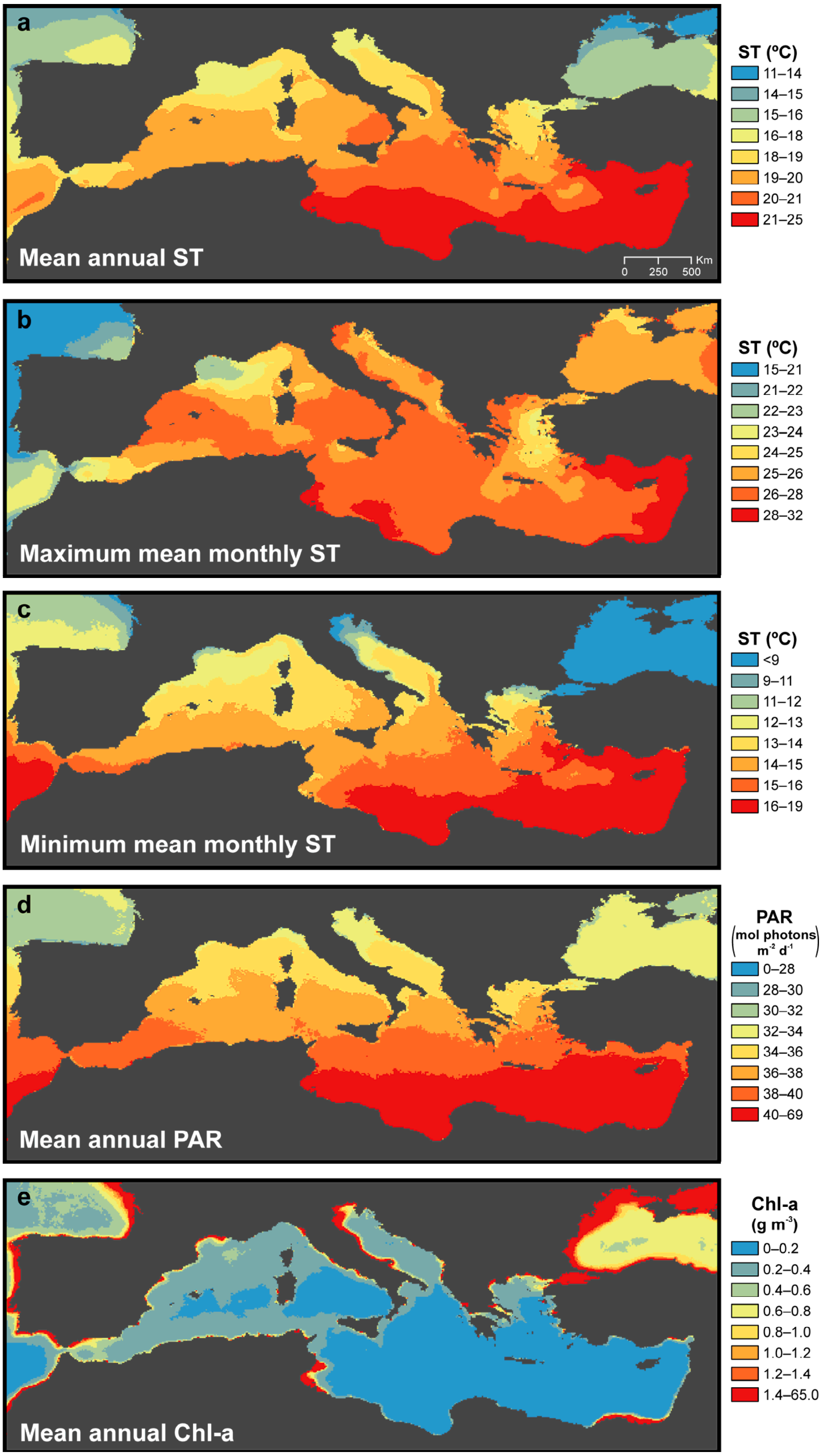


Fig. 5.7 Regional variation of key environmental parameters for the growth of *O. patagonica* in the Mediterranean Sea. **a** Mean annual seawater temperature (ST). **b** Maximum mean monthly ST. **c** Minimum mean monthly ST. **d** Mean annual photosynthetic active radiation (PAR) at sea surface. **e** Mean annual chlorophyll-a (Chl-a). Mean annual data over 2002-2009 (a-c, e) and over 1997-2009 (d) were obtained from Bio-Oracle dataset (Tyberghein et al. 2012).

Coral reefs typically occur in tropical and subtropical areas at low-latitudes, characterized by high light (PAR) and low nutrients (i.e., oligotrophic waters), with low seasonal variability (Zabala and Ballesteros 1989). Thanks to the presence of algae symbionts, zooxanthellate corals display higher growth rates than azooxanthellate corals (i.e., a process termed 'light-enhanced calcification'; Gattuso et al. 1999; Allemand et al. 2004). Thus, high solar radiation is a primary driver for the growth of coral reefs at low-latitudes (i.e., high diversity of zooxanthellate corals and reef-building conditions), where the amount of photo-assimilates transferred by autotrophic symbionts is sufficient to meet a large part of the nutritional needs for basal respiration of reef corals (Davies 1984; Muscatine et al. 1984; Muscatine 1990; Kleypas et al. 1999; Muir et al. 2015). Low light at high-latitudes diminish the amount of photo-assimilates and thus, native zooxanthellate corals in temperate areas such as the Mediterranean are generally scarce (i.e., less diversity and abundance, and generally non-reef building conditions; Schuhmacher and Zibrowius 1985; Zabala and Ballesteros 1989), and are facultative zooxanthellate species able to inhabit low-light and circa-littoral habitats (see Box 1.1 and references therein). The ability to tolerate different habitats reflects the plasticity of some temperate corals in the symbiosis with zooxanthellae and in turn, their ability to shift between auto- and hetero-trophic nutrition. In fact, despite the Mediterranean is an oligotrophic sea, its high seasonal variability (e.g., high-nutrients and low-light conditions during spring-winter) has been suggested as one of the main factors hindering the development of coral reefs in the high-latitude Mediterranean Sea (Zabala and Ballesteros 1989). In this sense, current knowledge on the cryptogenic Mediterranean species *O. patagonica* indicate autotrophic nutrition as the primary energy source, and a secondary role of heterotrophy, for the growth of coral colonies. First, it inhabits shallow-waters and is rare at depths >10 m (Table 5.1; **Chapter 4.5**) subjected to <10% of the surface irradiance (e.g., Weinberg 1978). Second, the annual colony growth cycle is positively correlated with PAR and is enhanced with increased PAR intensities at shallower waters (Rodolfo-Metalpa et al. 2008). Third, the daily heterotrophic carbon input corresponds to a percent contribution to daily respiration of 29% (estimated in mesocosm experiments; Tremblay et al. 2011). Finally, even though *O. patagonica* colonies can thrive only by heterotrophic feeding in dark habitats, azooxanthellate colonies are rare and restricted to habitats with high currents that likely enhanced food-availability (Coma and Ribes 2003; Aichelman et al. 2016). In **Chapter 4.5**, we showed that the demographics of *O. patagonica* (i.e., at both colony and population growth levels) within the ~1300 km Iberian coast were positively correlated with light (PAR at 3 m depth), and negatively correlated with chlorophyll-a (i.e., an estimate of plankton availability for heterotrophy; **Chapter 4.5**). These results reinforce the hypotheses of autotrophy (i.e., light nutrition) as the primary energy source, and light as a primary driver, for the colony and population growth dynamics of *O. patagonica* in the temperate Mediterranean Sea, such as documented in *Oculina arbuscula* (Leal et al. 2014) and generally in zooxanthellate tropical corals (Kleypas et al. 1999; Miller and Hay 1996; Miller 1998; Houlbrèque et al. 2004; Houlbrèque and

Ferrier-Pagès 2009). Nevertheless, further field and laboratory studies may elucidate the relative importance of autotrophy and heterotrophy on *O. patagonica* growth in relation to the seasonal and spatial variation in energy sources within the Mediterranean (Estrada 1996; Millot 2005), particularly during stressful conditions (Coma and Ribes 2003; Aichelman et al. 2016).

The variation in the thermal regime appears as a crucial factor contributing to explain the growth of *O. patagonica* colonies and populations within the Iberian coast. This is consistent with previous studies on the growth rate of coral colonies in the western Mediterranean, in which although the species behaved like a tropical coral with respect to growth enhancement with increasing ST and PAR, the relationships with PAR were weaker (Rodolfo-Metalpa et al. 2008; Rubio-Portillo et al. 2014b) and even absent under low-ST stressful conditions at high-latitudes (**Chapter 4.4**). The performance of zooxanthellate coral species is closely related to their limits of thermal tolerance, and both extremely high and low STs could cause bleaching and mortality, which in turn likely diminish coral population success (e.g., Hoegh-Guldberg et al. 2005; Angilletta 2009; Roth et al. 2012; Sunday et al. 2012; Hughes et al. 2017; see Fig. 1.2). At colony level, the thermal performance curve of *O. patagonica* is characterized by a minimum at 11-16ºC, enhancement up to a threshold of 24-27ºC, and a somewhat decline thereafter (>26-30ºC; Rodolfo-Metalpa et al. 2008, 2014; **Chapter 4.4**). Indeed, exposure to both extremely low- and high-STs has been related to cause bleaching and/or mortality in *O. patagonica* colonies during field experiments (reviewed in Table 5.2, see references therein). On the basis of this review, we identified thresholds that have been related to partial mortality events in *O. patagonica* colonies. Regarding low-ST sub-lethal thresholds, a previous 18-months study documented an episode of colony partial mortality during winter 2005-2006 in the Ligurian Sea (Rodolfo-Metalpa et al. 2008), while in **Chapter 4.4** we showed that coral partial mortality episodes occurred recurrently in winter over the 4-yr period study (winters 2008-2009 to 2011-2012) in the northward range-expanding area from the north-eastern Iberian coast (North-Balearic Sea). In these studies, no colony bleaching episodes were described during winter. In sum, the low-ST conditions during these partial mortality episodes on *O. patagonica* colonies occurring in winter characterized by 81-108 days at <14ºC, 44-73 days <13ºC and 0-29% days <12ºC (Table 5.2a). In accordance, no winter-related mortality and/or bleaching episodes were recorded in studies from warmer regions (e.g., Mid-Balearic Sea and Levant Sea; 0-62 days at <14ºC and 0 days <13ºC; Table 5.2a).

The review on high-ST sub-lethal thresholds for *O. patagonica* showed differences among regions and inter-annual differences within the same region (Table 5.2b and references therein). Within the Mid- and North-Balearic Sea, the high-ST conditions during summer-related partial mortality and/or bleaching episodes on *O. patagonica* colonies characterized by 56-79 days >26ºC and 9-46 days >27ºC. However, similar high-ST conditions (41 days >26ºC and 22 days >27ºC) did not cause colony mortality during summer 2009 at the North-Balearic Sea (**Chapter 4.4**; Table 5.2b). In the Ligurian

Sea, a previous 18-months study documented an episode of colony mortality the first summer (83 days >24ºC and 0 days >25ºC), whereas more severe high-STs did not cause mortality in 2006 (46 days >24ºC and 27 days >27ºC; Rodolfo-Metalpa et al. 2008). The most severe and recurrent bleaching and mortality episodes (~1993-2005) have been documented in the Levant Sea, which represents the warmest region throughout the Mediterranean Sea (i.e., 134 days >26ºC and 13 days >30ºC; Table 5.2b). These differences in sub-lethal high-ST thresholds may be related to a regional variation in the type of zooxanthellae symbionts (Leydet and Hellberg 2016; Grupstra et al. 2017), in the occurrence of pathogens (e.g., Rubio-Portillo et al. 2014c), in the availability of energy sources (e.g., the minimum food availability for heterotrophy occur during summer, which is an important driver of mass mortality events; Coma and Ribes 2003; Coma et al. 2009) and/or to the cumulative impact of consecutive stress events, as observed during consecutive high-ST-related mortality events during summer in *Porites astreoides* (Schoepf et al. 2015). In accordance with the hypothesis of cumulative effects of recurrent impacts on corals, we documented that the cumulative impact of consecutive low-ST-related mortality events during winter may affect the physiological status (energy budget) of the colonies of *O. patagonica*, thus diminishing their resilience and recovery capacity from further stresses (**Chapter 4.4**).

Table 5.2. Review on field studies from the literature which have evaluated associations between seasonal regimes of seawater temperature and the occurrence of mortality and/or bleaching events on *O. patagonica* colonies in the Mediterranean. **a** Low seawater temperature (Low-ST). **b** High-ST. *BL*: visually apparent bleaching, brown coloration (no) or white coloration (yes). *PM*: colony partial mortality, no/yes or proportion of the colony surface (%). Bleaching and mortality episodes are highlighted in bold.

a Low-ST					Temperature (ºC)						
Region	Location	Cold season	BL	PM	≤16	≤15	≤14	≤13	≤12	≤11	References
North-Balearic Sea	L'Ampolla	2008-2009	no	**26**	**162**	**143**	**94**	**63**	**0**	**0**	**Chapter 4.4**
		2009-2010	no	**48**	**161**	**129**	**104**	**73**	**29**	**0**	
		2010-2011	no	**57**	**151**	**135**	**108**	**63**	**15**	**0**	
		2011-2012	no	**66**	**141**	**112**	**81**	**44**	**17**	**0**	
Mid-Balearic Sea	Alacant harbor	2010-2011	no	no	140	111	62	0	0	0	Rubio-Portillo et al. 2014b, 2014c
	Tabarca Island	2010-2011	no	no	128	99	35	0	0	0	
Ligurian Sea	Monaco	2005-2006	no	**5-20**	**137**	**127**	**105**	**66**	**0**	**0**	Rodolfo-Metalpa et al. 2008
Levant Sea	Sdot-Yam	~1993-1994 to 2004-2005	no	no	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	Fine and Loya 1995; Kushmaro et al. 1997, 1998; Fine et al. 2001; Israely et al. 2001; Shenkar et al. 2005, 2006; Ainsworth et al. 2008

b High-ST		Warm			Temperature (ºC)							
Region	Location	season	BL	PM	≥24	≥25	≥26	≥27	≥28	≥29	≥30	References
North-Balearic Sea	L'Ampolla	2009	no	no	90	75	41	22	0	0	0	**Chapter 4.4**
		2010	no	no	69	60	0	0	0	0	0	
		2011	no	no	66	47	34	0	0	0	0	
Mid-Balearic Sea	Alacant harbor	2010	**yes**	no	**99**	**89**	**65**	**46**	**17**	**0**	**0**	Rubio-Portillo et al. 2014b, 2014c
		2011	**yes**	no	**112**	**89**	**79**	**30**	**0**	**0**	**0**	
	Tabarca Island	2010	no	no	99	82	61	0	0	0	0	
		2011	**yes**	**35**	**108**	**90**	**56**	**17**	**0**	**0**	**0**	
		2015	no	**30**	**>80**	**maximum daily ST of 28.2ºC**						Rubio-Portillo et al. 2016
Ligurian Sea	Monaco	2005	no	**30**	**83**	**0**	**0**	**0**	**0**	**0**	**0**	Rodolfo-Metalpa et al. 2008
		2006	no	no	46	42	33	27	0	0	0	
Levant Sea	Sdot-Yam	~1993 to 2005	**yes**	**yes**	**171 ± 2**	**151 ± 2**	**134 ± 2**	**110 ± 2**	**88 ± 3**	**56 ± 3**	**13 ± 5**	Kushmaro et al. 1997, 1998; Fine et al. 2001; Israely et al. 2001; Shenkar et al. 2005, 2006; Ainsworth et al. 2008; Armoza-Zvuloni et al. 2011

ST data from the Levant Sea (Sdot-Yam, Israel) are the mean ± SE of seven cold periods (2003-2004 to 2009-2010). ST data was obtained using HOBO® data-loggers (L'Ampolla and Alacant harbor: 2010, 2011, 2010-2011) and from satellite MODIS (Aqua) sensor system for the other locations and years. ST data from Alacant harbor (i.e., the study site was a concrete seawall located ~1km inside the harbor, in enclosed waters) was courtesy facilitated by Esther Rubio-Portillo. Surface ST time series were obtained from satellite-derived measurements performed by NASA's Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov/), which were made available as 'Ocean Level-2' HDF data. A ST time series was obtained on a 9-km^2 area (3x3 km) for each location. For the analysis, we considered only high-quality ST readings (flag values of 0 or 1). The ST series were linearly interpolated to obtain continuous series with daily values. ST thresholds are based on mean daily values. To examine whether exposure to low-ST thresholds (≤16 to ≤11ºC) could impact the species, we determined the fall/winter days on which ST dropped below each threshold and the days in spring/early summer of the next year on which it rose above each ST. To examine whether exposure to high-ST thresholds (≥24 to ≥30ºC) could affect the species, we determined the days in spring/summer on which the ST reached each threshold and the days in late summer/fall on which it dropped below each ST. To avoid any bias introduced by short-term ST oscillations, we determined that the daily mean ST values had to remain ≤ or ≥ each threshold on at least 80% of the days throughout the following two weeks (i.e., 11 of 14 days) after the date on which the ST crossed the threshold to be considered.

Interestingly, the annual growth cycle of *O. patagonica* colonies has shown contrasting patterns between the extreme ST regimes (low- and high-ST areas) found within the Mediterranean (Fig. 5.7a-c), which exceed both species-specific sub-lethal ST thresholds causing stress and delayed effects of ST on coral colony growth. In the North-Balearic Sea (low-ST area), the annual cycle of colony growth is positively correlated with ST, and is characterized by recurrent colony partial mortality episodes during severe winter (<12-14ºC) and lesion recovery and growth during summer (>16-27ºC; **Chapter 4.4**). In contrast, colony growth in the Levant Sea (high-ST area) is negatively correlated with ST, and is characterized by recurrent bleaching and colony partial mortality episodes during severe summer (>26-30ºC) and lesion recovery and growth during winter (<26-18ºC; e.g., Israely et al. 2001; Shenkar et al. 2005). Both sub-lethal low- and high-ST thresholds have been linked to reduced survival, growth and/or reproduction in *O. patagonica* colonies (e.g., Fine et al. 2001; Rodolfo-Metalpa et al. 2008; Armoza-Zvuloni et al. 2011), which in turn likely diminish coral population growth. At population level (i.e., population growth dynamics), the results obtained in **Chapter 4.5** are contributing to identify the most appropriate thermal regime for the success of *O. patagonica* colonies and populations within the Iberian coast, which appear to be generally constrained by cold-ST regimes, with thresholds that limit coral growth of annual mean ST <19ºC, P10th-ST <14ºC and P90th-ST <25ºC, but without severe high-ST periods (i.e., percentile 90th-ST >27ºC). Interestingly, the adverse low- and high-ST thresholds obtained at population level within the Iberian coast (i.e., mean annual P10th-ST <14ºC and P90th-ST >27ºC) generally coincided with previously described sub-lethal thresholds for the colonies of *O. patagonica* (e.g., 81-108 days at <14ºC and 9-46 days >27ºC, respectively; Table 5.2 and references therein). Despite the lower mean annual ST (chronic and acute stresses) appear as an important driver constraining the occurrence and demographics of *O. patagonica* within the low-ST biogeographic areas of the Iberian coast (Alborán Sea, Balearic Sea and Gulf of Lyons), the episodic exceed of high-ST species-specific sub-lethal threshold (P90th-ST >27ºC) also appeared to constrain coral colony and population growth in the Mid-Balearic Sea (Rubio-Portillo et al. 2014b, 2016; **Chapter 4.5**).

In the framework of the consistent relationship between the performance of *O. patagonica* and the different ST regimes found within the Iberian coast (**Chapter 4.5**), the analysis of the thermal regime of the other Mediterranean areas with available data on species demographics allowed us to further examine the role of ST on the population growth dynamics of the species. The coral *O. patagonica* has established in the low-ST areas (mean annual ST <19-17ºC and P90th-ST <25-22ºC), either with or without severe low-ST periods (P10th-ST <15-12ºC), such as the Algerian and Tunisian waters, Alborán Sea, North-Balearic Sea, Gulf of Lyons, Ligurian Sea and the central-Adriatic Sea (Fig. 5.7a-c). However, although the species had an ancient presence in most of these low-ST areas (i.e., >50 years of first record, or on the basis of maximum colony size), they currently have a limited number of recorded locations (i.e., fragmented distribution) with isolated large colonies but incipient populations (i.e., isolated to tens of colonies per location; Table 5.1). Lag-phases related to Allee effects (e.g., skewed sex ratio at locations with very low abundance of *O. patagonica*; Fine et al. 2001; **Chapter 4.3**) may be further constraining coral spread in these low-ST areas (Taylor and Hastings 2005). In contrast, the largest abundances of *O. patagonica*, with a high number of recorded locations (i.e., continuous distribution) and large populations (i.e., up to hundreds of colonies per location, locally reaching up to >50% in cover) have been documented in the South-Balearic Sea and in the South-Aegean Sea, both characterized by a warmer thermal regime (mean annual ST >19-21ºC, P90th-ST >25-27ºC) without severe low-STs (P10th-ST >14ºC; Table 5.1, 5.2a; Fig. 5.7a-c). Accordingly, the highest-ST area in the Mediterranean (Levant Sea; i.e., mean annual ST >23ºC and P90th-ST >29-30ºC) sustain abundant coral populations continuously distributed along ~250 km coastline, although the common exceed of high-ST sub-lethal thresholds (i.e., P90th-ST >27-30ºC) has been related to cause annually bleaching and mortality episodes during the reproductive season in summer (April-

September; Table 5.1, 5.2b; Fig. 5.7), which likely constrain the growth of coral colonies and populations (Fine et al. 2001; Armoza-Zvuloni et al. 2011). These evidences further reinforce the thresholds documented in this **PhD Thesis** to limit coral success within the Iberian coast, and overall indicate moderate high-ST regimes (i.e., mean annual ST >19-21ºC and P90th ST >25-27ºC), without severe cold-ST periods (P10th ST >14ºC) and/or warm-ST periods (P90th-ST <28ºC), as the optimal thermal conditions for the successful growth of *O. patagonica* colonies and populations within the Mediterranean Sea. Further long-term monitoring studies of coral populations at large-spatial scales may elucidate the underlying effects of distinct thermal regimes on the population growth dynamics of *O. patagonica*. For instance, knowledge of reproductive biology and its plasticity in scleractinian corals dealing with natural and anthropogenic disturbances is essential for understanding their population dynamics and dispersal (Fadlallah 1983; Harrison and Wallace 1990; Harrison 2011). The annual cycle of gametogenesis of *O. patagonica* is similar between the eastern and western Mediterranean basins, being positively correlated with the annual cycle of ST (i.e., starting with the increase in ST in April, and spawning during the beginning of ST decrease in September, overlapping the full moon period). In this context, preliminary data on the regional variation in coral reproduction output (i.e., fecundity estimates prior to spawning) indicate that reproduction may act as a key parameter modulating the regional variation in the success of *O. patagonica* within the Iberian coast (Correa 2013; authors' unpublished data).

The uptake of anthropogenic CO_2 by the oceans (i.e., seawater acidification) has already resulted in a decrease in pH of ~0.1 units compared to pre-industrial times and is projected to further decrease by 0.3-0.5 points by 2100 (Gattuso and Lavigne 2009; Calvo et al. 2011; Orr et al. 2005). The seawater acidification (i.e., a decrease in the saturation state of seawater aragonite) is considered among the main threats reducing the rate of biogenic calcification in calcifying organisms such as corals (e.g., Orr et al. 2005; Pandolfi et al. 2011; Doney et al. 2009; Jokiel et al. 2016). In this sense, mesocosm experiments have shown that *O. patagonica* reduced colony growth rate by 32% in projected pH by 2100 (i.e., at 7.8 pH units; Movilla et al. 2012) and that a complete dissolution of the skeleton occurs at 7.4 pH units (Fine and Tchernov 2007), suggesting that ocean acidification may constrain the success of *O. patagonica* in the near future. In addition, photosynthetic algae, which compete with *O. patagonica* for benthic space occupancy, may take advantage of a greater availability of CO_2 (Koch et al. 2013; Kroeker et al. 2013). Further studies may elucidate the interactive and long-term negative effects of ocean acidification, as an accompanying component of global change, on the changes in demographic processes and ecological interactions modulating the population growth dynamics of *O. patagonica*.

5.3. Future perspectives for the expansion of *Oculina patagonica* in the Mediterranean Sea

Shallow-water rocky ecosystems in temperate areas are dominated by macroalgae and not corals, which are generally scarce (Kleypas et al. 1999; Miller 1998; Sunday et al. 2012; Veron et al. 2015). However, the distributional limits and abundances of zooxanthellate coral species are closely related to their physiological limits of thermal tolerance, and are expected to range shift poleward, tracking the warming-related migration of suitable STs (e.g., Burrows et al. 2011, 2014; Poloczanska et al. 2013, 2016; Pörtner et al. 2014; see Fig. 1.2). Sea warming appears as the main driver of the widespread phase shifts from zooxanthellate coral- to macroalgal-dominance, and under even lower greenhouse gas emission scenarios, most coral reefs in tropical and subtropical regions may enter a non-coral-dominant stage before the end of the century (e.g., Hoegh-Guldberg and Bruno 2010; Pandolfi et al. 2011; Frieler et al. 2013; Hughes et al. 2017; Fig. 1.3). In fact, the area covered by zooxanthellate scleractinian corals has already declined by 50% since the 1980s (Bruno and Selig 2007; De'ath et al. 2012; Graham et al. 2015). In turn, some zooxanthellate corals in temperate areas are responding to sea warming by increasing in abundance, while tropical and subtropical corals are shifting poleward into temperate areas, and suitable habitats for coral reefs are predicted to expand poleward in future climate scenarios (Burrows et al. 2011; Vergés et al. 2014a; Freeman 2015; Fig. 1.4). The spread of corals in temperate areas is further favored by the warming-related depletion of algal forests (Harley et al. 2012). Given the rapid rate of change in species' distribution boundaries and abundances, including key structural species (i.e., macroalgae and corals), due to the cumulative effects of sea warming and other natural- and human-related impacts (i.e., global change), marine ecosystems are reorganizing in alternative states, causing dramatic phase shifts that are persistent in time (Conversi et al. 2015). In this context, understanding the ability of zooxanthellate coral species to adapt to environmental conditions at temperate, high-latitude areas is crucial to predict future ecosystem shifts in response to global change.

The coral-mediated tropicalization of macroalgae-dominated temperate ecosystems is a global scale phenomenon, in which the interaction of natural- and human-related impacts has first led to widespread phase shifts from macroalgae- to barren-dominance, and lately the poleward shift of subtropical and tropical zooxanthellate corals is leading to coral-dominated assemblages, challenging the dominant functional benthic group (reviewed in Vergés et al. 2014a). Regions with continuous tropical-temperate coastlines influenced by poleward currents (i.e., transport warm tropical water into temperate areas) are potential hotspots for such ecosystem shifts in response to gradual warming (Wu et al. 2012; Yang et al. 2016). In fact, a decline in cold-water macroalgae and a poleward influx and/or increase in abundance of subtropical and tropical organisms (i.e., herbivorous sea urchins and fishes, and zooxanthellate corals) have been already described in most temperate areas with continuous tropical-temperate coastlines. In fact, the tropicalization of temperate ecosystems by zooxanthellate scleractinian corals have been described in Japan (33ºN, *Acropora* spp. and *Pavona decussata*; Serisawa et al. 2004; Yara et al. 2011; Yamano et al. 2011, 2012; Denis et al. 2013), Korea (33ºN, *Alveopora japonica*; Denis et al. 2015; Vieira et al. 2016), eastern North-America (26-28ºN, *Acropora cervicornis* and *A. palmata*; Vargas-Ángel et al. 2003; Precht and Aronson 2004), eastern Australia (30ºS, *Acropora* spp.; Baird et al. 2012), western Australia (29-31ºS, e.g., *Acropora* spp., *Goniopora norfolkensis*, *Plesiastrea versipora*; Marsh 1993; Thomson 2010; Richards et al. 2016; Tuckett et al. 2017). The tropicalization of shallow-water temperate ecosystems by zooxanthellate scleractinian corals is a phenomenon also occurring in the semi-enclosed Mediterranean Sea (31-44ºN, *O. patagonica*; this **PhD Thesis**). In addition, some zooxanthellate species of zoanthid corals (Zoantharia, Zoanthidae) are also expanding poleward and experiencing population outbreaks within their distribution ranges, such as in Korea and Japan (*Zoanthus sansibaricus*, 33-36ºN; Reimer et al. 2016).

Similarly to their tropical counterparts, the few native zooxanthellate corals from the temperate Mediterranean Sea have also been already affected by extremely high-ST events and show a decreasing demographics along an increasing-ST regional gradient, pointing that the threats posed by sea warming would further deplete native coral populations (e.g., Goffredo et al. 2008; Kersting et al. 2013; Airi et al. 2014; Kružić et al. 2016; see Box 1.1). In contrast, the cryptogenic coral *O. patagonica* has been range shifting its geographical distribution in multiple directions, and establishing abundant populations along wide areas (i.e., >100 km in coastal length) in several regions throughout the Mediterranean (Table 5.1). The successful proliferation of the zooxanthellate scleractinian *O. patagonica* across the Mediterranean Sea only resembles that of the invasive azooxanthellate scleractinian *Tubastraea coccinea* (Scleractinia, Dendrophylliidae), which is also experiencing a rather recent invasive behavior (Blackburn et al. 2011) in the tropical and subtropical western Atlantic Ocean, both in the northern (Caribbean and Gulf of Mexico) and southern hemispheres (Brazil; Fenner and Banks 2004; Creed and De Paula 2007; Sammarco et al. 2012; Silva et al. 2014; Carlos-Júnior et al. 2015; Creed et al. 2017). As a native of the tropical Indo-Pacific, its occurrence in the western Atlantic was first recorded from some Caribbean islands, where it may have been introduced in the 1930s as a fouling organism on an oil platform or a ship hull (Cairns 2000). The capacity of *T. coccinea* to reproduce both sexually and asexually (Glynn et al. 2008; Capel et al. 2014), and to settle and grow readily on man-made substrates (oil and gas platforms, buoys and ships) may have assisted its wide geographic dispersal (reviewed in Creed et al. 2017), and these life-history traits are similar to those documented for the range-expanding coral *O. patagonica* in the Mediterranean. In fact, both species have a broad tolerance to varying environmental parameters, are opportunistic colonizers of high fecundity, generalists in terms of substratum utilization (e.g., can successfully outcompete the surrounding native benthic organisms for space occupancy), and benefit from current human-related impacts (e.g., their population growth is enhanced in artificial habitats, which likely act as corridors for successful dispersal; Fig. 1.8; Fig. 5.4; e.g., Fine et al. 2001; Creed 2006; Mantellato et al. 2011; Riul et al. 2013; Mantellato and Creed 2015; Creed et al. 2017; **Chapters 4.1**, **4.5**).

Understanding of the threats of global change on the structure and dynamics of benthic macroalgae assemblages (i.e., the dominant group in shallow-water rocky communities; Box 5.1), and the biotic interactions of *O. patagonica* (i.e., competition, facilitation and predation; Fig. 5.6), is especially relevant to determine the interactive effects of global change on the expansion dynamics of *O. patagonica*. However, some aspects remain poorly understood. For instance, the primary production of macroalgal assemblages in the Mediterranean is dynamic and exhibit a strong seasonality, with most algal communities showing maximum production and biomass from late-winter to summer (Ballesteros 1989, 1991). Therefore, the success of *O. patagonica* larvae, spawning in early autumn, likely may benefit from the natural reduction of algal biomass occurring during autumn and early winter (i.e., higher open space availability for settlement and overwinter survival of coral recruits, and to grow enough calcareous skeletons to outcompete soft macroalgae during algal bloom of first spring). Further field studies are needed to understand the effects of distinct composition of benthic algal communities, and its seasonal changes in biomass, on *O. patagonica* population growth dynamics. Nevertheless, healthy shallow-water rocky reefs dominated by canopy-forming macroalgae (i.e., algal forests) are generally being lost throughout the Mediterranean due to the combined effects of natural- and human-related disturbances (e.g., severe storms, sea warming, pollution, habitat destruction and artificial reefs, and increased grazing by sea urchins outbreaks and invasive rabbit fish), shifting the diverse and productive algal forests to other non-canopy-forming algal assemblages and deforested barrens (Box 5.1 and references therein). The dynamics of sea urchin-mediated regime shifts show a globally coherent pattern in temperate seas worldwide, in which sea urchin grazing cause a discontinuous regime shift with hysteresis effect of about one order of magnitude in sea urchin biomass between critical thresholds of overgrazing *versus* recovery, thus making these shifts hard to reverse (Ling et al. 2015; Boada et al. 2017). In addition, the invasive rabbitfish species entered the Mediterranean via the Suez Canal and rapidly expanded westward (Sala et al. 2011; Vergés et al. 2014b), suggesting that global change impacts on native macroalgal assemblages will increase open space availability in the near future, which likely further pave the way for *O. patagonica* expansion.

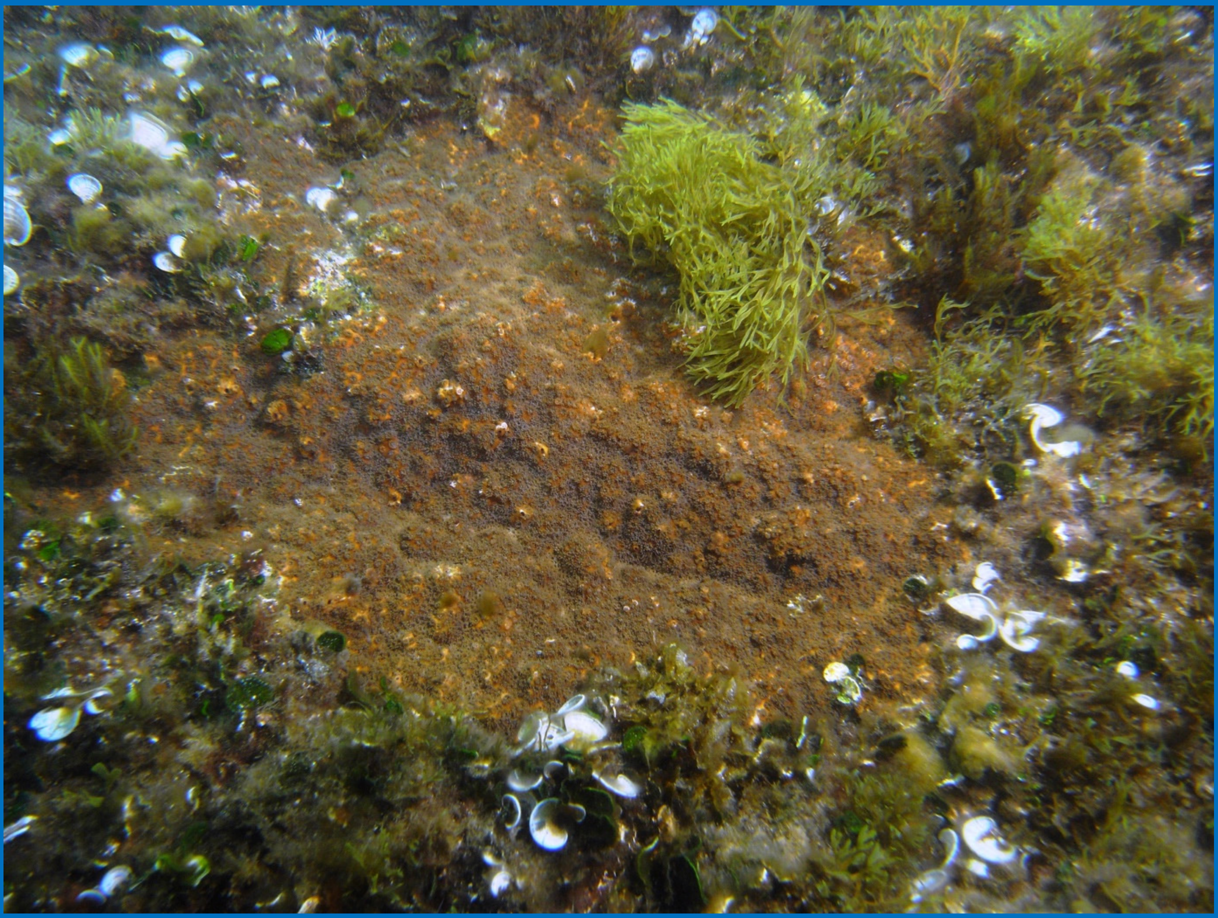
The sea warming trend in shallow waters from the western Mediterranean over the period 1980-2010 has been estimated in ~0.03ºC yr^{-1}, but no warming trends in mean annual ST were detected before the 1980s (Belkin 2009; Coma et al. 2009; Nykjaer 2009; Vargas-Yáñez et al. 2010). The ~1ºC increase in mean annual ST after 1980s was somewhat concomitant with the time period (2000s) in which the spread of *O. patagonica* (i.e., at both population growth and distributional range levels) has been documented in this **PhD Thesis** along the Iberian coast (western Mediterranean), and coincided with the 90% of warming-related impacts reported since year 1950 (Conversi et al. 2010; Marbà et al. 2015). Note that the establishment and growth of long-lived scleractinian corals such as *O. patagonica* needs several years for changes in recruitment and recruit survival to manifest in visibly expanding populations. Besides the increase in mean annual ST, sea warming has also been related to a significant increase in mean ST of the warmest month of the year (0.011ºC yr^{-1} over 1950-2009 throughout the Mediterranean; Hoegh-Guldberg et al. 2014), including the occurrence of single extremely high-ST events after the 1990s (Belkin 2009; Coma et al. 2009; Nykjaer 2009; Vargas-Yáñez et al. 2010). Whether a change in mean ST of the coldest month of the year throughout the Mediterranean has occurred is still uncertain because although Shaltout and Omstedt (2014) observed a significant pattern of ST increase over 1982-2012 (0.016 ºC yr^{-1}), other studies encompassing similar time periods (1985-2006) only observed a significant increase in winter ST in the eastern Mediterranean (e.g., Nykjaer 2009), and no warming trends in mean winter-STs were detected before the 1980s (e.g., 0.004ºC yr^{-1} over 1950-2009; Hoegh-Gulberg et al. 2014). Under future warming scenarios, *O. patagonica* is expected to benefit from a lengthening of its growing season at the low-ST areas of its distribution (western and north-eastern Mediterranean) and from a reduction in the severity of recurrent mortality episodes during winter at high-latitudes, and therefore, it is expected that this species will further expand its distribution range and abundances within low-ST regions. In contrast, the faster warming rate in mean ST (~0.06ºC $year^{-1}$ over 1980-2010) documented in the high-ST area (i.e., Levant Sea; Belkin 2009; Nykjaer 2009; Vargas-Yáñez et al. 2010) is expected to further diminish *O. patagonica* population growth by diminishing the optimum growth conditions which only occur during the low-ST period of the year, and by increasing the severity of mortality episodes that already annually occur during summer (e.g., Fine et al. 2001). Nevertheless, our survey within the Iberian coast represents only one sampling point in time and limit the rating of the importance between the components of thermal regime (annual mean ST, and P90th-ST and P10th-ST) in determining the population growth dynamics of *O. patagonica*. In fact, coral populations exposed to contrasting thermal regimes can exhibit different degrees of acclimatization and resilience to sea warming (Hughes et al. 2003). In addition to chronic sea warming, the occurrence of single extremely low- or high-ST events are considered key drivers of population dynamics for long-lived species such as corals (e.g., Easterling et al. 2000; Kersting et al. 2013; Takao et al. 2015; Tuckett et al. 2017), and both severe summers and winters have episodically occurred in the Mediterranean (Coma et al. 2009; Nykjaer 2009; Vargas-Yáñez et al. 2012).

The ongoing coral-mediated tropicalization of the temperate Mediterranean Sea is being solely driven by the range-expanding zooxanthellate coral *O. patagonica*. In fact, the surveys conducted along the Iberian coast indicate that *O. patagonica* is the most abundant zooxanthellate coral species in shallow-waters, whereas the native zooxanthellate coral *C. caespitosa* is generally scarce (i.e., isolated colonies; authors' unpublished data), in accordance with the fact that only few living bioconstructions of *C. caespitosa* currently exist in the Mediterranean (reviewed in Chefaoui et al. 2017). Given that the Mediterranean is a semi-enclosed basin that does not have continuous tropical-temperate coastlines influenced by poleward currents (Vergés et al. 2014a), the northward range shift (i.e., northward migration) of zooxanthellate coral species is not plausible (i.e., zooxanthellate corals are rare in the Eastern Atlantic; Zibrowius 1980). However, some azooxanthellate scleractinian coral species, native from the eastern Atlantic and adjacent Mediterranean coasts, appear to be range shifting their distribution ranges and expanding their populations inside the Mediterranean, tracking the migration of suitable STs (Clemente et al. 2011; López-González et al. 2010; Burrows et al. 2011; Ocaña-Vicente et al. 2011).

Nevertheless, the Mediterranean has an intense maritime traffic and several alien species may have been introduced *via* shipping, either as a fouling organism or in larval stage in ballast waters (Bianchi 2007; Galil 2009, 2012; Zenetos et al. 2010, 2012). At present, only one alien zooxanthellate coral species has already been recorded in the central Mediterranean (i.e., *O. crispata* in Corsica; Hoeksema and Ocaña-Vicente 2014), and shipping can be considered a plausible vector for the introduction of this species in the Mediterranean, because although it is native from the Indo-Pacific, its native distribution range does not include the Red Sea (i.e., natural dispersion *via* the Suez Channel is not a plausible explanation). The thermal regime in several Mediterranean regions mimic the thermal conditions found in the native range of distribution of the cold-tolerant coral *O. crispata* (i.e., it can survive at 7°C; Yamashiro 2000), and has a reputation of being an opportunistic successful colonizer (i.e., it can settle on a wide variety of artificial substrates and reproduces both sexually and asexually; Nakano and Yamazato 1992; Yamashiro 2000; Lam 2000a, 2000b; Chen et al. 2011), suggesting that this coral could expand throughout in the near future (Hoeksema and Ocaña-Vicente 2014). In addition, thermal conditions at least in the Levant Sea, with minimum monthly ST around 18ºC, are already suitable for most reef-building coral species (Kleypas et al. 1999). Therefore, given the predicted trends of sea warming and the ongoing alien biodiversity enrichment in the Mediterranean, with currently more than 1,000 alien and cryptogenic species (Lejeusne et al. 2010; Hoegh-Guldberg et al. 2014; Zenetos et al. 2017), and its connection *via* the Suez Channel to the Indo-Pacific' coral reefs (i.e., Red Sea), it seems feasible the suggestion made by Por (2009) indicating that 'it is probably only a matter of time till, by accidental means, other alien zooxanthellate scleractinians will emerge'. In fact, several alien species of non-scleractinian cnidarians (i.e., hydroids and jellyfish) have already been introduced into the Mediterranean, most of which are of tropical origin and were likely introduced *via* shipping (reviewed in González-Duarte et al. 2016). For instance, the alien zooxanthellate hydrocoral *Millepora* sp. (Hydrozoa, Anthoathecata) was first discovered in 2004 in the neighboring subtropical eastern Atlantic (11ºN, Canary Islands; Clemente et al. 2011) and genetic studies indicated that the source populations where from the Caribbean (western Atlantic; López et al. 2015). Some alien species of non-scleractinian cnidarians have experienced population outbreaks and an invasive behavior in the warming Mediterranean Sea (i.e., spreading their distribution range and increasing abundances within invaded ranges; González-Duarte et al. 2016). For instance, the increased occurrence of population outbreaks documented in the native jellyfish *Pelagia noctiluca* has been related to the cumulative effects of human-related impacts (Canepa et al. 2014).

The broad spread of the zooxanthellate coral *O. patagonica* across the Mediterranean Sea, and its invasive behavior at both distribution range shift and population outbreak levels, able to drive phase shifts from macroalgal to coral dominance in natural and artificial reefs, is consistent with the ongoing process of coral-mediated tropicalization of shallow-water rocky ecosystems documented in other worldwide subtropical and temperate areas under current sea warming. While this **PhD Thesis** apply specifically to the zooxanthellate coral *O. patagonica* in the Mediterranean, the conceptual approaches we have used have a more general applicability, and the shallow-water rocky ecosystems responses we document are likely valid for other temperate ecosystems worldwide. The study of the ecology of the range-expanding coral *Oculina patagonica* has just started and during the development of this **PhD Thesis** many interesting and unresolved questions have arisen. Future research is needed to further understand the population ecology of *O. patagonica* and the main factors modulating its invasive behavior, and the general process of coral-mediated of tropicalization in temperate ecosystems worldwide. We encourage authorities to pay attention to the spread of range-expanding zooxanthellate coral species at large spatial-scales, determine their impact on shallow-water marine ecosystems, and facilitate research-driven making of management decisions.

6. GENERAL CONCLUSIONS



Chapter 6

6. GENERAL CONCLUSIONS

The main conclusions that arise from the manuscripts of this **PhD Thesis** are described below:

- **Chapter 4.1. A phase shift from macroalgal to coral dominance in the Mediterranean**

- The study case of a particular natural location in the South-Balearic Sea (37ºN) provide evidence that the bioconstructions formed by the range-expanding zooxanthellate coral *Oculina patagonica* can drive a persistent regime shift from macroalgal- to coral-dominance in shallow-water rocky ecosystems from the Mediterranean Sea.

- The high density and the positively skewed size-frequency structure of *O. patagonica* colonies indicate high recruitment and a fast-growing population.

- Physical disturbance from sand scouring appear as the main source of open space (i.e., algal-depleted benthic assemblages) for *O. patagonica* to colonize, which likely have facilitated the high development of this coral population.

- **Chapter 4.2. Sea urchins predation facilitates coral invasion in a marine reserve**

- Over an 8-yr period (2002–2010), the zooxanthellate coral *O. patagonica* has experienced populations outbreaks (i.e., an increase in coral density at a rate of ~0.1–0.2 colonies m^{-2} yr^{-1} and in cover at 0.9–1.4% yr^{-1}) in a marine reserve from the South-Balearic Sea (38ºN).

- The coral *O. patagonica* reached a mean density of 1.4–2.0 colonies m^{-2} and a mean cover of 10–15% of the rocky bottom in 2010, becoming the most abundant invertebrate species in the shallow-water ecosystems from the marine reserve.

- The increase in the density and cover of *O. patagonica* over time and the colony size-structure of the populations indicate that high recruitment, colony survival and sustained growth played an important role in increasing coral abundance.

- A trophic interaction facilitated the population outbreak of *O. patagonica*. Over the ~8-yr period (2002–2010), the biomass of sea urchins increased 4-fold, and the colonies of *O. patagonica* settled preferentially on barren areas cleared by sea urchins, indicating that the grazing of sea urchins on macroalgae facilitated coral recruitment, and the survival and growth of coral colonies.

- **Chapter 4.3. Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean**

- Over a 19-yr period (1992–2010), the zooxanthellate coral *O. patagonica* has experienced a northward distributional range shift along ~400 km of coastline in the north-eastern Iberian coast, from the North-Balearic Sea (40º31'N) to the Gulf of Lyons (42º13'N).

- The northward range shift of *O. patagonica* was at a rate of 22 km yr^{-1}, and was driven by the join action of two spatial scales of dispersal: neighborhood and long-distance.

- The spread curve of *O. patagonica* over time (i.e., the cumulated number of locations with the species) characterized by a 9-yr lag phase during which the spreading rate was much lower than in the exponential phase. The exponential phase began shortly after the species established some foci in the area.

- The occurrence and abundance of *O. patagonica* was higher in artificial locations than in natural locations within each zone of the north-eastern Iberian coast, indicating that artificial reefs foster the population growth of this species.

- The pattern of the spread curves of *O. patagonica* diverged between artificial and natural locations, with a half-reduced duration of the lag phase and a 2-fold higher slope for the exponential phase in the former, indicating that artificial reefs act as corridors that enhance the distributional range shift of this range-expanding coral.

- Lengthening of the growing season of *O. patagonica* over 1992–2010 due to sea warming (i.e., a 10% increase in the number of days with seawater temperature (ST) >18ºC, the period in which the species growth is 2-fold higher than that at lower ST) may have favored the northward spread of the species at high-latitudes.

- **Chapter 4.4. Recurrent partial mortality events in winter shape the dynamics of the zooxanthellate coral *Oculina patagonica* at high latitude in the Mediterranean**

- The colonies of the zooxanthellate coral *O. patagonica* can survive and grow at high-latitudes (41ºN) under a wide seasonal variation in ST (monthly mean ranging from 11.7 to 27.1ºC) at the range-expanding area in the north-eastern Iberian Peninsula (North-Balearic Sea).

- The colonies of *O. patagonica* exhibit a strong seasonal cycle that includes partial mortality and cessation of growth during winter (December to April), tissue regeneration starting in late spring (May) and linear extension during summer and fall (June to November).

- The annual pattern of partial mortality on *O. patagonica* colonies is negatively correlated with ST, and the annual pattern of linear extension is positively correlated with ST, but were not correlated with photosynthetic active radiation (PAR), indicating that the annual dynamics of *O. patagonica* colonies at this high-latitude area are primarily driven by ST.

- The low-ST conditions during partial mortality episodes on *O. patagonica* colonies occurring in winter characterized by 81–108 days at <14ºC, 44–73 days <13ºC and 0–29 days <12ºC, and the severity of partial mortality events appear to be related to the extent of exposure to low-ST conditions and the cumulative impact of consecutive winter-related mortality events.

- The high capacity of *O. patagonica* colonies to recover from lesions occurring in winter, and the subsequent survival and resumption of colony growth during the favorable summer season, is a decisive biological trait that enables this species to withstand unfavorable environmental conditions affecting zooxanthellate corals at high-latitudes.

- The Dalmatian mortality pattern of *O. patagonica* occurring in winter, which characterized by leaving the polyps alive and isolated within their calices, appear as a crucial stress response mechanism that allowed the high regeneration capacity of this species.

- The severe and recurrent pattern of colony partial mortality in winter indicate that low-ST conditions may be exerting both a direct effect on the linear extension dynamics of *O. patagonica* and an indirect effect *via* partial mortality, and thus, play a crucial role in constraining the colony growth dynamics of this species at high latitudes.

- **Chapter 4.5. Variation in demographics of the zooxanthellate coral *Oculina patagonica* along the Mediterranean Iberian coast in relation to environmental parameters**

- The Mediterranean coast of the Iberian Peninsula is the most invaded region by the zooxanthellate coral *O. patagonica*, in terms of both the cumulated number of locations with species' records and coastal length.

- This study provides a reference baseline quantitative assessment of current *O. patagonica* occurrence and demographics along ~1,300 km of the Mediterranean Iberian coast.

- Within the Iberian coast, the colony size-frequency distributions of *O. patagonica* were unimodal and positively skewed, indicative of non-stable and growing populations.

- The occurrence and abundance of *O. patagonica* was higher in artificial locations than in natural locations within each zone of the Iberian coast, indicating that artificial reefs foster the demographics of this species.

- The relevant abundance of artificial reefs (i.e., 100 m artificial reef km^{-1} coast) and the high availability of open space to colonize in natural locations (i.e., 33% cover of algal-depleted reefs and barren grounds) found within the Iberian coast may have facilitated the proliferation of *O. patagonica*. However, the zonal variation in species' demographics on natural locations within the Iberian coast cannot be directly attributed to a zonal variation in the availability of open space, nor in the abundance of artificial reefs.
- The demographics of *O. patagonica* (i.e., occurrence, density, cover, and colony partial mortality and size-structure) on natural locations displayed significant correlations and showed a marked zonal pattern along the Iberian coast that conform to the 'abundant-center' hypothesis (i.e., a most abundant center that declines toward the edges of a geographic range).
- The results on *O. patagonica* demographics showed that the 'abundant-center' pattern is not only related to the time of establishment but points to the relevant role of differences in coral population growth that correlate with key environmental variables.
- The success of *O. patagonica* colonies and populations within the Iberian coast appear to be generally constrained by low ST and light conditions, with thresholds that constrain colony and coral population growth of mean annual PAR-3m <30 mol photons m^{-2} d^{-1}, mean ST <19ºC, P10th-ST <14ºC, and P90th-ST <25ºC and >27ºC.

From a broader perspective, the synthesis of current knowledge obtained from this **PhD Thesis** allow to conclude that:

- The zooxanthellate coral *O. patagonica* generally inhabits shallow-water rocky bottoms (~0 to 8 m), up to ~25 m depth.
- The current distribution range of *O. patagonica* span 7ºW–35ºE in longitude and 31–44ºN in latitude, and include most Mediterranean biogeographic regions.
- The estimated time period of establishment indicates that *O. patagonica* may have been present before 1900 in the Mediterranean Sea and that was established in most regions by ~1950s.
- The number of locations in which *O. patagonica* has been recorded across the Mediterranean since its first record in 1966 to 2017 has increased exponentially. The spread dynamics of *O. patagonica* over 1966–2017 have followed over ~40 years in a slow undetectable motion until the 2000s, when accelerated being exponentially recorded in additional locations.
- The minimal sampling effort for estimates of *O. patagonica* demographics is an area of 40 m^2 for coral density and cover (variance about <10% of the mean), and 20 colonies for colony size and partial mortality (variance about <20% of the mean).

- The coral *O. patagonica* has exhibited a northward expansion along the north-eastern Iberian coast. The rate of spread of *O. patagonica* is the highest reported for a zooxanthellate scleractinian coral (22 km yr^{-1}).
- The current distribution pattern of *O. patagonica* is continuous (i.e., ≥1 location with the species per 10 km coastal length) and coral abundance is high (i.e., tens to hundreds of colonies per location) in the south-western Mediterranean (Algerian and Tunissian waters, Alborán Sea and Balearic Sea) and in the eastern Mediterranean (Aegean Sea and Levant Sea), whereas the species' distribution is fragmented and coral abundance is low in the north-western areas (Balearic Islands, Gulf of Lyons, Ligurian Sea and Adriatic Sea).
- The Mediterranean Iberian coast is a hot-spot for the coral *O. patagonica*, in terms of both the cumulated number of locations and coastal length, with the largest and spreading coral populations recorded in the central Iberian coast of the South-Balearic Sea. The results on species' demographics show that the observed 'abundant-center' pattern is not only related to the time of establishment but also to differences in coral population growth that correlate with key environmental variables.
- Artificial reefs foster the population growth and the distributional range shift of the range-expanding coral *O. patagonica*.
- Low ST and light conditions (i.e., mean annual ST <19ºC and PAR-3m <30 mol photons m^{-2} d^{-1}) appear as relevant drivers constraining performance of *O. patagonica*, which is in accordance with previous studies on tropical zooxanthellate coral species.
- Moderate high-ST regimes (i.e., mean annual ST >19–21ºC and P90th-ST >25–27ºC), without severe low-ST periods (P10th-ST >14ºC) and/or warm-ST periods (P90th-ST <28ºC), appear as the optimal thermal conditions for the successful growth of *O. patagonica* colonies and populations within the Mediterranean Sea.
- The invasive behavior of the zooxanthellate coral *O. patagonica* (i.e., spreading geographically and locally increasing population densities) is consistent with the ongoing process of coral-mediated tropicalization of shallow-water rocky ecosystems in the Mediterranean Sea, such as documented in other worldwide subtropical and temperate areas under current sea warming.
- Photosynthetic macrophytes are the main trophic group and source of primary production in shallow-water rocky reefs from the temperate Mediterranean Sea, but the interaction between the cumulative effects of global change and the spread of *O. patagonica* could greatly modify underwater seascape, which challenges the current structure and function of shallow-water ecosystems.

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Photograph by Juan Carlos Calvín

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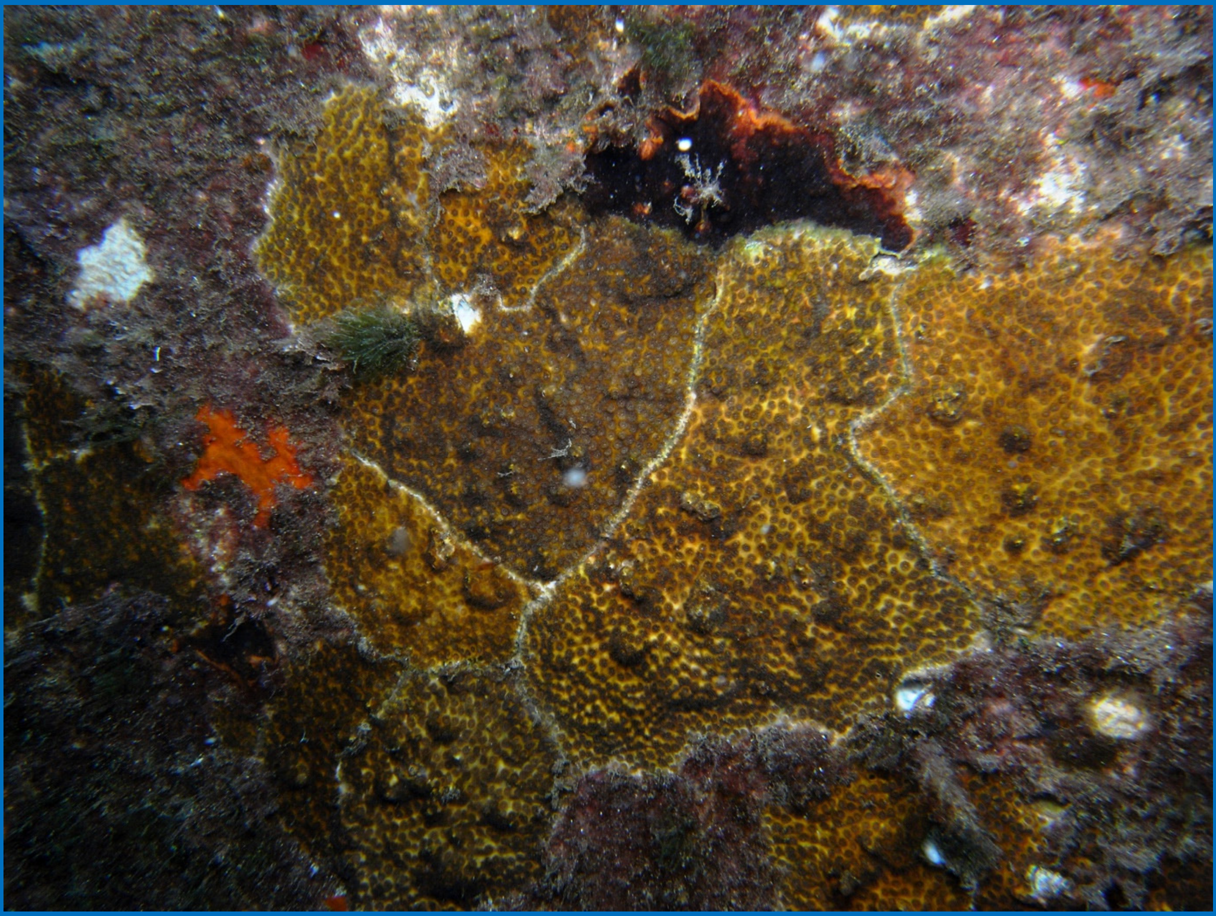
APPENDICES



Appendices

A phase shift from macroalgal to coral dominance in the Mediterranean

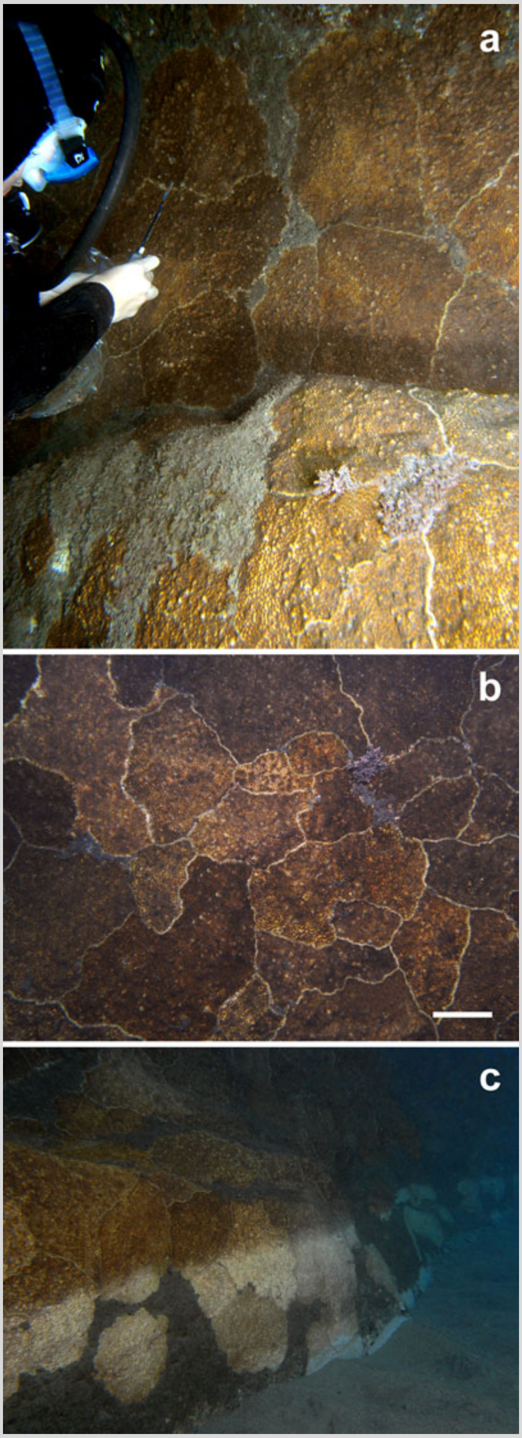


Fig. 1 **a**, **b** Community dominated by *Oculina patagonica* in the western Mediterranean. *Scale bar* 20 cm. **c** The shallow water community was severely affected by sand scouring

Macroalgae dominate Mediterranean shallow water assemblages, whilst corals are extremely rare. *Oculina patagonica* is a zooxanthellate coral that was first recorded in the Mediterranean in 1966 and is thought to originate in the SW Atlantic. Although it is spreading in the Mediterranean, it has never been observed as main component of a natural community. In 2009, *O. patagonica* was found to be abundant in shallow water (0–3-m depth) at Torre Pirulico in SE Spain (37°4′70″N, 1°50′59″W). Based on 25 random 1-m^2 plots, the mean density was 24 (±2 SE) colonies m^{-2}, covering 55 ± 5 % of the 750 m^2 study area (Fig. 1a, b). Coral colonies ranged from 0.07 to 3578 cm^2 (mean = 229 ± 11 cm^2, n = 603) and their size distribution was positively skewed with 37.5 % colonies <100 cm^2, indicating that strong recruitment was the main cause of the species' high abundance. Other components of the benthic community included turf algae (36.6 %), erect algae (7.3 %), sponges (0.9 %), calcareous-encrusting macroalgae and bare rock (0.2 %) (n = 30 random 0.25-m^2 quadrats). Sea urchins were absent and physical disturbance from sand scouring (Fig. 1c) was the main source of open space for *O. patagonica* to colonise.

Whilst high cover of *O. patagonica* has been recorded on artificial habitats, cover on natural substrata is generally sparse (<15 %, Fine et al. 2001; Sartoretto et al. 2008; Coma et al. 2011). It is unclear how *O. patagonica* outcompetes algae and other invertebrates. Densities at Torre Pirulico are the highest ever reported. This is a coral community dominated by *O. patagonica*.

Our finding of a persistent phase shift from macroalgal to coral dominance in the Mediterranean contrasts with the reported trend in many coral reef ecosystems. Macroalgae are important primary producers in temperate coastal ecosystems and this change in the dominant trophic group may affect ecosystem function.

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Sea Urchins Predation Facilitates Coral Invasion in a Marine Reserve

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Abstract

Macroalgae is the dominant trophic group on Mediterranean infralittoral rocky bottoms, whereas zooxanthellate corals are extremely rare. However, in recent years, the invasive coral *Oculina patagonica* appears to be increasing its abundance through unknown means. Here we examine the pattern of variation of this species at a marine reserve between 2002 and 2010 and contribute to the understanding of the mechanisms that allow its current increase. Because indirect interactions between species can play a relevant role in the establishment of species, a parallel assessment of the sea urchin *Paracentrotus lividus*, the main herbivorous invertebrate in this habitat and thus a key species, was conducted. *O. patagonica* has shown a 3-fold increase in abundance over the last 8 years and has become the most abundant invertebrate in the shallow waters of the marine reserve, matching some dominant erect macroalgae in abundance. High recruitment played an important role in this increasing coral abundance. The results from this study provide compelling evidence that the increase in sea urchin abundance may be one of the main drivers of the observed increase in coral abundance. Sea urchins overgraze macroalgae and create barren patches in the space-limited macroalgal community that subsequently facilitate coral recruitment. This study indicates that trophic interactions contributed to the success of an invasive coral in the Mediterranean because sea urchins grazing activity indirectly facilitated expansion of the coral. Current coral abundance at the marine reserve has ended the monopolization of algae in rocky infralittoral assemblages, an event that could greatly modify both the underwater seascape and the sources of primary production in the ecosystem.

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Introduction

Natural and human-caused disturbances can trigger the fall of a dominant trophic group of organisms and the rise of another [1]. The relevance of this change to the ecosystem varies. But, if the affected group has an important impact on elemental cycles, the change in composition can affect the flows of energy and materials [2,3]. In the marine realm, the decline of coral reefs and the shift from coral to macroalgae-dominated communities are the clearest examples of the widespread implications and consequences of these changes [4–6]. In contrast, the dominance of macroalgae in the rocky shallow infralittoral zone is a common pattern in temperate marine environments [7] where they represent the primary source of energy and organic matter [8]. Macroalgae usually represent the dominant trophic group on Mediterranean infralittoral rocky bottoms [9], although suspension feeders (e.g., mussels, some polychaetes) can occasionally outcompete algae in enriched (eutrophic) waters [10–12]. Native zooxanthellate corals (e.g., *Cladocora caespitosa*) can also constitute the dominant trophic group [13,14]. However, the exotic coral *Oculina patagonica* (De Angelis D'Ossat 1908) has become widespread in the Mediterranean [15–17] since its discovery in 1966 in the Gulf of Genova (Italy) [18], which challenges present conceptual framework [9].

Populations of *O. patagonica* were first described in 1973 as isolated colonies at some locations in the western Mediterranean. Abundant populations were observed only in areas highly affected by humans [19]. Later reports have discovered populations in natural habitats [15,20–22]. Therefore, in addition to its geographical spread in the Mediterranean, the species appears to be increasing in abundance in some areas. This population increase may affect the stability of algae as the dominant trophic group in shallow Mediterranean rocky communities and prompts an investigation into what mechanisms are likely to be involved in the increase of *O. patagonica*.

Short- and long-term changes in shallow Mediterranean communities from natural habitats are known to be regulated by bottom-up mechanisms (nutrient availability, irradiance, catastrophic events) as well as top-down controls (mainly herbivory) [8,23–25]. But the Mediterranean is being affected by the main global change threats (i.e., overfishing, habitat degradation, pollution, species introduction and global warming, [26,27]). Then, anthropogenic impacts (i.e., nutrient uploads, climate change, overfishing and their associated cascading effects) interact with natural mechanisms to ultimately shape the underwater seascape on most Mediterranean shores. In this context, our understanding of the synergistic effects of global change threats on the dynamics of invasion of exotic species is still scarce. To avoid some of the anthropogenic impacts, mainly overfishing, the study was conducted at a Marine Protected Area (MPA), where management plans permit underwater assemblages to attain and maintain their natural population status [28].

The effects of global change threats on the population dynamics of species are unlikely to be additive but mediated by their biotic interactions [29]. Then, occurrence and determination of the effects of key species is especially relevant. Key species are species that are important to ecosystem structure and function by driving ecosystem processes or energy flow [30]. Although invasion of exotic species is a widespread threat to the integrity and functioning of native ecosystems, the role that key species play in invaded communities is still poorly known. Therefore, a major challenge to our understanding of ecosystem functioning is determining whether a few species have a preponderant role in shaping community composition [31–33].

The pattern of dominance of macroalgae in shallow habitats from temperate ecosystems is especially evident in the rocky shallow infralittoral zone from oligotrophic seas such as the Mediterranean [23], where erect algae dominate [9]. The only exception to this pattern occurs under extreme physical disturbance and/or high sea urchin densities wherein encrusting coralline algae predominate [34,35].

In the Mediterranean, the reduction of fish abundance is one of the main factors causing changes in the structure of rocky infralittoral assemblages [36–38]. However, the grazing activity of fishes, mostly *Sarpa salpa* do not create open spaces and/or coralline barrens [34]. The most important biological perturbation that generates open space in Mediterranean shallow rocky habitats is herbivory by sea urchins [24,39–41]. Grazing activity by sea urchins can remove algal canopies and/or prevent their recovery, providing and maintaining cleared patches in the substratum on which other organisms can settle and survive [25,42]. Mediterranean herbivorous fishes play a secondary role in shaping infralittoral assemblages (but see [43,44]), and some predators (e.g., *Diplodus* spp.) even benefit algae by altering the behavior and abundance of sea urchins [45].

Studies of trophic cascades in which sea urchins play a pivotal role have contributed to an understanding of benthic community structure [24,37,38,46]. Therefore, sea urchins, considered a key species in Mediterranean shallow infralittoral ecosystems because they control the growth of seaweed populations [47,48], may contribute to an understanding of the cause of coral increase. Sea urchin densities seem to be controlled mainly by the abundance of predators, the presence of refuges and resource availability [25,49–51]. Thus, the hypothesis is that an increase in the abundance of a zooxanthellate coral that spatially competes with macroalgae could be mediated by sea urchins through the creation of barren areas that enhance coral settlement or survival.

Other factors that can affect the structure and dynamics of benthic communities such as predation, competition, facilitation, diseases and environmental conditions [52–54] should not be disregarded to contribute to the understanding of the coral pattern of variation. They were examined on the basis of our observations as well as from those of other studies in the area (see Text S1 in supporting information, SI).

In order to understand the dynamics of *Oculina patagonica*, in 2002 we started an assessment of the coral population in the shallow infralittoral environments of Islas Hormigas (Murcia, SE Spain), a well-conserved Marine Protected Area (MPA) excluded of major human impacts where *O. patagonica* was already present. The aims of the study were twofold: (1) to examine abundance and the pattern of variation of the coral *O. patagonica* over time in the MPA Cabo de Palos-Islas Hormigas, and (2) to contribute to the understanding of the main mechanisms that may have allowed the coral's abundance and its variation to occur.

Results

Density and coverage of *Oculina patagonica* over time

The density of coral colonies of *O. patagonica* increased at La Hormiga and El Hormigón (Figure 1) over the study period (2002–2010; Figure 2a,b). Mean density varied from 0.60 to 1.37 colonies m^{-2} at La Hormiga and from 0.75 to 1.97 colonies m^{-2} at El Hormigón. These measurements represent an average density increase of 0.091 ± 0.021 (slope ± SE) and 0.176 ± 0.027 colonies m^{-2} $year^{-1}$ (Figure 2a,b), respectively, resulting in total increases of 128% and 163% for each respective location over the 8 year time period (Figure 2a,b).

The proportion of surface bottom occupied by *O. patagonica* varied from 2.75 to 10.34% at La Hormiga and from 5.55 to 15.09% at El Hormigón. These variations represent an average increase in cover of $0.923 \pm 0.267\%$ per year (slope ± SE) and $1.350 \pm 0.281\%$ per year (Figure 2c,d), respectively, resulting in total increases of 276% and 172% for each respective location over the 7 year time period (2003–2010, Figure 2c,d).

Size structure of *O. patagonica* over time

The increase in mean colony size between 2003 and 2010 was not statistically significant [El Hormigón: $p = 0.0704$, $N = 8$; La Hormiga: $p = 0.1063$, $N = 8$, Table 1]. The coefficient of variation (SD/mean) did not vary over time (El Hormigón: 1.52 ± 0.23, mean ± SD, $p = 0.3453$, $N = 8$; La Hormiga: 1.71 ± 0.39, $p = 0.9315$, $N = 8$).

The proportion of the smallest size class (0–100 cm^2) over the study period ranged from 17 to 28% at El Hormigón and from 17 to 36% at La Hormiga, indicating the prevalence of small size classes at both locations (Figure S1, Figure S2, Table 1; skewness provided similar information and, therefore, it is not shown). The proportion of the smallest size class exhibited its highest values from 2006 to 2007 at both locations (Table 1). These results indicate that recruitment success of the coral contributed to the density increase observed in both populations during these years. The kurtosis coefficient of the size structure of colonies at both locations showed results that were more peaked than normal distributions (Table 1) which indicates that the change in demographic parameters was recent.

Sea urchins population over time

Density of urchins increased over time (Time effect, Figure 3, Table 2). However, the pattern of variation over time differed between both species (Time-Species interaction, Table 2). The density of both species was constant and low from 2003 to 2005 (*P. lividus* mean density: 1.73 and 2.05 individuals per m^2 (ind m^{-2}) at La Hormiga and El Hormigón, respectively; *A. lixula* density: 0.14 and 0.21 ind m^{-2} at La Hormiga and El Hormigón, respectively). Density of *P. lividus* increased and then remained constant and high from 2007 to 2010 (mean density: 4.36 and 5.51 ind m^{-2} at El Hormigón and La Hormiga, respectively). This density increase was mainly caused by the high recruitment observed in 2006 and 2007 (Figure 3a). In contrast, the density of *A. lixula* increased steadily from 2006 to 2010 (Figure 3b).

The abundance of *P. lividus* was about 8 times greater than the abundance of *A. lixula* (mean density 3.52 ind m^{-2} versus 0.41 ind m^{-2}, respectively, Species effect, Table 2). Therefore, the pattern of variation in abundance of both sea urchins over time was mainly driven by *P. lividus*. Density varied from 1.46 to 7.02

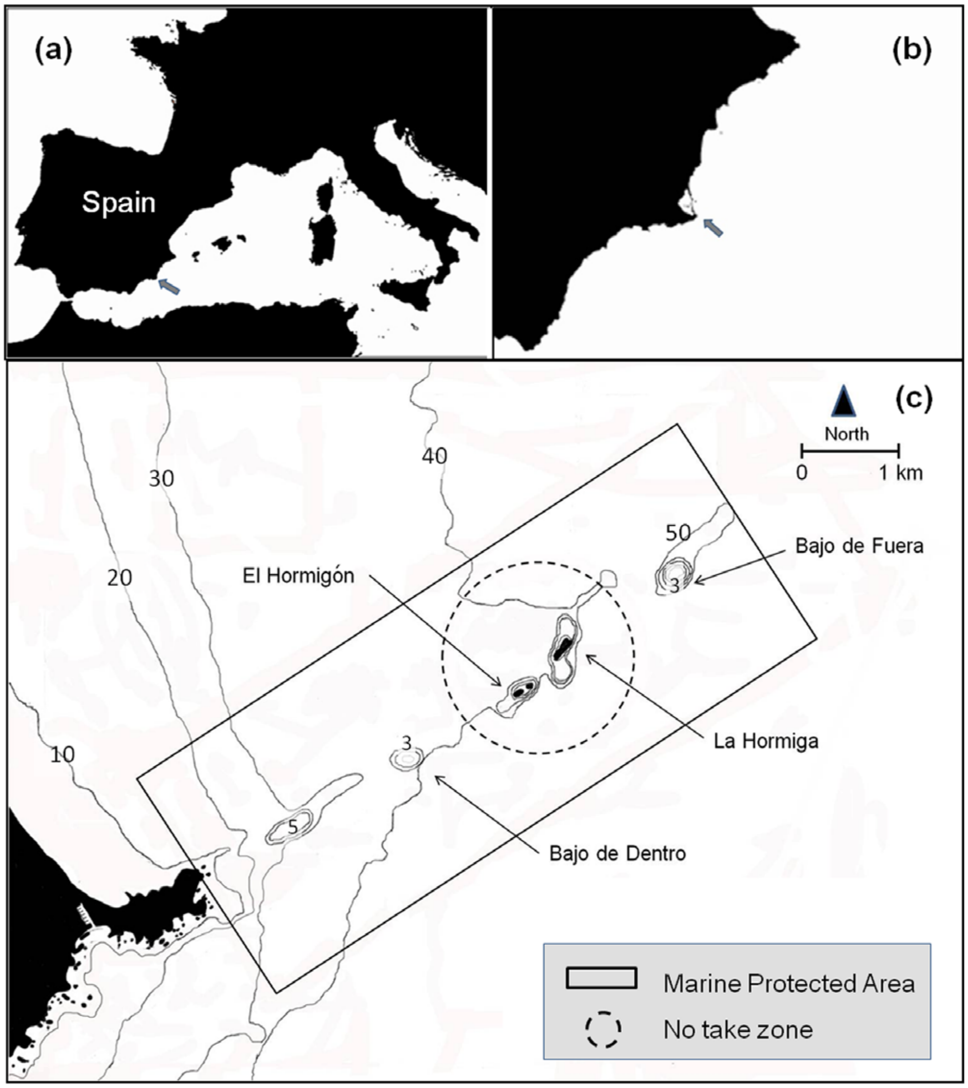

Figure 1. Study sites. (a) Location of Cape of Palos (south-east Spain) in the NW Mediterranean. (b) Location of the Marine Reserve of Cape of Palos-Islas Hormigas. (c) Location of 4 study sites at the Cape of Palos-Islas Hormigas Marine Reserve: Bajo de Dentro, Bajo de Fuera, La Hormiga and El Hormigón.
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ind m^{-2} at La Hormiga and from 1.62 to 4.96 ind m^{-2} at El Hormigón, which represent an increase of 381 and 206%, respectively over the 7 years time period, although mainly due to the increase during the 2006–2007 time-period (Figure 3c).

We studied size structure of *P. lividus* between 2006 and 2010. The highest frequencies of small sea urchins (size class 2, >2–3 cm MTD) were found in 2006 and 2007, suggesting a high level of recruitment in the preceding years (Figure S3). This recruitment appears to form the basis of the overall urchin density increase observed during this time period. However, although density stopped increasing after 2007 (Figure 3c), the biomass of *P. lividus* demonstrated a similar increase over time at La Hormiga and El Hormigón (Figure 4, two-way ANOVA comparing *P. lividus* biomass among locations and time, time effect $F_{4,10} = 18.9034$, $p = 0.0073$), mainly due to the increase in mean size of the individuals (Figure S3). This effect was similar in both locations (location-time interaction $F_{4,\ 10} = 0.4040$, $p = 0.8018$).

Sea urchins and coral abundance

The abundance of *O. patagonica* (density and coverage) at the scale of 50 m^2 was strongly related to sea urchin densities at La Hormiga and El Hormigón over the study period 2003–2010 (Figure 5).

In 2002 and 2010, an examination of coral density at two other locations (Bajo de Dentro and Bajo de Fuera, Figure 1) allowed us to determine whether the increase in abundance observed at La Hormiga and El Hormigón was also present at other locations. Density of coral colonies increased over time at all four locations (2-way ANOVA comparing coral colonies density among locations and time, $F_{1,-} = 48.057$, $p = 0.0056$, Figure 6). However, the increase in coral colony density did not differ among locations ($F_{3,3} = 1.6838$, $p = 0.3396$, Figure 6).

Levels of sea urchin density at Bajo de Dentro (8.6±0.8 ind m^{-2}, mean ± SE) and Bajo de Fuera (9.6±0.7 ind m^{-2}) were similar to those observed at La Hormiga (7.0±0.8 ind m^{-2}), and higher than those observed at El Hormigón (5.0±0.5 ind m^{-2})

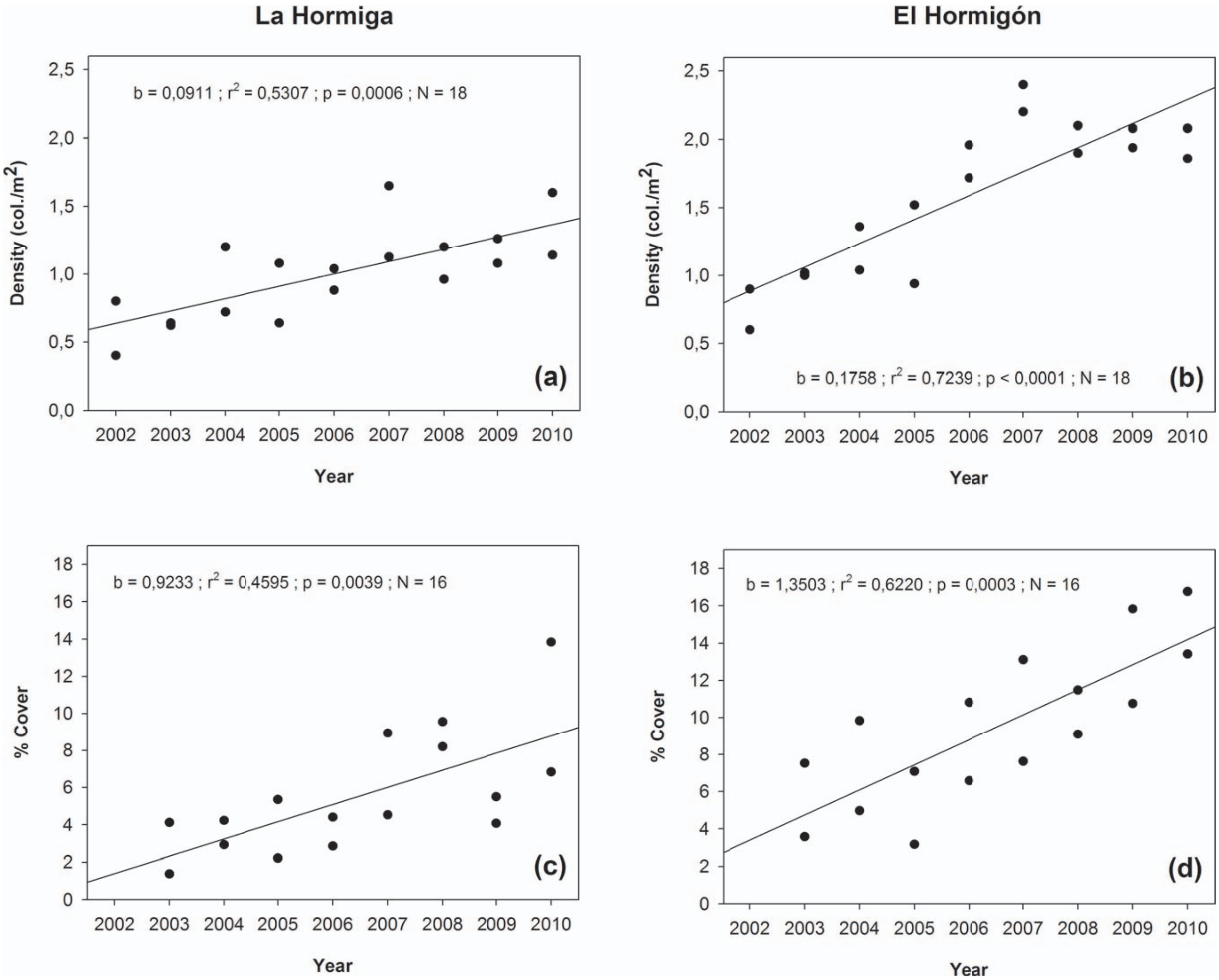

Figure 2. Trends exhibited by the density and the coverage of *Oculina patagonica* over time at La Hormiga and El Hormigón. Pearson product moment correlations between coral density and time and between coral coverage and time are indicated.
doi:10.1371/journal.pone.0022017.g002

(one-way ANOVA comparing sea urchins density among locations in 2010, $F_{3,36} = 4.9260$, $p = 0,0057$; Scheffe's contrast test).

These results reveal a local-scale pattern of increase in the abundance of both coral colonies and sea urchins. The pattern has occurred in four places that are nearby to each other (within 4 km distance) but separated by 50–80 m deep channel (two of the locations are small islands, La Hormiga and El Hormigón, and the other two, Bajo de Dentro and Bajo de Fuera, are rocky bommies).

Colony size and presence in open spaces

Open spaces on the substrata were common at La Hormiga and El Hormigón and were covered by encrusting corallines or bare rock. The number of open spaces associated with *O. patagonica* did not differ between the two locations (La Hormiga and El Hormigón; two-way ANOVA comparing abundance of open spaces associated to coral colonies among locations, main effect location: $F_{1,3,1501} = 0.0152$, $p = 0.9093$) or over time, despite showing an increasing trend (2005, 2006, 2007, 2010; main effect time: $F_{3,-} = 1.4271$, $p = 0.3886$). On average, the mean number of open spaces associated with coral colonies over the entire study period was 3.68±0.23 (SE) per 10 m^2. The mean size of these open spaces was 0.81±0.34 (SE) m^2 in 2010. The proportion of space occupied by open spaces (16.0%±1.9; mean ± SE) did not differ between both locations (One-way ANOVA comparing proportion surface bottom occupied by open spaces among both locations, $F_{1,38} = 2.4673$, $p = 0.1245$).

The contrast between the expected proportion of small colonies (up to 100 cm^2) associated with open spaces and the observed proportion (see methods) is shown in Figure 7. The observed number of small colonies associated with open spaces was larger than that expected on the four sampled occasions (2005, 2006, 2007 and 2010, Chi-square, $X^2 = 25.79$, $df = 3$, $p < 0.00001$). Thus, small colonies were found to be present on open spaces about 68% more frequently than expected according to random distribution.

Discussion

Causes of variation in coral abundance

The increasing abundance of coral colonies of *Oculina patagonica* at the studied MPA from 2002 to 2010 is likely driven by environmental conditions that favor coral's growth. Two main

Table 1. *Oculina patagonica.*

Locality	Year	Area	N	-------------- Colony size (cm^2) ------------------				kurtosis (g2)			%Ni colonies
		(m^2)		Mean	SE	Min.	Max.	g2	SEg2	sig(>2)	<100 cm^2
Hormigón	2003	100	98	417.2	63.9	4.9	4128.3	18.05	0.48	37.36	27.55
	2004	50	60	617.0	99.1	15.9	3848.5	5.23	0.61	8.60	21.67
	2005	100	123	416.7	43.5	19.6	3068.0	8.05	0.43	18.59	17.89
	2006	100	184	473.1	63.8	9.6	7854.0	40.11	0.36	112.53	28.26
	2007	100	230	451.1	50.0	7.1	7854.0	45.23	0.32	141.50	26.96
	2008	80	160	514.4	63.7	12.6	5345.6	15.63	0.38	40.99	18.75
	2009	100	201	661.6	80.2	7.1	8576.8	24.16	0.34	70.78	17.91
	2010	100	197	766.2	79.7	0.8	6013.2	7.24	0.34	21.01	17.26
Hormiga	2003	100	63	436.7	117.6	15.9	7088.2	42.95	0.59	72.20	19.05
	2004	50	48	372.8	63.0	19.6	2164.8	8.50	0.67	12.61	16.67
	2005	100	86	434.5	79.3	19.6	6361.7	50.37	0.51	98.01	25.58
	2006	100	95	382.3	49.0	4.9	2375.8	4.85	0.49	9.90	35.79
	2007	80	111	485.3	101.6	4.9	8251.6	32.81	0.46	72.10	29.73
	2008	100	108	822.3	158.4	7.1	11309.8	19.18	0.46	41.59	16.67
	2009	100	117	409.6	57.1	7.1	5674.5	45.62	0.44	102.81	22.22
	2010	100	137	754.6	109.3	0.8	9940.2	29.94	0.41	72.80	18.25
Bajo Fuera	2002	100	100	392.7	72.8	7.1	6361.7	46.15	0.48	96.49	34.00
	2010	50	148	402.3	44.1	0.8	2827.4	6.34	0.40	16.00	30.41
Bajo Dentro	2002	100	55	262.1	62.9	8.3	2375.8	12.23	0.63	19.30	49.09
	2010	100	231	257.8	24.9	0.2	3318.3	30.91	0.32	96.91	35.50

Descriptive statistics regarding the size distribution of the populations at study sites. Area: sampled area at each site and year; N: number of colonies examined at each site; sig(>): kurtosis is significant if absolute value of coefficient/SE >2.

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requirements must be met for *O. patagonica* to be able to increase its abundance in a space-limited habitat such as the one in this study: 1) an increase in space availability driven by physical disturbances (i.e., storms) and/or biological interactions (i.e., overgrazing); and 2) the capacity of the species to recruit, grow and survive.

Physical perturbations, such as large storms, can create open spaces [55] such as those observed at the study sites. However, over the study period, open spaces have regularly been observed at the study sites despite a lack of large storms over the study period (authors' observations) [56].

Abundance of the main herbivorous fish species (*Sarpa salpa*) did not vary over the study period [56], nor can they create open spaces [39]. In fact, the most important biological perturbation that generates open space in Mediterranean shallow rocky habitats is herbivory by sea urchins [24,34]. A threshold of 7–9 adult sea urchins m^{-2} may cause an ecological shift from macroalgae assemblages to coralline barrens [35,39]. Current sea urchin abundance in the study area (5–9 ind m^{-2}) is similar to densities known to cause barrens, and is therefore great enough to be considered a feasible explanation for the open spaces regularly present at our study sites.

The second requirement necessary for coral colonies to increase in abundance is the capacity of the coral species to recruit, grow and survive. Statistical results concerning the size structure of the coral colonies identifies high recruitment as a main factor causing this increase in coral abundance. This result is consistent with evidence that recruitment can also be a critical cause of changes in coral-macroalgae abundance [57–59]. However, in this study, recruitment did not result in a decrease in mean colony size (Table 1), which indicates that the species is indeed meeting its requirements for growth and survival.

The polychaete *Hermodyce carunculata* appears to be the main predator of *O. patagonica* in the Mediterranean [60]. The presence and the effects of this worm were observed on very rare occasions during the study (see Text S1). Therefore, predation does not seem to be an important factor affecting the coral populations at our study sites.

Sea surface temperature in the NW Mediterranean is exhibiting a pattern of increase [61] and current evidence indicates that the coral species may benefit from the lengthening of the growing season due to the warming pattern [62,63]. However, analysis of the SST data showed that lengthening of the growing season did not vary over the study period nor did mean annual temperature (see Text S1). These results are most probably related to the short-term oscillatory pattern that sea water temperature exhibits in the NW Mediterranean [61]. Therefore, the observed pattern in coral abundance can not be attributed to a variation in sea water temperature.

At the study area, an increase in sea urchin population density would increase the availability and persistence of cleared patches, the first crucial step for the establishment of coral colonies. This observation is in agreement with the observed relationship between sea urchins abundance and that of *O. patagonica* (Figure 6). Furthermore, the presence of small coral colonies that have settled preferentially on areas cleared by sea urchins (Figure 7) and the size of the cleared spaces provide compelling evidence about the positive relationship between sea urchin density and coral abundance. This result, together with the observed pattern of coral recruitment, implies that the increase in sea urchins

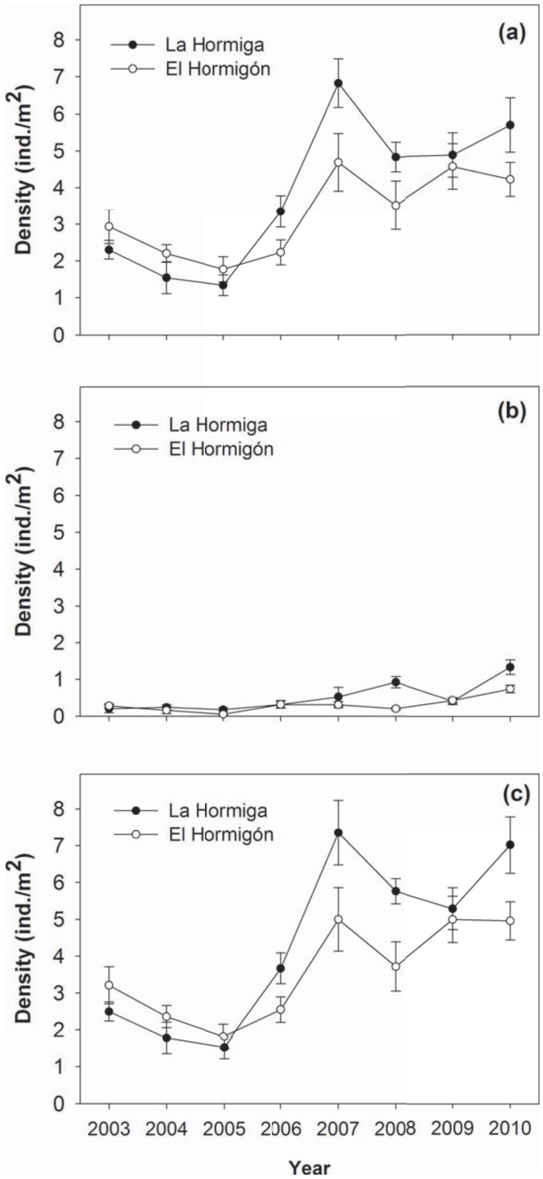

Figure 3. Density of sea urchins (ind m^{-2} ; mean ± SE) over time. Only sea urchins with >2 cm in test diameter were counted. a) *Paracentrotus lividus*. b) *Arbacia lixula*. c) both sea urchins species together.
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abundance is one of the main causes of the increase in density and coverage of coral colonies (Figure 8).

Although a causal relationship cannot be inferred from the statistical correlation observed between the abundance of coral and sea urchins, the existence of the correlation is a proof of concept of the basic idea underlying the hypothesis. It is apparent that sea urchin grazing promotes the recruitment of *O. patagonica* colonies, in accordance with results obtained in coral reef ecosystems [64–66]. Thus, interspecific facilitation appears to be one of the main mechanisms involved in the observed increase in abundance of coral colonies (Figure 8). These results highlight the crucial role that herbivory by sea urchins appears to play in increasing the abundance of coral colonies.

Table 2. Summary of a three-way ANOVA comparing sea urchins density among locations (La Hormiga, El Hormigón), time (2003 to 2010) and species (*Paracentrotus lividus*, *Arbacia lixula*).

Effect	df	MS	F	p
Location	1	0.3080	13.17	0.1644
Time	7	0.7637	14.52	0.0011
Species	1	23.9064	20937.67	0.0044
Location × Time	7	0.0526	1.73	0.2427
Location × Species	1	0.0011	0.04	0.8517
Time × Species	7	0.1609	5.30	0.0214
Location × Time × Species	7	0.0304	0.68	0.6856
Error	32	0.0445		
Cochran's test			ns	
Transform			Nil	

The species and time factors were considered as fixed in the analyses and location was randomized.
doi:10.1371/journal.pone.0022017.t002

The main fish species identified as successful sea urchin predators are the Sparidae *Diplodus sargus*, *Diplodus vulgaris* and *Sparus aurata*, and the Labridae *Coris julis*, *Labrus merula*, *L. viridis*, *Symphodus roissali* and *S. tinca* [67–70]. Populations from all these fish species have not varied significantly over the study period [56]. Nutrient levels and the presence of sea urchins refuges did also not vary over the study period [56]. Therefore, recruitment appears to be the primary factor contributing to the increase in sea urchins abundance. Although the factors responsible for large fluctuations in sea urchin abundance remain poorly understood, there is evidence that high level of recruitment can outweigh fish predation [24,71]. Our study provides evidence that a change in the demography of a sea urchin species can drive a relevant change in community structure. Under unchanged fish predation, nutrients and refuge conditions, the increase of *P. lividus* biomass resulted from both a high recruitment and a good period of growth for sea urchins. Two non-exclusive causes may have contributed to the success of *P. lividus*: i) favourable climatic conditions, and ii) low predation on reproductive populations and on planktonic larvae. However, this study can not distinguish between both causes and, most probably, it may have been a combination of them.

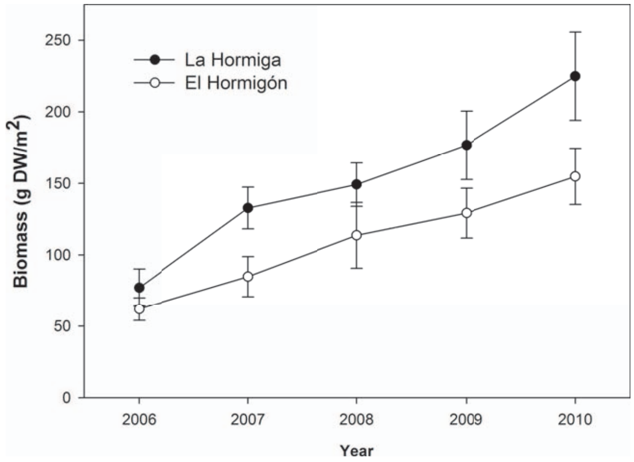

Figure 4. Biomass (g dry weight m^{-2}; mean ± SE) of the sea urchin *Paracentrotus lividus* at La Hormiga and El Hormigón between 2006 and 2010.
doi:10.1371/journal.pone.0022017.g004

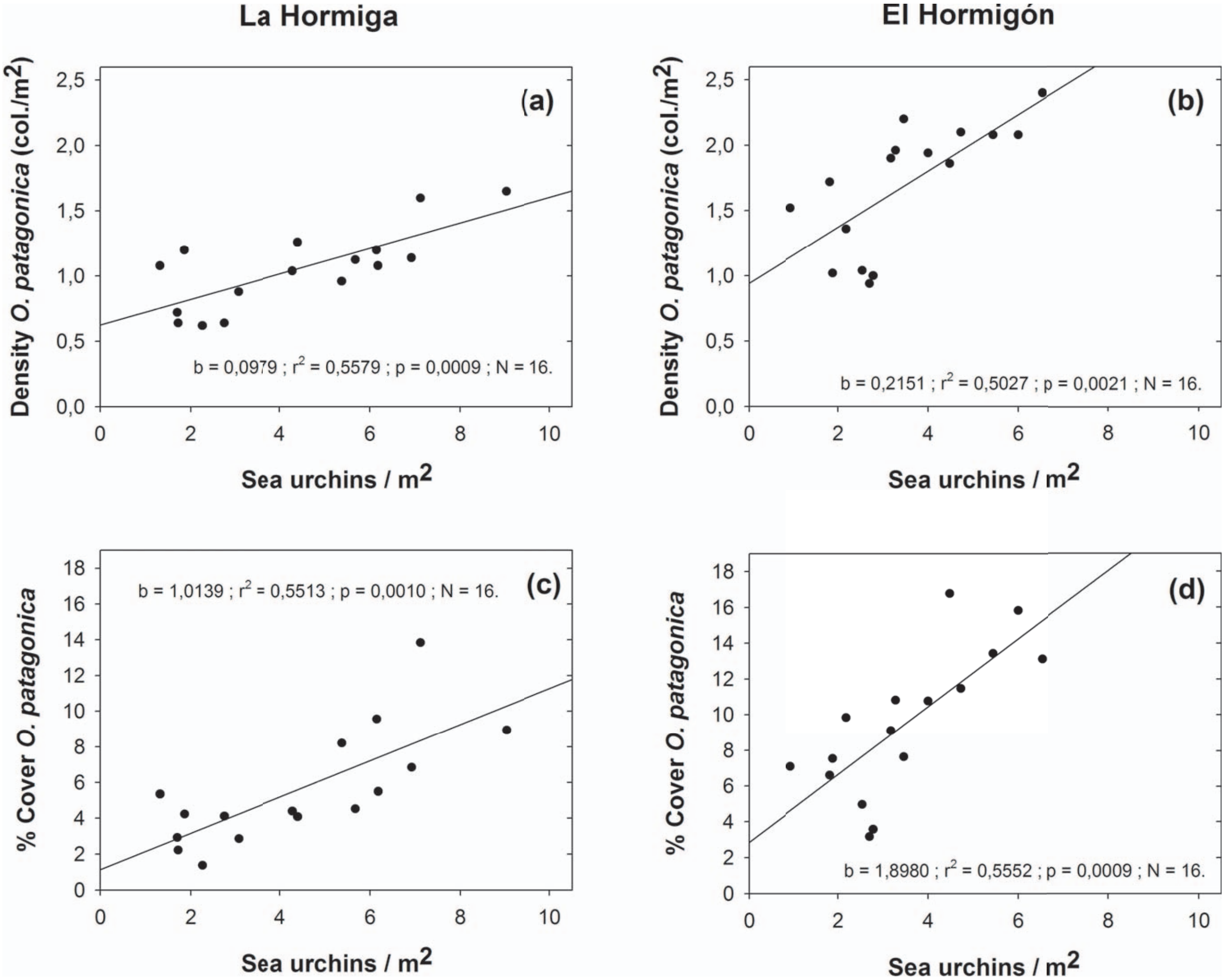

Figure 5. Pearson product moment correlation between the density of both sea urchin species (*P. lividus* and *A. lixula*) and abundance of the coral *Oculina patagonica* at both studied locations [La Hormiga. a) density and c) cover; El Hormigón. b) density and d) cover].

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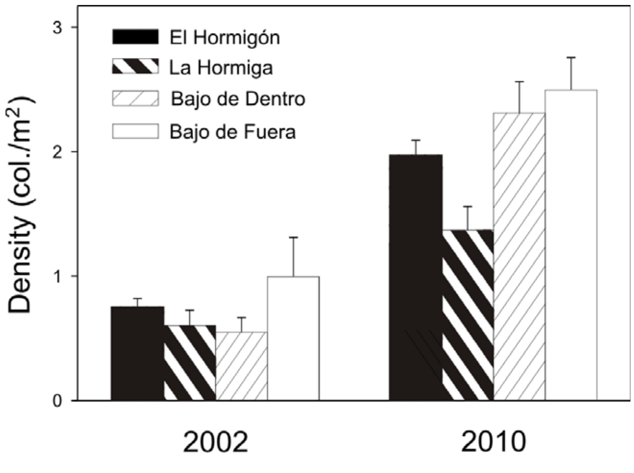

Figure 6. Density of *Oculina patagonica* colonies in 2002 and 2010 at the four studied sites.

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Relevance of the current coral abundance

The percent cover observed for *O. patagonica* at our study sites (10–15%) was only slightly lower than those reported for total coral cover in coral reef ecosystems (e.g., Great Barrier Reef: 27%, Indo-Pacific: 22%, Caribbean: 7%, Florida Keys: 16%, [5,6,72]), emphasizing the importance of this species within the benthic community of this temperate ecosystem.

Macroalgae species composition exhibits regional, bathymetric and seasonal changes in the biomass of the dominant species [23]. Interannual changes have also been documented in relation to species substitution, sea urchin activity and overfishing [24,73,74]. However, none of these spatial and temporal variations imply a change in the dominant trophic group (i.e., all changes involve algal species). Even in the case of successfully introduced species, changes in dominant species generally involve the replacement of the dominant algal species by an exotic algae species [75].

Algal assemblages at the study sites were dominated by different species of macroalgae as it is the case in other well-conserved areas in the central western Mediterranean [76,77]. No relevant changes on relative abundance of the main dominant macroalgae species was observed over the study period but a decrease in abundance of *H. scoparia* (see Text S1).

Detailed data using photo-quadrats [77] in similar shallow infralittoral habitats illustrate that erect macroalgae account for roughly 69.9–91% of surface cover, calcareous encrusting macroalgae account for 28.6–7.5% cover and invertebrates (mainly sponges) account for the remaining 1.5%. Therefore, the current coverage of *O. patagonica* at the study sites is unusual for Mediterranean shallow water assemblages, matching the abundance of several species of dominant erect macroalgae. Thus, *O. patagonica* is able to initiate an important change in community structure and end the monopolization of algae in shallow assemblages, an event that could greatly modify both the underwater seascape and the sources of primary production in the ecosystem.

Despite the differences between the temperate Mediterranean and coral reef environments, the observed processes may be similar to those observed in the Caribbean, where the recovery of *Diadema antillarum* populations is known to have enhanced coral recruitment [65,66]. However, in Caribbean coral reef communities, as in those in other areas, the positive effects of urchins on coral may be diminished or even negated by increases in coral diseases, temperature-related mortality, and coastal habitat degradation [4,78,79]. Like the Caribbean, the Mediterranean is also affected by coastal habitat degradation, rising temperatures and diseases [61,63,80,81]. However, in the western Mediterranean these disturbances appear to be affecting *O. patagonica* less

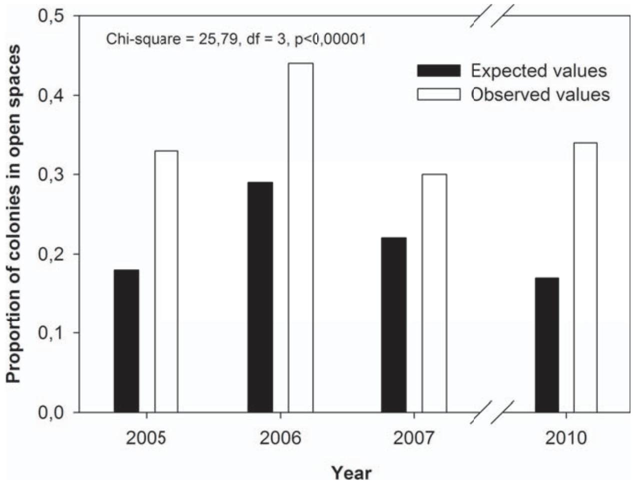

Figure 7. Contrast between the observed proportion of small colonies (up to 100 cm^2) on open spaces and that expected from the consideration of the abundance of the different colony size classes and their random distribution on open spaces in 2005. 2006. 2007 and 2010.
doi:10.1371/journal.pone.0022017.g007

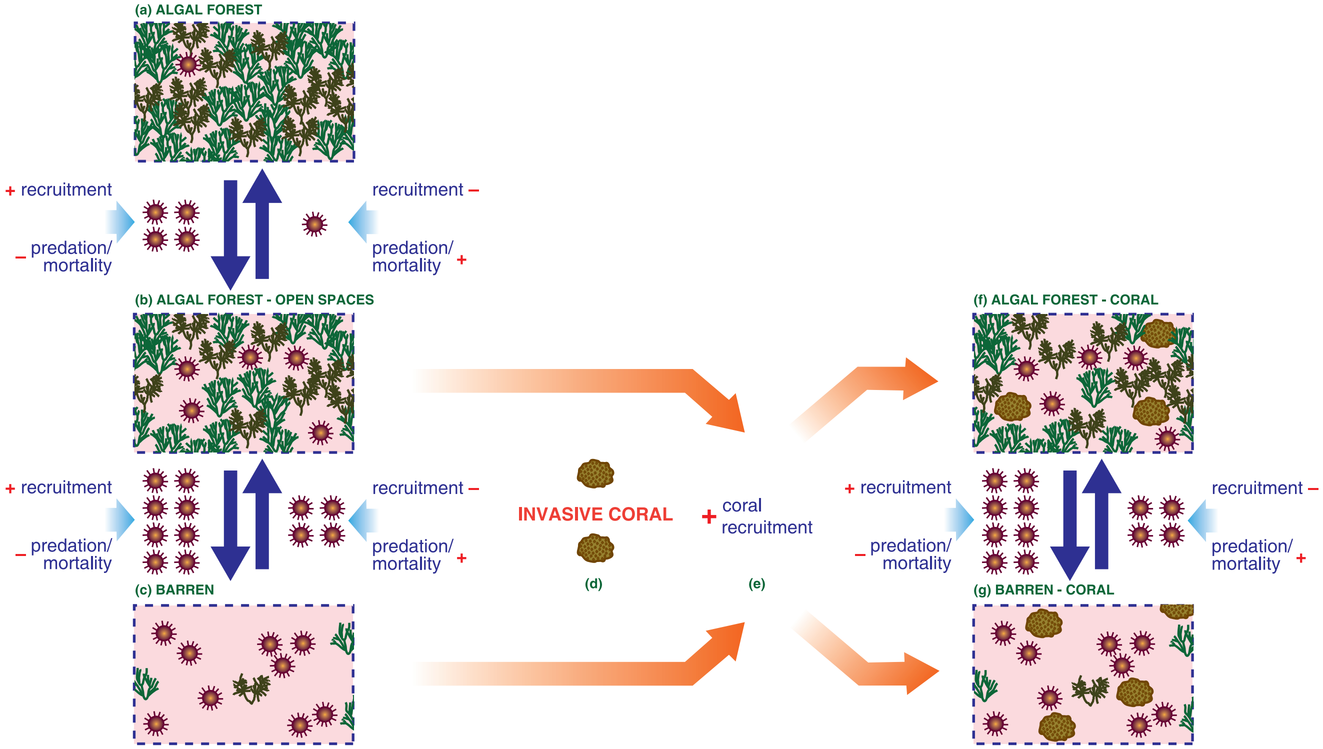

Figure 8. Schematic representation of the observed interactions. The two major assemblages in Mediterranean rocky infralittoral ecosystems are represented at the left side: erect algal forest (a) and coralline barrens (c). Variations in sea urchins density and their grazing impact is the main driver of the shift from algal forests to coralline barrens and *vice versa*. Intermediate densities of sea urchins create and maintain open spaces in the space-limited algal forest (b). These open spaces are usually filled up again by erect algae in a dynamic process of creation and removal of open spaces. However, under the presence of the invasive coral *Oculina patagonica* (d), these open spaces facilitate coral recuitment (e) and increase the abundance of the coral to the extent of matching that of some dominant erect macroalgal species. Therefore, under the presence of *Oculina patagonica* and high to medium sea urchin grazing, two new assemblages flourish: an algal forest-coral assemblage (f) and a coral-coralline barren assemblage (g), depending on the abundance and grazing impact of sea urchins.
doi:10.1371/journal.pone.0022017.g008

than other suspension-feeders thriving in similar habitats, such as *Cladocora caespitosa* and different species of sponges, which have been severely affected by recent mass mortality events [82–84].

Our study describes the processes causing the increase of *O. patagonica* inside a single MPA. However, the increasing number of areas that this coral has been reported in the western Mediterranean [17] suggests that the processes described here could also be underway in other areas. In addition, this growth and expansion could be linked to an increase in sea urchin populations related to changes in the food web directly or indirectly enhanced by overfishing or pollution [24,46,48,74,85].

Shallow infralittoral rocky bottoms in the Mediterranean are undergoing profound changes that result in the disappearance of important habitat engineering species [25,74]. These changes are often linked to overfishing [24], habitat destruction [74], invasive species [75], mass mortality events [84,86,87] or pollution [88]. In this work, we document that the selective predation by sea urchins on the dominant species (macroalgae) created open spaces that enhanced coral settlement and survival. Therefore, within the conditions of the study, trophic interactions contributed to the success of an invasive coral in the Mediterranean because sea urchins grazing activity indirectly facilitated expansion of the coral (Figure 8). We have also presented evidence that the invasive zooxanthellate coral is growing in abundance to levels completely unexpected in the Mediterranean, an event that challenges the current conceptual framework [9], offering an excellent opportunity to study the mechanisms that sustain present benthic communities in this habitat. Furthermore, we discovered new evidence regarding the crucial role of sea urchins in Mediterranean infralittoral communities by demonstrating that sea urchin grazing activity not only causes changes in algal composition, but also facilitates the expansion of an invasive coral.

Materials and Methods

Study area

The study was conducted at the Cabo de Palos-Islas Hormigas Marine Reserve which is located in the southeastern part of the Iberian Peninsula (Cape of Palos: 37°38′01″N, 0°41′04″W).

Sampling

The density and size of coral colonies of *Oculina patagonica* was assessed at 4 locations (Figure 1) in 2002 and 2010. Yearly assessments of the coral populations were conducted in spring at two locations (La Hormiga and El Hormigón) within the marine sanctuary of the Marine Reserve (where no activities other than scientific research can be conducted since 1995) from 2003 to 2010. Although the species is abundant at depths from the surface to 9 m, the greatest abundance was observed around 6 m [89]. At this depth, two randomly located transects (50 m×1 m) were performed by SCUBA divers. Only colonies with at least 50% of their surface area lying within the belt-transect were counted to avoid boundary effect biases to the spatial sampling method [90].

Within the study area, the colonies of *O. patagonica* displayed a predominantly encrusting growth form with a circular-ellipsoidal shape. The surface area of the colonies was estimated by means of *in situ* measuring of the longest dimension of the colony (length, L) and its perpendicular axis (width, W) with a ruler to the nearest millimeter. The surface area was calculated (S, cm^2) using the formula $S = \pi[L+W]/4]^2$ according to [15].

The abundance of sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) along the same 50 m^2 transects was also recorded every year from 2003 to 2010. Sea urchin abundance was recorded in plots measuring 10 m^2. Between 2006 and 2010 size-structure of sea urchins was also estimated by measuring maximum test diameter without spines (MTD). All individuals larger than 2 cm in test diameter were counted and measured with calipers along the whole transect.

To determine whether coral recruitment was facilitated by the presence of open spaces we examined small coral colonies (up to 100 cm^2) associated with open spaces (a discrete area deprived of, but bordered by, erect macroalgae). A colony was considered to be associated with an open space if a minimum of 50% of the perimeter of the coral colony was in contact with the open space. We examined whether or not each coral colony within the random transects was associated to an open space on a minimum of a 100 m^2 in 2005, 2006, 2007 and 2010. The observed number of small colonies associated with open spaces was contrasted to that expected. Expected values were estimated by multiplying the total of colonies associated with open spaces by the proportion that the small colonies size class represents from the overall coral population. Observed and expected values from the four different year assessments was tested using Chi-square.

The size of the open spaces within the transects in contact with *O. patagonica* was estimated in 2010. Percent cover of open spaces was assessed within randomly located 1 m^2 squares ($n = 20$) by estimating abundance of open spaces in 20 randomly distributed square meters at La Hormiga and El Hormigón. Each square meter estimate was conducted by adding the estimates of 4 adjacent 0.50×0.50 m quadrats. Quadrats were subdivided into 25 squares (each representing 4% of the quadrat), and the open spaces in each subdivision were recorded.

Statistical analysis

Variation of coral density over time at La Hormiga and El Hormigón was examined using a Pearson product moment correlation. Variation of coral cover (proportion of surface occupied by coral colonies in each 50 m^2 transect) over time was examined with the same method. A two-way ANOVA was conducted comparing coral density among 4 locations (La Hormiga, El Hormigón, Bajo de Fuera and Bajo de Dentro) and time (2002 and 2010) to examine whether the abundance of the species varied over the study period at the four locations. Prior to analysis, normality was checked using a Kolmogorov test. Homogeneity of variance was tested using Cochran's test, and whenever necessary, data were transformed [91]. Statistics were performed using STATISTICA 6 software package.

Coral size distribution was analyzed by estimating mean colony size, the coefficient of variation (i.e., standard deviation as percentage of the mean), skewness and kurtosis. Variation of the mean colony size over time (2003 to 2010) was examined using a Pearson product moment correlation. Variation of the coefficient of variation over time was examined with the same method. Skewness and kurtosis coefficients were considered significant if g_1 per SES (standard error of skewness) or g_2 per SEK (standard error of kurtosis) was greater than 2 [92].

A two-way ANOVA was used to determine whether the number of open spaces varied between locations (La Hormiga and El Hormigón) and over time. Time was considered to be fixed in the analyses, and location was randomized. A one-way ANOVA was used to determine whether the amount of space occupied by open spaces varied between both locations.

A three-way ANOVA was used to compare sea urchin densities among species (*Paracentrotus lividus* and *Arbacia lixula*), locations (La Hormiga and El Hormigón) and time (2003–2010). The factors of species and time were considered to be fixed in the analyses, and location was random. A one-way ANOVA was used to examine variation in the density of both sea urchin species among the four locations in 2010. Pearson product moment correlation was used to examine the relationship between the abundance of both sea urchin species and the abundance (density and coverage) of *O. patagonica*.

The following equation was used to transform *P. lividus* density and size structure into *P. lividus* biomass:

$$DW = 0{,}0013 \times D^{2{,}571}$$

where DW is dry weight in grams and D is the test diameter without spines [35]. A two-way ANOVA was conducted to compare *P. lividus* biomass among locations (La Hormiga and El Hormigón) and time (2006–2010) to examine whether the species exhibited a similar pattern over the study period at both locations. Time was considered to be fixed and location was randomized in the analyses.

Supporting Information

Figure S1 Size-frequency distribution of *Oculina patagonica* populations between 2003 and 2010 at La Hormiga.
(EPS)

Figure S2 Size-frequency distribution of *Oculina patagonica* populations between 2003 and 2010 at El Hormigón.
(EPS)

Figure S3 Size-frequency distribution of the populations of the sea urchin *Paracentrotus lividus* between 2006 and 2010 from La Hormiga and El Hormigón.
(EPS)

Text S1 Assessment of other factors that may affect the dynamics of the coral and sea urchin populations.
(DOC)

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Author Contributions

Conceived and designed the experiments: RC ES CL. Performed the experiments: RC CL ES DD EB. Analyzed the data: RC ES MR. Contributed reagents/materials/analysis tools: RC EB MR. Wrote the paper: RC ES EB MR.

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Rapid Northward Spread of a Zooxanthellate Coral Enhanced by Artificial Structures and Sea Warming in the Western Mediterranean

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Abstract

The hermatypic coral *Oculina patagonica* can drive a compositional shift in shallow water benthic marine communities in the northwestern Mediterranean. Here, we analyze a long-term, large-scale observational dataset to characterize the dynamics of the species' recent northward range shift along the coast of Catalonia and examine the main factors that could have influenced this spread. The variation in the distributional range of *Oculina patagonica* was examined by monitoring 223 locations including natural and artificial habitats along >400 km of coastline over the last 19 years (1992–2010). Abundance of the species increased from being present in one location in 1992 to occur on 19% of the locations in 2010, and exhibited an acceleration of its spreading over time driven by the join action of neighborhood and long-distance dispersal. However, the pattern of spread diverged between artificial and natural habitats. A short lag phase and a high slope on the exponential phase characterized the temporal pattern of spread on artificial habitats in contrast to that observed on natural ones. Northward expansion has occurred at the fastest rate (22 km year^{-1}) reported for a coral species thus far, which is sufficiently fast to cope with certain climate warming predictions. The pattern of spread suggests that this process is mediated by the interplay of (i) the availability of open space provided by artificial habitats, (ii) the seawater temperature increase with the subsequent extension of the growth period, and (iii) the particular biological features of *O. patagonica* (current high growth rates, early reproduction, and survival to low temperature and in polluted areas). These results are indicative of an ongoing fundamental modification of temperate shallow water assemblages, which is consistent with the predictions indicating that the Mediterranean Sea is one of the most sensitive regions to global change.

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Introduction

Human activities (e.g., overfishing, trawling, coastal development, deployment of man-made infrastructures, transportation, use of fossil fuels and pollution) are currently affecting marine ecosystems worldwide [1–3]. Two main phenomena – climate change and the introduction of alien species – appear to be increasing the rate of change in species distribution boundaries, making it possible to examine such changes on a decade time-scale [4–7]. The distributions of a wide range of taxa are expanding poleward [6,8], and at the same time, coral reefs are undergoing rapid degradation due to increasing anthropogenic impacts, particularly climate change [9–12]. The poleward expansion of corals favored by increasing temperatures could compensate for the degradation of corals in their normal distribution range because of warming. However, it has been argued that coral species appear to be unable to disperse or adapt rapidly enough to cope with the current rate of change [12–15], but see [16–17].

The Mediterranean Sea is an optimal study site for early detection and characterization of the effects of global change on marine species ranges for several reasons. First, it is a semi-enclosed sea that is being affected by climate change at a faster rate than many other marine areas [18], and second, it is a hot spot for alien species, some of which are of tropical origin and have entered the Mediterranean via the Suez Canal [19–21]. An understanding of the spread dynamics of alien species and the main processes determining this spread are crucial for predicting future changes in their distributions in the context of global environmental change [4,22]. Accurate predictions of the future distribution ranges of alien species that are able to change the structure and functioning of native ecosystems [23–25] are essential for determining their effects and for supporting management actions.

The most accurate records regarding the rate and the spatial pattern of the spread of alien species come from annual field surveys [26]. However, surveys repeated with high frequency in areas ranging from tens to hundreds of kilometers are rare, mainly due to the cost of monitoring large areas in detail. Thus, distributional data for most introduced species have low accuracy given that they comprise a relatively limited number of observations [27–28].

Oculina patagonica (De Angelis D'Ossat 1908) is an alien, non–lessepsian scleractinian zooxanthellate coral that presumably originated from the southwest Atlantic and was first recorded in the Mediterranean Sea in 1966 (when a single colony was found in the Gulf of Genoa, [29]). The unsolved problem is that the original description of *O. patagonica* is based on fossil material from Holocene deposits on the temperate coast of South America, and living specimens have not been found in this area. In the late 1970s, *O. patagonica* was abundant along ~300 km of the southeast coastline of the Iberian Peninsula, indicating that this species had been present in this area for a long time when it was first recorded [30–32]. This species is also currently abundant on the coast of Israel where it was first recorded in 1993 [31]. During the last decade, *O. patagonica* has exhibited a 3-fold increase in certain littoral locations in southeastern Iberia [24], and isolated colonies have been found in several new areas throughout the Mediterranean (see [32] for a review), suggesting that *O. patagonica* is spreading geographically. The species presumably spread from the western basin to the levant basin via the intense intra-Mediterranean maritime traffic [31]. Both asexual dispersal in the form of polyp expulsion [33] and the release of gonads from colonies attached to ship hulls [29], which is favored because the species is capable of reproducing sexually when colonies are small [31], have been proposed as the primary vectors of invasive transport. Moreover, the species' ability to thrive and reproduce despite wide variations in temperature, salinity, UV radiation, turbidity and hydrodynamic conditions [31,34] may have favored the species' spread throughout the Mediterranean.

In this study, the spread of *O. patagonica* was examined by monitoring >400 km of coastline over the last 19 years on the Catalan coast (northwestern Mediterranean). Whereas *O. patagonica* is abundant ~30 km south of the Catalan coast ([35], authors' unpublished data), it was not recorded in the adjacent area to the north prior to 1992 [32]. Here, we analyze a long-term, large-scale observational dataset in order to characterize the dynamics of the species' recent northward range shift along the Catalonian coast and examine the main processes that could have influenced this spread.

Materials and Methods

Distribution surveys

The study was performed along the Catalan coast in the northeastern region of the Iberian Peninsula (northwestern Mediterranean). The study area encompassed more than 400 km of coastline from Les Cases d'Alcanar in the south (40°31′N, 0°30′E) to Portbou in the north (42°26′N, 3°10′E, Fig. 1). A total of 223 locations were examined for the presence of the scleractinian coral *O. patagonica* over a period of 19 years (1992–2010) at intervals ranging between 1 and 2 years as part of a monitoring protocol designed to determine the arrival and occurrence of alien species in the shallow infralittoral zone. We surveyed both natural ($n = 169$) and artificial ($n = 54$) habitats. The natural habitats were rocky reefs, while the artificial habitats included man-made structures, primarily dikes, breakwaters and harbor walls. The mean linear distance between the examined locations was ~2 km. At each location and sampling date, the presence or absence of the coral was determined through close examination of at least 1500 m^2 of the sea floor using SCUBA.

The results of the systematic monitoring of *O. patagonica* were translated into absence/presence records over time at each location. The cumulative numbers of locations where the species was present were used to reconstruct the pattern of its spread [36–37]. The initial detection of the coral was unequivocal for colonies larger than 5–10 cm in diameter; however, smaller colonies could be overlooked. It was noteworthy that over the study period, the species did not disappear from any location after its initial detection there. Thus, although the initial detection underestimates spread rate of *O. patagonica*, this species persistence in all locations where it was found over the study period indicates that the detection of small colonies provides a fair estimation of when this species became established. This pattern is most likely related to the size-dependent nature of coral mortality [38–39]. To reduce the bias introduced by the fact that not all locations were examined every year, gaps in the data obtained at a particular location after the coral was first detected were marked as the species being present based on species persistence. Then, to examine the pattern of *O. patagonica* spread over the study period, we calculated the cumulative number of locations where the species was present and expressed this as a percentage of the total number of locations.

Regression models were fitted to the standardized cumulative number of locations where the species was present over time (termed standardized spread curves [37,40]), and the slope of the linear regression of the log-transformed cumulative number of locations was used as a measure of spreading success [37,41]. A standardized spread curve was calculated separately for each of the two habitat types (i.e., natural and artificial).

The different phases of the spreading process (lag, exponential and saturation; [42]) were examined in the standardized spread curves. The beginning of the exponential phase was defined as the year in which the parameters of the standardized spread curve changed. This phase was detected using a maximum likelihood estimation of classic regression parameters for partitioned models [43–44]. The shift was set at the F-value of maximum significance ($p < 0.0001$). The coefficient of the linear regression of the cumulative number of locations after the lag phase over time was used as a measure of the rate of the exponential phase. Differences in the slopes of the overall standardized spread curves and in the slopes of the exponential phase were tested using the homogeneity of slopes test [45].

We examined whether the northern limit of the distribution of *O. patagonica* varied over time. The linear correlation coefficient of the northern distribution limit of the species over time was used to estimate the expansion rate (km $year^{-1}$).

Current distribution and abundance (2008–2010)

Between 2008 and 2010, field surveys also included measurements of all coral colonies and an annotation of the depth of each colony. Within the study area, the *O. patagonica* colonies displayed a predominantly encrusting growth form with a circular-ellipsoidal shape. A colony was defined as any distinct, single coral skeleton with living tissue. A specimen divided by partial mortality into separate patches of living tissue that was morphologically still one entity was considered as a single colony. Neighboring colonies in close proximity, which were found on several occasions, were measured as distinct. The surface area of the colonies was estimated by means of *in situ* measurements of the longest dimension of the colony (length, L) and its perpendicular axis (width, W) to the nearest millimeter using a ruler. The surface area (S, cm^2) was calculated using the formula $S = \pi[(L + W)/4]^2$ according to [31].

Two methods were used to estimate coral abundance on hard substrata between 0 and 10 m in depth (or until the maximum depth when the depth was <10 m), which is the depth range within which *O. patagonica* has been reported to be the most

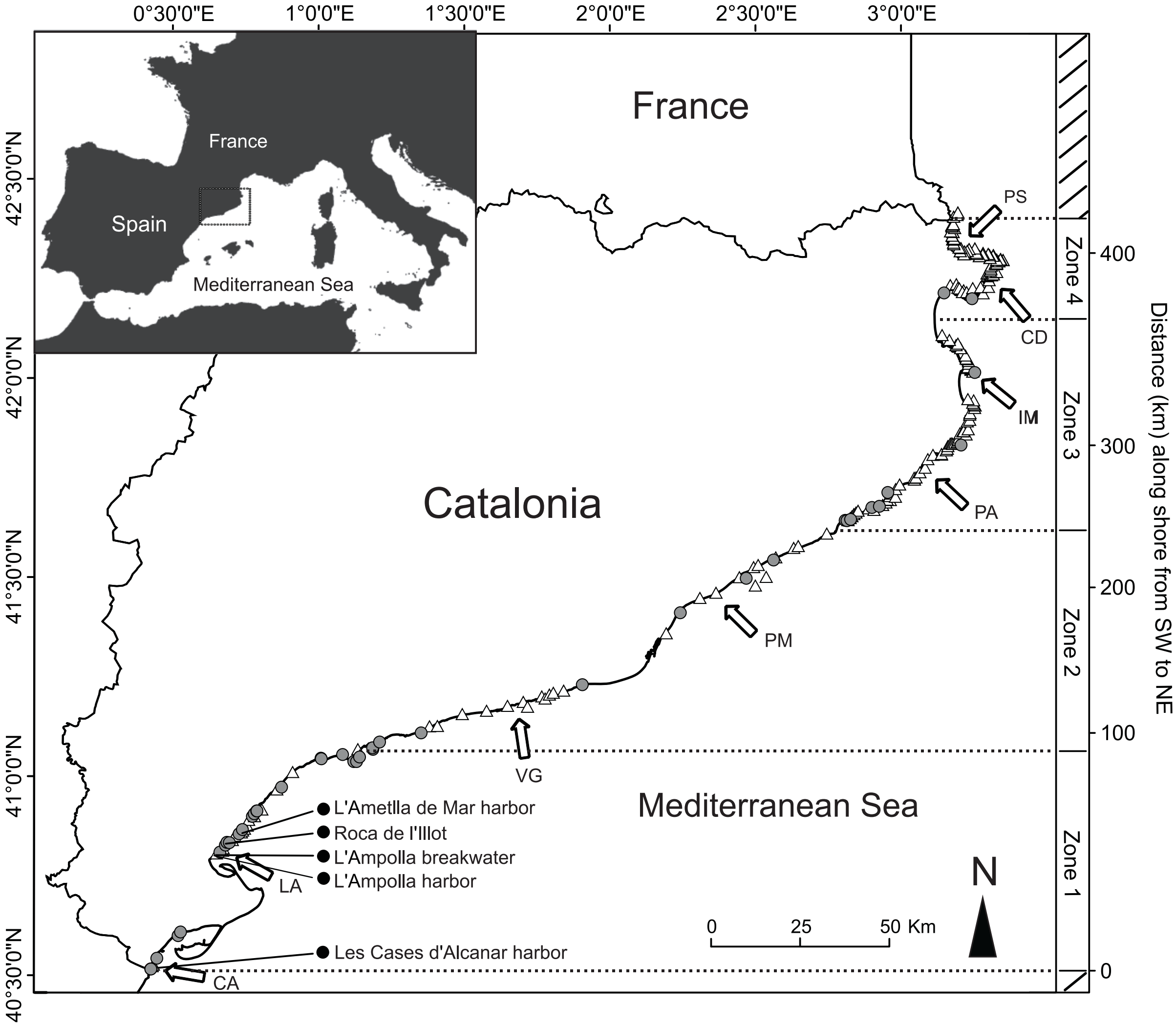

Figure 1. Map of the Catalan coast in the northeastern region of the Iberian Peninsula (northwest Mediterranean Sea). The positions of the 223 surveyed locations are indicated. Blank triangles (n = 180) represent surveyed locations in which *Oculina patagonica* was not found. Locations in which *O. patagonica* was found are represented by grey circles (n = 38; density $<$0,05 col. m^{-2}) and black circles (n = 5; density $>$0,05 col. m^{-2}). The linear coastal length from the southernmost location (in kilometers) is represented on the right-hand y-axis. Four zones of ~100 km in length have been distinguished from the south (zone 1) to the north (zone 4) to examine the patterns in coral abundance. Sea surface temperature (SST) data have been obtained from two locations in each zone (indicated by white arrows): Les Cases d'Alcanar (CA), L'Ampolla (LA), Vilanova i la Geltrú (VG), Premià de Mar (PM), Port d'Aro (PA), Illes Medes (IM), Cadaqués (CD) and Port de la Selva (PS).
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abundant [31–32, authors' observations]. When the species was scarce (hereafter, present), we assessed its abundance by counting and measuring all colonies present on 1500 m^2 of the seabed using SCUBA. When the species was abundant (hereafter, populations), we conducted three replicates of randomly localized 40 m^2 transects (40×1 m, Fig. S1). Only colonies with at least 50% of their surface area lying within the belt transect were counted and measured to avoid boundary effect biases in the spatial sampling method [46]. Coral abundance data were standardized based on the area surveyed, and the species density and percent cover values were calculated for each location.

We utilized the standard error (SE) sample size function to determine the minimal sampling area needed to assess the density and percent cover of the coral populations [47–48]. Preliminary sampling to obtain coral abundance estimates was conducted at one of the study locations (Les Cases d'Alcanar) by examining an area of 200 m^2 using 5 m^2 belt transects (5×1 m) set randomly on the substrate between depths of 2 and 4 m.

We partitioned the entire coast into four similar zones (each ~100 km of coastal length, Fig. 1) to identify the mechanisms that contribute to the variation in the abundance of *O. patagonica* colonies across the study area. The number of locations where the species occurred was calculated separately for each zone to examine whether the coral exhibited an identifiable pattern along the coast. The proportion of locations where the coral occurred in each of the four zones was calculated separately for the two habitat types (i.e., natural and artificial).

Temperature

Temperature has long been considered to be one of the main environmental factors controlling coral species distributions (e.g., [49–50]). We obtained a sea surface temperature (SST) time series from 8 locations distributed along the ~400 km Catalan coast

(Fig. 1). The cumulative distances between the locations at which temperature was examined, ordered from south to north, are indicated in Table S1.

Daily mean SSTs were obtained from January 2003 to December 2010 from satellite measurements performed by the MODIS (aqua) sensor system (http://oceancolor.gsfc.nasa.gov/), which were made available as "Ocean Level-2" HDF data by NASA's Goddard Space Flight Center. HDF files were read and processed using Matlab R2009a (MathWorks Inc., Natick, MA, USA). In the analysis, we considered only high-quality temperature readings (flag values of 0 or 1), and we discarded less reliable readings (flag values of 2 or 3). The suitable SST readings used in our analyses corresponded to the daily means in a 9-km^2 area centered on the geographic coordinates indicated in Table S1.

Over the SST study period, the mean annual temperature and mean annual 95th and 5th percentiles were determined for each location along the Catalan coastline. On the basis of the SST data recorded daily, we also calculated the number of days that the temperature was above or below different thresholds specifically chosen because of their biological consequences (i.e., relying on previous field observations and/or thermo-tolerance experiments performed on *O. patagonica* [51–52]). To examine whether exposure to summer conditions ($>$18°C, [53]) and to upper sub-lethal temperatures (24 and 26°C) could affect the target species, we determined the day in spring/summer on which the SST reached $\geq$18°C, $\geq$24°C, and $\geq$26°C and the day in late summer/fall on which it dropped below each temperature. To avoid any bias introduced by short-term temperature oscillations, we determined that after the date on which the SST reached $\geq$X°C, the daily mean SST values had to remain $\geq$X°C on at least 80% of the days throughout the following two weeks (i.e., 11 of 14 days). These temperature thresholds were used to assess the temperature regimes among 8 locations distributed along the 400 km of the Catalan coastline.

Due to the assumptions made by the Pearson's correlation analyses, we estimated the confidence intervals when the n value was $<$12. The 95% confidence intervals were calculated using bias-corrected bootstrapping with 1,000 resamples, which were considered significant when the confidence limits did not include zero [54]. All analyses were computed using STATISTICA 7.0, except for the bootstrapping analyses, which were implemented with R [55].

Results

Current distribution along the Catalan coast

We found that *O. patagonica* was present in wide areas along the study coast at a depth range of 0–10 m. The species was rarely observed below this depth, although a few colonies were found down to 28 m depth.

O. patagonica abundance decreased from south to north, and significant populations (defined as those with a density of $>$0.05 colonies m^{-2}) were found in 5 locations, all of which were situated in the southernmost zone of the studied region (Fig. 2a). At all other locations where this species was observed, it occurred at a density of $<$0.05 colonies m^{-2}. Occurrence of the species at densities of $<$0.05 colonies m^{-2} was defined as presence. Four of these populations were located in artificial habitats, and one was located in a natural habitat. The density of *O. patagonica* populations in the artificial habitats ranged from 0.24 to 1.07 colonies m^{-2} (0.46±0.20 colonies m^{-2}, mean ± SE), which was approximately three-fold higher than the density observed in the single natural habitat (0.17±0.02 colonies m^{-2}, mean ± SE). The percentage of the sea floor occupied by the species (percent cover) in artificial habitats ranged from 0.51 to 5.51% (2.48±1.13%, mean ± SE), which was approximately two-fold higher than that of the population in the single natural habitat (1.35±0.48%, mean ± SE). The species density at the 38 locations where it was present was also two-fold higher in artificial habitats than in natural habitats (0.0042±0.0009 vs. 0.0020±0.0004 colonies m^{-2}, respectively; mean ± SE; One-way ANOVA, $F_{1,36} = 4.6563$, $p = 0.0377$). Of the total number of *O. patagonica* colonies measured ($n = 670$), 80% were found in artificial habitats, and 20% were located in natural habitats.

In accordance with the species abundance, the maximum colony size decreased from south to north. The locations with the largest colony sizes ($>$1000 cm^2) were mainly found in the southernmost zone of the region (Fig. 2b). The maximum colony size was less than 1000 cm^2 at all other locations, with the exception of the location where a discrete long-distance dispersal event occurred in the year 2000 (see below). The maximum colony size did not vary between the artificial and natural habitats (1156±363 vs. 925±255 cm^2, mean ± SE, respectively; One-way ANOVA, $F_{1,\ 38} = 0.2623$, $p = 0.6115$).

The proportion of locations where the species occurred decreased steadily from 61% in the southernmost zone to 3% in the northernmost zone (Fig. 3), although this pattern differed depending on habitat type (i.e., natural and artificial). In artificial

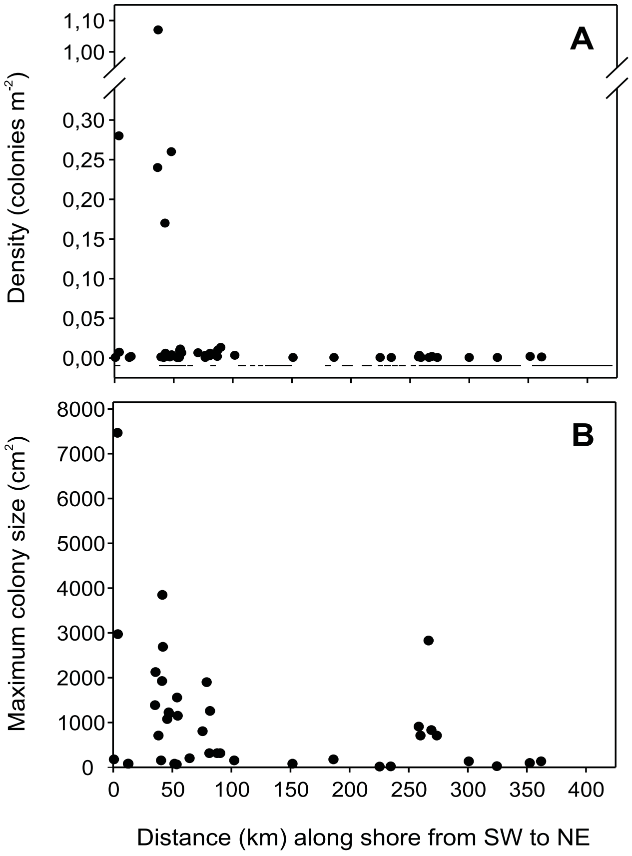

Figure 2. Density and maximum colony size of *Oculina patagonica* along the Catalan coast. A) Current coral density (colonies m^{-2}) in the locations at which the species was observed along the linear length of the Catalan coast (km). Horizontal lines below the zero line indicate locations at which *O. patagonica* was not encountered. B) Maximum colony size (cm^2) in the locations at which the species was observed in 2010.
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habitats, the proportion of locations where the species occurred decreased steadily from 94% in the southernmost zone to 11% in the northernmost zone (Fig. 3), while in natural habitats, the proportion of locations where the species occurred decreased steadily from 38% in the southernmost zone to 2% in the northernmost zone (Fig. 3).

Temporal variation of species distribution

A solitary colony of *O. patagonica* was discovered for the first time in a natural habitat located in the southernmost area of the Catalan coast (Les Cases d'Alcanar) in 1992. A year later, an *O. patagonica* colony was recorded for the first time in an artificial habitat. From 1993 until 2010, the number of locations at which the species was present along the Catalan coast increased exponentially (Fig. 4a). In 2010, the species was present in 19% of all explored locations (43 of the 223 explored locations, Fig. 4a). However, this pattern diverged markedly between the two distinct habitat types; the species was observed in 44% of the artificial habitats and only in 11% of the natural habitats (Fig. 4b).

Exponential regression models provided the best fit to the increase in the cumulative number of locations over time. The cumulative number of locations where *O. patagonica* has been found over the 19-year study period increased $\sim$1% every year (Fig. 4a) and showed a pattern of geographic spreading (Fig. 5). The overall pattern of geographic spreading was characterized by a lag phase of 9 years and a steady increase since 2001 (Fig. 4a, Table 1). However, this pattern diverged between natural and artificial habitats (Fig. 4b); the duration of the lag phase for the natural habitats was approximately twice that of the lag phase associated with artificial habitats (Table 1). The number of locations at which the species was present at the end of the lag phase was low for both habitat types (2–9% of the examined locations), indicating that the exponential phase began immediately after *O. patagonica* established foci in a particular region (Table 1). Throughout the entire study period, the slope associated with the artificial substrata was slightly higher than that associated with the natural substrata. This effect was accentuated in the exponential phase, during which the slope for the artificial substrata was significantly higher than that for the natural substrata ($F = 29.1849$, $p<0.05$, Table 2). Between 2001 and 2006, the overall slope of the exponential phase was reduced because the natural habitats were still in the lag phase. After 2006, the slope exhibited an increasing trend because both habitats were in the exponential phase (Fig. 4, Table 2). Therefore, the species is spreading faster among artificial habitats than natural habitats.

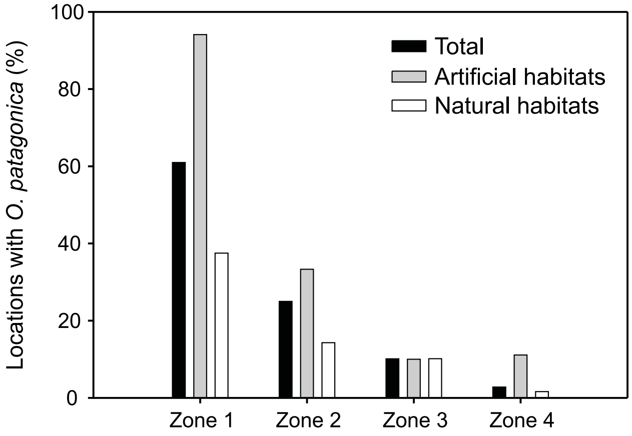

Figure 3. Proportion of locations where *Oculina patagonica* was observed in four zones along the Catalan coast. See Fig. 1 for a description of the four zones. The proportion of locations at which the species was encountered in 2010 is given based on the total number of locations and the habitat type (i.e., natural and artificial).
doi:10.1371/journal.pone.0052739.g003

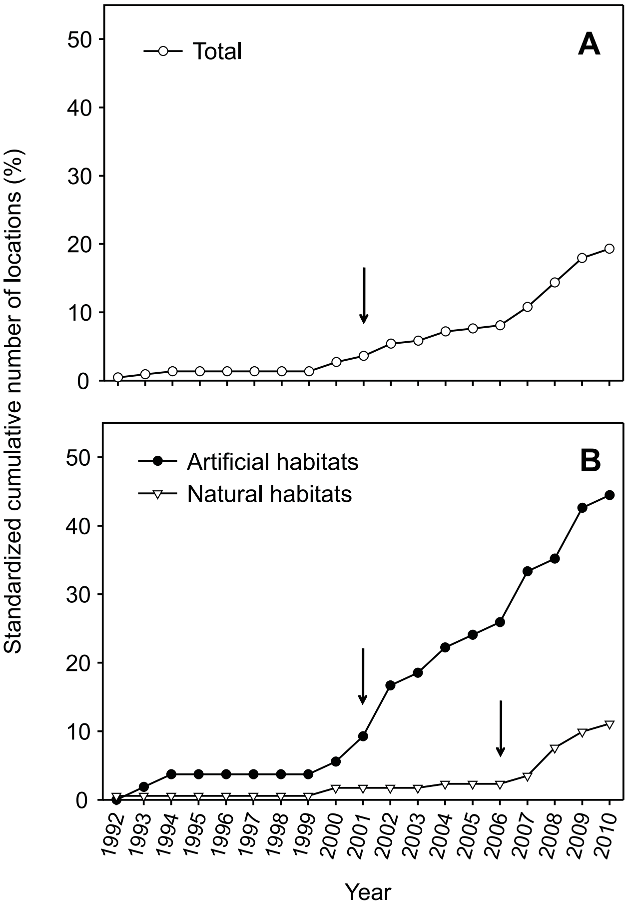

Figure 4. Standardized spread curves of *Oculina patagonica* from 1992 to 2010 along the Catalan coast. The standardized cumulative number of locations where the species occurred is given for (A) the total data and (B) the habitat type (i.e., natural and artificial). The beginning of the exponential phase is indicated by an arrow (see Methods).
doi:10.1371/journal.pone.0052739.g004

Latitudinal distribution limit and spreading patterns

The northern limit of the distribution of *O. patagonica* varied over time, exhibiting a northward geographic spread (Fig. 5). Over the 19-year study period, this limit spread 361 km northward at a mean rate of 21.67 ± 3.70 km year^{-1} (mean ± SE). The presence of *O. patagonica* in the littoral zone underwent lag phases over time (see above), and some long-distance dispersal events ranging between 76 and 182 km (120 ± 32 km; mean ± SE, Fig. 5) created new invasion foci. After the lag phase, the mean square displacement (MSD) between the locations at which the species was present over time showed a scaling exponent of $\alpha \sim 2$ (MSD is proportional to t^{α}, where t is time and α is the scaling exponent, Fig. 6), which indicates an acceleration of spreading over time [56]. This accelerating pattern is strongly driven by a few intermittent long-distance dispersal events. To distinguish local dispersal from long-range dispersal, we estimated the MSD in the southern region of the coral's distribution (first $\sim$100 km of coastline, Fig. 5), which is separated from the northern region by

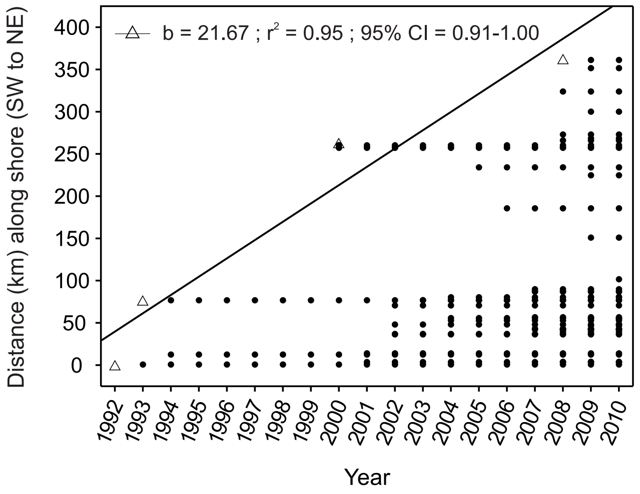

Figure 5. *Oculina patagonica* records obtained on the Catalan coast throughout the study period (1992–2010). Records of the coral occurrence (full circles) throughout the Catalan coastal length (km) from 1992–2010 illustrate the spreading of the species over time. Blank triangles indicate the change in the northern latitudinal limit over time. The expansion rate (km year^{-1}) was calculated as the slope of the Pearson product-moment correlation between the change in the northern latitudinal limit of the coral species and time (n = 4). 95% CI: 95% confidence interval calculated with bootstrapping.
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~50 km of coastline where the species is not present (Fig. 2a). After the lag phase (in 2001), the MSD of the southern region (0–150 km) showed a scaling exponent of $\alpha = 0.43$, indicating a decline of spreading over time (Fig. 6).

Latitudinal temperature analysis

The SST along the studied coastline displayed a northward latitudinal decrease in the mean annual temperature of 0.55±0.05°C/100 km, ranging from 18.72±0.13°C (mean ± SE) in the south (CA) to 16.68±0.13°C in the north (PS) (Fig. 7a). The mean annual temperature did not vary over 8 years according to the available satellite data (2003–2010) at any of the 8 examined locations (data not shown). This is most likely related to the short-term oscillatory pattern in northwest Mediterranean temperatures [57]. The mean annual 95th percentile (p95) decreased by 0.91±0.09°C/100 km with increasing latitude, ranging from 26.84±0.35°C (mean ± SE) in the south (CA) to 23.24±0.44°C in the north (PS) (Fig. 7b). The mean annual 5th percentile (p5) did not vary significantly due to the local temperature conditions of the southernmost location (CA), which is subjected to discharge from the Ebro River (Fig. 7c). However, when this local effect was not considered, p5 exhibited a similar significant pattern of a northward decrease [0.26±0.09°C/100 km, $r^2 = 0.62$, 95% confidence interval = 0.41–1.00 (bootstrap analysis), n = 7]. We are aware that the n value was inappropriate for the Pearson's correlation method, but bootstrapped confidence intervals provided an estimate of the probability that the true correlation coefficient do not include zero.

We calculated the number of days on which the SST was ≥18°C as a temperature indicator of warm conditions that favor *O. patagonica* growth [52] as long as the upper sublethal threshold is not reached [51]. The mean annual number of days on which the SST was ≥18°C exhibited a decreasing latitudinal pattern from south to north, ranging from 188±4 days year^{-1} in the south (CA; mean ± SE) to 143±5 days year^{-1} in the north (PS) (Table 3). Additionally, the mean annual number of days on which the SST was ≥18°C was 24% lower in the north (PS-CD) than in the south (CA) and exhibited an average decrease of 12.35±1.13 days year^{-1} (slope ± SE) for each 100 km northward (Table 3). We calculated two indicators of elevated temperature conditions that have been documented to cause colony damage and decrease the growth of *O. patagonica* after a certain period of exposure: (1) the annual number of days on which the SST was ≥24°C [52] and (2) the annual number of days on which the SST was ≥26°C [51]. The mean annual number of days on which the SST was ≥24°C exhibited a northward decrease, ranging from 90±4 (mean ± SE) days in the south (CA) to 8±5 days in the north (PS). The mean annual number of days on which the SST was ≥24°C was 91% lower in the north (PS) than in the south (CA) and exhibited an average decrease of 22.41±2.05 days year^{-1} (slope ± SE) for each 100 km northward (Table 3). The mean annual number of days on which the SST was ≥26°C exhibited a northward decrease of 7.21±1.15 days/100 km (Table 3), ranging between 31±7 days in the south (CA) and 0 days in the north (PA and upper northern locations). Colony damage related to high temperature was not observed during exposure to summer temperature conditions from 2008–2010 at the southern location (LA), where the SST was ≥24°C for 61–82 days year^{-1} and was ≥26°C for 0–28 days year^{-1} (colonies monitored seasonally over the period 2008 and 2010, authors' unpublished data). In contrast, colony damage that was apparently related to exposure to low temperature during the winter was observed every year (authors' unpublished data).

Discussion

Small cryptic alien species may be present at low numbers for years before they are detected [58]. However, this is most probably not the case for the alien coral *O. patagonica* in Catalonia because (1) it occurs mainly in the shallow infralittoral zone, which has been well studied in previous taxonomic surveys during the 1970s

Table 1. Characteristics of the standardized spread curves of *Oculina patagonica* along the Catalan coast.

	N	First detection in Catalan waters	Duration of L (years)	Beginning of E Year	Loc. no.	% N
Total	223	1992	9	2001	8	3.59
Artificial	54	1993	8	2001	5	9.26
Natural	169	1992	14	2006	4	2.34

A standardized spread curve is given for the total data and the distinguishing habitat type (i.e., artificial and natural). N: number of studied locations; L: lag phase; E: exponential phase; Loc. no.: number of locations; %N: percentage of the cumulative number of locations at which the species was observed at the beginning of the exponential phase.
doi:10.1371/journal.pone.0052739.t001

Table 2. Spread rate of *Oculina patagonica* along the Catalan coast.

	Entire study period					Exponential phase				
	Slope (b)	**SE of b**	**r^2**	**p-value**	**N**	**Slope (b)**	**SE of b**	**r^2**	**95% CI**	**N**
Total	0.08	0.00	0.96	<0.0001	19	1.71	0.19	0.91	(0.83–0.98)	10
Artificial	0.08	0.01	0.94	<0.0001	18	3.74	0.20	0.98	(0.94–1.00)	10
Natural	0.07	0.01	0.88	<0.0001	19	2.40	0.28	0.96	(0.90–1.00)	5

Coral spread rate for the 19-year study period (left side of the Table), is expressed as the slope of the linear regression of the log-transformed standardized cumulative number of locations where the species was present versus time. For the exponential phase (right side of the Table), the spread rate is expressed as the slope (b) of the linear regression of the standardized cumulative number of locations where the species was present versus time. In each case, estimates were calculated separately for the total data and the distinguishing habitat type (i.e., natural and artificial). SE: Standard error. N: number of years. 95% CI: 95% confidence interval calculated with bootstrapping.

doi:10.1371/journal.pone.0052739.t002

and early 1980s [59–63]; (2) it achieves a large colony size (>50 cm in diameter); (3) it is easy to identify and has previously been detected in other Mediterranean areas [29–30]; and (4) the Catalan coast was regularly explored (every 1–2 years) at a high resolution (mean distance between locations of 2 km) throughout the entire study period (1992–2010) with the specific objective of detecting alien species in this habitat. We therefore conclude that *O. patagonica* should be a recent addition to the studied coast.

Although the regular monitoring of *O. patagonica* has allowed us to characterize the dynamics of its spreading, the initial detection of the species at a sampling station did not necessarily correspond to the date of its arrival because we were not able to detect very small colonies with one polyp or a very low number of polyps. In fact, according to Lodge [64], the proportion of species introduced outside of their original range that become established is generally low for a wide variety of reasons, and the time of establishment is ecologically more relevant than the time of first arrival. The fact that *O. patagonica* did not disappear from any of the locations where it had been detected over the 19-year monitoring period indicates that our time of initial detection is a conservative estimate of the time of establishment.

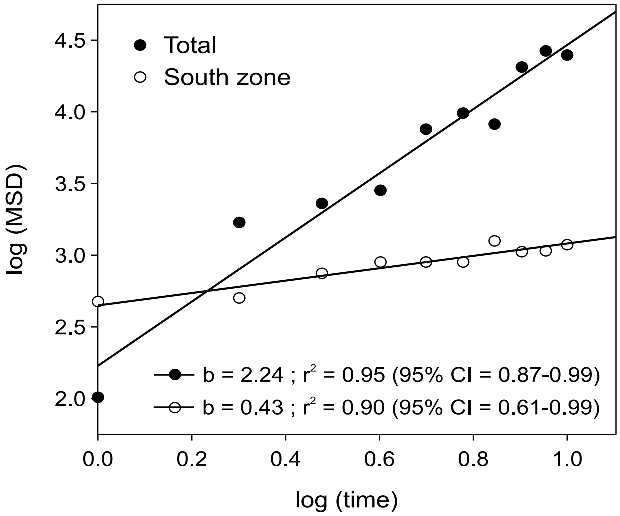

Figure 6. Patterns of *Oculina patagonica* dispersal. Mean square displacement (MSD) between the locations at which the coral species was found after the lag phase. The dispersal of the species during the exponential phase of spreading is provided separately for the overall distribution (Total) and for the southern zone (0 to 100 km coastal length). MSD is proportional to t^{α} where t is time and α is the scaling exponent. 95% CI: 95% confidence interval calculated with bootstrapping.

doi:10.1371/journal.pone.0052739.g006

Spreading dynamics

The use of a standardized spread curve has allowed us to characterize a 9-year lag period, during which the spreading rate was much lower than that in the exponential phase. After the establishment of the species at a particular location, its colonies begin to grow and reproduce. Thus, the observed lag phase could be related to the fact that broadcast spawning corals, such as *O. patagonica* [31], rely on an external fertilization process (in which gametes are released into the water column for dispersal) that requires a critical density of adults to ensure successful fertilization [65–68]. Additionally, the species is a gonochoric coral, and a skewed sex ratio has been documented at certain locations with low coral abundance [31]. Therefore, Allee effects could be contributing to the observed lag phase in this species' spreading dynamics. Surprisingly, the lag phase of this coral species is within the range documented for most invasive benthic macroalgae (5–10 years, [28]), which is likely attributable to the particular biological characteristics of *O. patagonica* (see below). The beginning of the exponential phase occurred when *O. patagonica* was present at 3.6% of the total number of investigated locations, indicating that the exponential phase began shortly after the species established foci in the region.

The observed northward spread of *O. patagonica* across the study area coupled with the northward decrease in coral abundance and maximum colony size provides strong evidence of a recent and ongoing poleward expansion. The MSD estimate for the southern region of *O. patagonica* distribution, which is indicative of the pattern of dispersal to nearby locations, showed a decrease in spreading over time [56]. This finding is consistent with the fact that the species faces less favorable conditions while spreading northward [69–70]. However, the MSD estimate for the overall distribution indicated a pattern of spreading acceleration over time. The differences in the patterns emerging from the two estimates are based on the occurrence of a few intermittent long-distance dispersal events (i.e., punctuated dispersal, [71]). The occurrence of intermittent long-distance dispersal events exerted a large effect on the overall pattern of spreading of the species by promoting a regime shift from a decreased to an accelerated pattern of spreading over time. Thus, the rapid spreading of *O. patagonica* appears to have been accomplished through the interplay of two spatial scales of dispersal: neighborhood dispersal and long-distance dispersal interspersed with lag periods. This rapid spreading is consistent with a large increase in the spreading rate that may be caused by a small number of long-distance

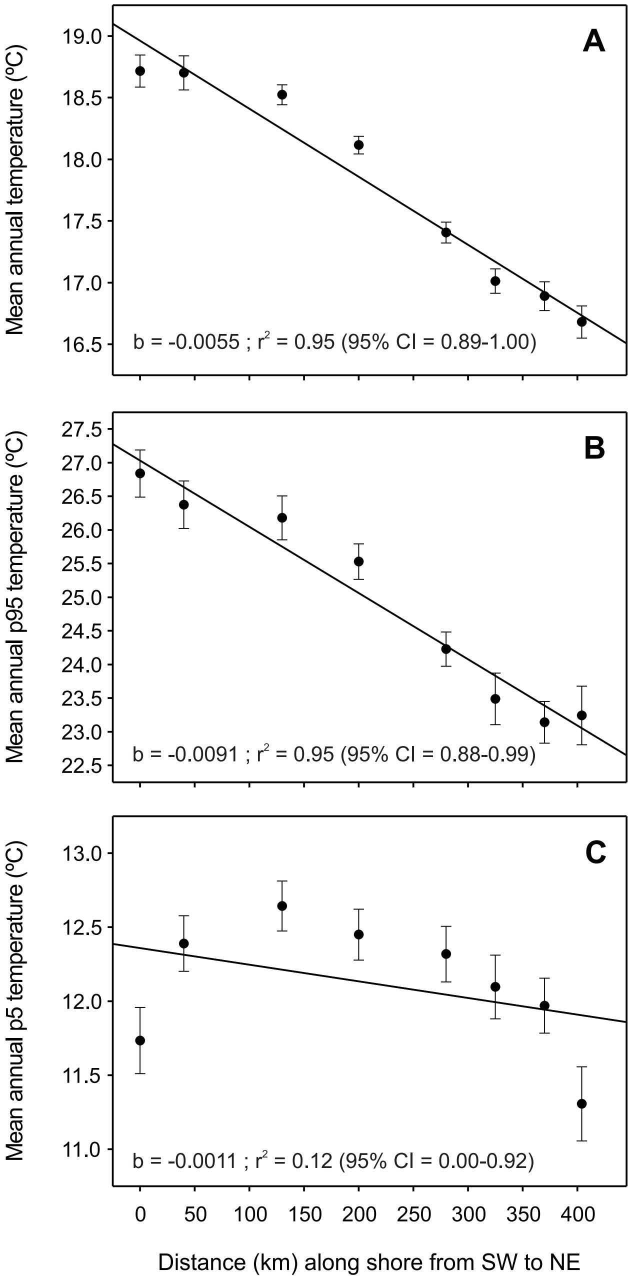

Figure 7. Sea surface temperature (SST) obtained from NASA satellite measurements over the last 8 years (2003–2010). See Fig. 1 and Table S1 for a description of the studied locations (n = 8). A) Mean annual temperature; B) mean annual temperature 95th percentile (p95); C) mean annual temperature 5th percentile (p5). Pearson product-moment correlation between the distance (km) along the shore from SW to NE (see Fig. 1) and the temperature along the Catalan coast. 95% CI: 95% confidence interval calculated with bootstrapping.
doi:10.1371/journal.pone.0052739.g007

Table 3. Sea surface temperature thresholds along the Catalan coast.

SST indicator	slope (b)	SE of b	r^2	95% CI	N
no. of days ≥18°C	−0.12	0.01	0.95	(0.86−1.00)	8
no. of days ≥24°C	−0.22	0.02	0.95	(0.89−0.99)	8
no. of days ≥26°C	−0.07	0.01	0.87	(0.71−0.98)	8

Pearson product-moment correlation between coastal length (km from south to north, see Fig. 1) and sea surface temperature (SST) indicators (mean annual number of days on which the temperature was above 18°C, 24°C and 26°C per year from 2003 to 2010) along the Catalan coast. SE: standard error of the slope (b). N: number of locations where SST was measured along the Catalan coast. Temperature values were obtained from satellite data, see Methods. 95% CI: 95% confidence interval calculated with bootstrapping.
doi:10.1371/journal.pone.0052739.t003

dispersal events, as documented in other observed and modeled populations [72–74].

Various tropical corals appear to be shifting their distributions to higher latitudes in the western Atlantic (6–10 km year^{-1}; [75], *sensu* [76]), the Indo-Pacific [77] and the western Pacific (2–14 km year^{-1}; [17]). The northward spreading rate of *O. patagonica* observed in this study (22 km year^{-1}) is the highest reported for a native or alien scleractinian coral to date and is consistent with the recently documented presence of isolated colonies of this species in distant zones throughout the Mediterranean [32].

Gametogenesis has been observed in colonies from the study area (authors' unpublished data). Dispersal to nearby areas can be achieved through the dispersion of planula larvae and via the polyp expulsion mechanism [33]. Long-distance dispersal can also be achieved through planula dispersion mediated either by currents or ballast waters as previously suggested [29,32]. However, the capacity of this species to settle on floating objects ([31], authors' observations) and to thrive in harbors and polluted areas [78] suggests that drifting on artificial substrata may be another vector favoring dispersal. Long-distance dispersal mediated by floating objects has been shown to contribute to the spreading of rapid colonizer species of coral [79–82]. Although sea surface circulation along Catalonia typically occurs in a southwestward direction [83], strong southern winds also occur regularly [84], which may help to explain the observed northward spreading of *O. patagonica* (Text S1). This spreading, via the above-mentioned dispersal mechanisms, indicates the high capacity of this species for dispersal, recruitment, growth and survival, which is consistent with its biological characteristics (see below).

Causes of northward expansion

Successful establishment in a new area is dependent on the physical environment and the life-history traits of the species together with biological interactions [85–86]. However, the response of a species to environmental change could affect the outcome of biotic interactions such as competition and predation [87–90]. For example, when *O. patagonica* comes into contact with a bryozoan species, the competitive outcomes vary depending on whether the coral is affected by bleaching [91]. Competition between macroalgae and corals plays a significant role in determining the composition of benthic communities [10,92–93]. Macroalgae are dominant in shallow habitats in temperate ecosystems [69,94–95], and this dominance is especially evident in the Mediterranean [96–98]. Although macroalgae have been strongly affected during the last century due to habitat alteration along the Catalan coast, the shallow infralittoral zone in which the species dwells is still spatially limited [99–100]. In the northwest Mediterranean Sea, extreme physical disturbances and/or the high sea urchin abundance are the main mechanisms that create significant open spaces in an otherwise spatially limited macroalgal community [101–102]. Although the Catalan coast was affected by several large storms (defined as storms with waves ≥3 m) during the study period, only the storm of December 2008 was sufficiently large to cause relevant changes in the availability of open spaces [103]. Thus, the observed pattern of northward spreading cannot be attributed to a variation in the occurrence of physical disturbances. With regard to herbivory pressure, an increase in sea urchin abundance has been shown to increase the availability of open spaces and facilitate an increase in the abundance of coral species by reducing the competitive dominance of algae [24,104–105]. However, sea urchin abundance did not increase over the course of the study, and in some areas, it decreased due to legal and illegal fishing [106–107]. Hence, the northward spread also cannot be attributed to a change in sea urchin abundance. Therefore, we conclude that physical and biotic disturbances have not varied much over the last twenty years, and although some changes in the composition of macroalgal communities have been detected, no major structural changes have occurred.

Although the main reasons for the northward expansion of *O. patagonica* are difficult to identify, the observed pattern of spread suggests some factors that must have played a relevant role in promoting the spread of this species. The high proportion of *O. patagonica* in artificial habitats in contrast to natural habitats (see Results) indicates that artificial habitats represent important places that foster the abundance and dispersal of this species. Space availability is the main initial difference between natural and artificial habitats. Assemblages flourishing in artificial habitats become similar to those of adjacent rocky bottoms over time; however, even after many decades, the assemblages do not usually resemble each other because artificial habitats are characterized by a higher space availability and a lower species richness, both of which are factors that increase habitat invasibility by primary space occupiers such as *O. patagonica* [22,71,108–110]. Thus, space availability plays a crucial role in explaining the differential spreading observed between the two types of habitats, which is consistent with previous results showing that open spaces created by the grazing activity of sea urchins enhances the settlement and survival of *O. patagonica* [24].

The deployment of coastal infrastructure causes ecological impacts by altering water flow, light penetration and sedimentation rates in shallow coastal waters [111], which negatively affects the growth of scleractinian corals [112]. However, field studies and laboratory experiments have revealed that *O. patagonica* has an exceptional capacity to grow under a wide range of environmental conditions [31]; as such, it is less affected than many native species by the above-mentioned side effects of artificial habitats. Therefore, the increased space availability on artificial substrata and the increasing deployment of artificial marine habitats in Catalonia (Fig. S2) appear to be the main causes of the observed differences in the spreading dynamics of the species between the two habitat types. Artificial habitats may be acting as corridors that facilitate the expansion of this species. Thus, although *O. patagonica* has been known to occur south of Catalonia since the 1970s [30–31], the fact that the species did not reach the study area until the early 1990s, despite the presence of significant amounts of artificial substrata prior to that time and several large populations within <30 km of the first discovery site on the Catalan coast (some with >20% cover [35], authors' unpublished data), is indicative of a change in the spreading dynamics at the end of the 1990s and throughout the 2000s, which may be related to temperature.

Water temperature is among the main factors affecting the distribution of corals [73,113–114] and has been increasing over the last decades in the northwest Mediterranean [18]. Temperature has been hypothesized to limit coral reef growth directly by reducing the capacity of corals to achieve successful reproduction and recruitment [115–117], reducing coral growth [118] and causing coral mortality as a result of cold temperature episodes [119]. Damage to *O. patagonica* colonies in winter (partial mortality) occurs in the southern locations of the study area (authors' unpublished data) and is likely to be related to cold temperatures as previously documented [52]. Despite this damaging effect, *O. patagonica* is especially abundant in these southern areas; therefore, current winter temperature (11.7°C, the lowest 5th percentile except for the km 400) is not preventing the northward expansion of the species. The results raise the questions of: a) whether extreme cold temperature events may have prevented the northward establishment of this coral in the past, and b) whether the current 5th temperature percentile at km 400 (11.3°C) may prevent further northward spread of the species.

A long-term data series (1974–2010) obtained *in situ* at 0.5 m depth was used to estimate the rate of the mean annual temperature increase on the Catalan coast (0.032°C year^{-1}) [18]. Based on this estimation, the mean annual temperature has increased ~0.6°C over the 19-year study period. Additionally, the growing season (number of days with SST ≥18°C) has been lengthened by 0.76 days year^{-1} due to the warming pattern; therefore, it has increased by ~14 days over the study period (1992–2010; authors' unpublished data). This corresponds to a 10% increase of the period in which the species growth is 2 folds higher than that at lower temperature [52]. However, the warming pattern also increases the occurrence of extreme high temperature episodes [53,120], and previous experiments have shown that high temperatures affect *O. patagonica* [51–52,121]. Interestingly, we have not observed coral bleaching and/or partial mortality in relation to high temperatures in the region; thus, the current high summer temperatures have not caused conspicuous harm to the species in the study area. This finding is consistent with the fact that the upper sea temperature thresholds that were documented to cause damage to this coral in Israel (i.e., >36–44 days above 26°C, [51]) have not been reached in the study area. Thus, the current pattern of seawater temperature increase favors coral growth by extending the growing period of the species, as has been documented in other species from terrestrial ecosystems [122]. The lack of apparent damage to the colonies submitted to the highest 95th temperature percentile (26.8°C) indicates that, if the current pattern of sea warming is maintained, lengthening of the species' fast growing period will continue to favor the species growth during the following decades because most of the study area is far below the value of this percentil. *Oculina patagonica* exhibited a rapid increase after 1999. The cause of this timing can not be addressed, however, it coincided with the time period in which warming accelerated in the Eastern Mediterranean Sea causing an amplification of the entry of alien species [7].

Although successful establishment is affected by environmental conditions and interspecific interactions, the expansion of a population mainly depends on growth and dispersal and, consequently, on the life-history characteristics of each species [58,123]. Therefore, biological traits that are characteristic of an opportunistic colonizer may have contributed to the observed pattern of *O. patagonica* expansion; these traits include (a) the ability to function as a facultative zooxanthellate species; (b) the capacity to reproduce both sexually and asexually and to be fertile at an early age (1–2 years, [31,33]); (c) the ability to survive extreme environmental conditions (i.e., in tide pools, at temperatures of 10–40°C and at salinities of 28–50‰, [31]); and (d) the capacity to survive and grow in harbors, polluted areas, and areas affected by severe sand scouring as well as on undisturbed natural rocky bottoms [78].

Although environmental conditions are among the major determinants that shape species distribution ranges [113–114] and represent the main factors controlling coral species [50], the abundance of artificial habitats and the biological characteristics of *O. patagonica* have played a significant role in the ongoing expansion of this species. In short, the rapid spread process appears to be a response to global change mainly mediated by the interplay of (i) the availability of open space provided by artificial habitats, (ii) seawater temperature increase (mainly by extending the growth period), and (iii) the particular biological features of *O. patagonica* (high current growth rates, early reproduction, and survival to low temperature and in polluted areas).

Despite the evidence that some coral species appear to be responding to climatic warming by expanding their distributions toward the poles ([70], see above), it has been argued that latitudinal migration is unlikely to occur rapidly enough to respond to the current projected temperature change (3–6°C over the next 100 years [124]) due to the significant distance involved (i.e., the latitudinal temperature gradient is ~1,5°C/1000 kilometers), the effects of temperature on reproduction and the decrease in carbonate ion concentrations at high latitudes [15,125–126]. The present study has characterized the rapid northward expansion of a coral species at high latitudes (40–42°N), a process that has been enhanced by artificial reef structures ahead of the migrating coral. Furthermore, *O. patagonica* is able to reproduce under the environmental conditions at these high latitudes (authors' unpublished data) and even adapt to the effects of repeated bleaching events [34]. Thus, a coral species with particular biological characteristics that allow it to withstand the temperature challenge that accompanies northward migration as well as the natural and anthropogenic side effects that this type of migration involves (i.e., competition with macroalgae, high sediment loads, turbidity, water chemistry) has accomplished a successful northward expansion and may be able to keep pace with the global warming prediction of ~3°C over the next 100 years.

It is crucial to develop an understanding of the characteristics and the spread rate of a coral that is able to profoundly alter the habitat within which it thrives. In the southeast region of the Iberian littoral zone in the Mediterranean Sea, *O. patagonica* has exhibited a large increase in cover over the last decade (from 3–5% to 10–15%, [24]). Furhermore, this species has been able to induce a persistent phase shift from macroalgal to coral dominance at a particular location [25], which challenges the current conceptual framework [96]. In this evolving context, the rapid northward spread of the species over the last two decades is indicative of an ongoing fundamental modification of temperate shallow water assemblages, which is consistent with predictions [18,127] that highlight the Mediterranean Sea as one of the ecosystems most sensitive to global change.

Supporting Information

Text S1 Sea surface circulation in the Catalan Sea, implications for *Oculina patagonica* northward dispersal (PDF).
(PDF)

Figure S1 *Oculina patagonica*. Minimal sampling area for colony density and cover estimates (PDF).
(PDF)

Figure S2 Trends on coastal development in the Catalan coast (1970s-2010) (PDF).
(PDF)

Table S1 Studied locations for sea surface temperature in the Catalan coast (PDF).
(PDF)

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Author Contributions

Conceived and designed the experiments: ES RC MR BW MG EB. Performed the experiments: ES BW MG RC EB. Analyzed the data: ES RC MR EB. Wrote the paper: ES RC MR EB.

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REPORT

Recurrent partial mortality events in winter shape the dynamics of the zooxanthellate coral *Oculina patagonica* at high latitude in the Mediterranean

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Abstract Global warming has many biological effects on corals and plays a central role in the regression of tropical coral reefs; therefore, there is an urgent need to understand how some coral species have adapted to environmental conditions at higher latitudes. We examined the effects of temperature and light on the growth of the zooxanthellate coral *Oculina patagonica* (Scleractinia, Oculinidae) at the northern limit of its distribution in the eastern Iberian Peninsula (western Mediterranean) by transplanting colonies onto plates and excluding them from space competition over a ~4-yr period. Each year, most of the colonies (~70%) exhibited denuded skeletons with isolated polyps persisting on approximately half of the coral surface area. These recurrent episodes of partial coral mortality occurred in winter, and their severity appeared to be related to colony exposure to cold but not to light. Although *O. patagonica* exhibited high resistance to stress, coral linear extension did not resume until the coenosarc regenerated. The resumption of linear extension was related to the dissociation of the polyps from the coenosarc and the outstanding regenerative capacity of this species (10.3 $\text{mm}^2\ \text{d}^{-1}$). These biological characteristics allow the species to survive at high latitudes. However, the recurrent and severe pattern of denuded skeletons greatly affects the dynamics of the species and may constrain population growth at high latitudes in the Mediterranean.

Keywords Zooxanthellate coral · Partial mortality · Lesion regeneration · Linear extension dynamics · Cold thermal stress · Mediterranean Sea

Introduction

Latitudinal variation in environmental parameters determines coral biogeography. Temperature, solar radiation, nutrients and the saturation state of seawater aragonite are critical factors for photosynthesis and the calcification of zooxanthellate corals, and these variables co-vary with increasing latitude, thus limiting coral growth at high latitudes (e.g., Kleypas et al. 1999; Muir et al. 2015). The scarcity of zooxanthellate corals in temperate areas is related to the effects of environmental parameters, competition with macroalgae and the synergistic interactions of biotic and abiotic factors (e.g., Miller 1998; Hoegh-Guldberg 1999). However, the current decline of coral reefs in both perturbed and unperturbed areas indicates that increasing temperature is a global stressor that is playing a crucial role in the regression of reef ecosystems (e.g., Hughes et al. 2010). Temperature has long been considered to be the primary factor controlling the distribution of coral species (e.g., Hoegh-Guldberg 1999; Kleypas et al. 1999), and exposure to both high and low stressful temperatures has been documented to reduce coral growth and cause bleaching and mortality (e.g., Saxby et al. 2003; Hoegh-Guldberg et al. 2005; Colella et al. 2012; Roth et al. 2012).

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Global warming is affecting many biological aspects of coral species; even the more conservative warming projections indicate that many tropical reefs may enter a non-coral-dominant stage before the end of the century (Hoegh-Guldberg and Bruno 2010; Pandolfi et al. 2011; Frieler et al. 2013). Corals are among the organisms least expected to exhibit poleward movement because their capacity to adapt is usually outpaced by the current, rapid rate of environmental change due to human activities (Hoegh-Guldberg 2012). However, the distribution of some zooxanthellate scleractinian corals has shifted to higher latitudes in some areas, tracking the movement of suitable temperatures (e.g., Takao et al. 2015), and marginal habitats for coral reefs are predicted to expand in future climate scenarios (Freeman 2015). Understanding the ability of such coral species to adapt to environmental changes at high latitudes is crucial to predict shifts in coral communities in response to climate change.

In the shallow rocky assemblages of the temperate Mediterranean Sea, both local evidence of phase shifts from macroalgal to coral dominance and the rapid expansion of *Oculina patagonica* (Scleractinia, Oculinidae) (Serrano et al. 2012, 2013; Salomidi et al. 2013; Rodolfo-Metalpa et al. 2014) provide evidence that this zooxanthellate coral may be displaying invasive behavior that could challenge the current conceptual framework of the ecosystem (Miller 1998). Such behavior is consistent with the fact that *O. patagonica*, first documented in the Mediterranean in 1966, is currently found in many areas throughout the Mediterranean Sea (Rubio-Portillo et al. 2014a and references therein). A recent study indicated that the species is not a recent introduction, and thus its current taxonomic status is unclear because it cannot be reliably classified as either "native" or "introduced" (Leydet and Hellberg 2015). The most abundant *O. patagonica* populations have been recorded along the coast of the eastern Iberian Peninsula (Balearic Sea; Fine et al. 2001; Coma et al. 2011; Serrano et al. 2012, 2013; Rubio-Portillo et al. 2014a). However, although this coral has been expanding northward from the north Balearic Sea (40°N) toward the Gulf of Lyon (42°N) over the last two decades (Serrano et al. 2013), little is known about its growth dynamics in the expansion zone.

Similar to tropical corals, the growth rate of *O. patagonica* in the western Mediterranean is positively correlated with a certain temperature range (Rodolfo-Metalpa et al. 2008). Prolonged exposure to sublethal warm-temperature thresholds has been reported to damage *O. patagonica* colonies in short-term field studies (<2 yr) and surveys (Rodolfo-Metalpa et al. 2008, 2014; Rubio-Portillo et al. 2014b), and long-term studies in the eastern Mediterranean have shown that the species suffers severe annual bleaching and mortality events in summer (Fine et al. 2001; Shenkar et al. 2005) that are mainly related to exposure to high temperature (Ainsworth et al. 2008). In this study, we addressed the effect of temperature and light on *O. patagonica* growth dynamics in the expansion zone at the northern limit of its population distribution along the Iberian Peninsula (Serrano et al. 2013), a critical first step toward understanding the response of this species to climate change. We assessed the seasonal variation in growth and mortality of *O. patagonica* colonies over a ~4-yr period. Although long-term monitoring studies are labor intensive, they are fundamental to acquiring a thorough understanding of the factors that influence the life cycles of long-lived species such as corals, and they enable predictions of how such species might be affected by climate change. The effects of these abiotic factors were examined by transplanting coral colonies onto plates and excluding them from space competition with other organisms. The results of this study provide new insights into the seasonal and annual growth dynamics of *O. patagonica* at the northern limit of its distribution and contribute to an understanding of the biological characteristics that allow some zooxanthellate corals to thrive in temperate systems.

Materials and methods

Sample collection

In August 2008, the encrusting colonial coral *O. patagonica* was sampled at L'Ampolla breakwater (40°49′N, 0°43′E) in the north Balearic Sea (northwest Mediterranean Sea; Fig. 1) by scuba diving at depths of 2–5 m. Coral fragments (~3 cm in diameter) were collected with a hammer and chisel from widely separated (>3 m) and healthy (<10% colony partial mortality) colonies ($n = 29$) that ranged between 25 and 40 cm in maximum diameter. The coral specimens were immediately placed in large seawater containers and transported to the Experimental Aquarium Zone at the Institute of Marine Sciences in Barcelona (<4 h). Shortly after, the coral samples were carefully cleaned of epiphytes and sediment, and each was glued onto a methacrylate plate (15 × 15 cm) with an inert mastic compound. The coral plates were placed in a 225-L acclimation tank equipped with a circulation pump and running natural seawater. The inlet and outlet pipes remained open so that the acclimation tank functioned as a flow-through open system, and the corals were maintained in aquaria under controlled conditions until the perimeter of the entire colony was growing onto the plastic plates. During the ~3-month acclimation period in the aquaria, the natural seawater temperature (ST) was gradually decreased from 25 to 18 °C, and the light conditions were adjusted to 150 µmol photons m^{-2} s^{-1} (12:12 light:dark

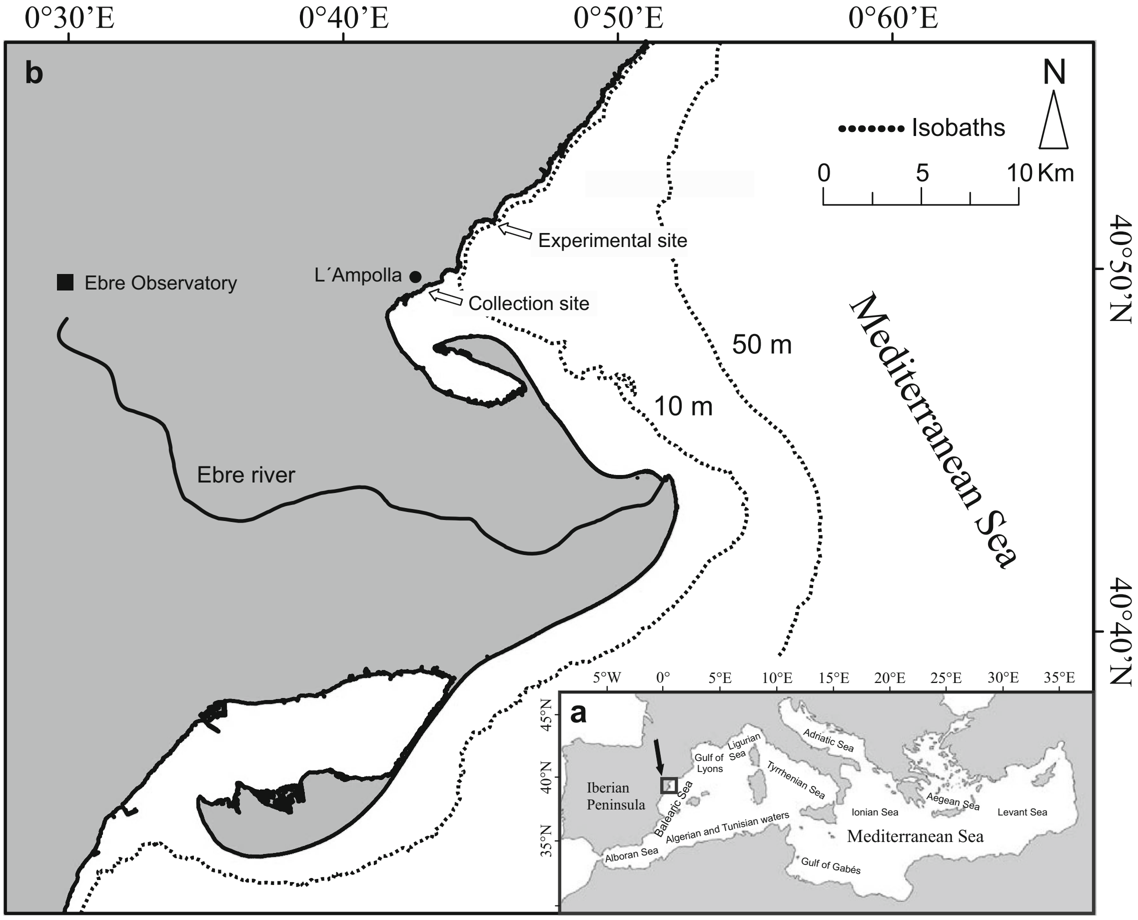

Fig. 1 **a** Map of the Mediterranean Sea showing the study area (L’Ampolla) in the north Balearic Sea. **b** Location of the collection site and the experimental site

photoperiod) to simulate late summer/early autumn conditions at the study area (Fig. 2).

Study site and experimental design

In November 2008, the 29 coral plates were transported back and randomly fixed onto a rocky reef located ~5 km north of the collection site (Fig. 1). The thermal and light regimes did not differ between the collection and experimental sites (Electronic Supplementary Material, ESM, Supplementary methods). Therefore, we will generally refer to the study area as L’Ampolla. In the study area, *O. patagonica* has a patchy distribution on shallow rocky reefs with locally abundant populations (Serrano et al. 2013). All coral plates were installed on slightly inclined surfaces (<45°) at depths of 4–5 m within a ~400-m^2 rocky area oriented parallel to the shore (80 × 5 m). The coral plates were monitored over a ~4-yr period (November 2008–August 2012, $n = 17$ sampling dates) at an average sampling interval of 87 ± 8 d (SE, $n = 16$). The benthic community surrounding the plates was dominated by algal communities with a canopy height >2 cm. On each sampling date, the coral plates were cleaned of settling organisms (commonly turf algae <1 cm in height) to ensure that the corals were not exposed to algal competition, and any algae that settled on the coral skeleton were removed during the surveys.

Colony partial mortality and growth

On each sampling date, all coral plates were photographed in situ using a ruler as a size reference. Because colonies of *O. patagonica* have an encrusting morphology, the colony surface area from a planar view and the area experiencing partial mortality were measured from photographs using ImageJ software. Colony partial mortality was evaluated for each sampling date as the percentage of the colony area showing signs of mortality (i.e., denuded skeleton or coverage by sessile organisms). Partial mortality was further classified into three levels of severity: mild (<15%), moderate (15–85%) or severe (>85%). At the beginning of the study (November 2008), mean partial mortality was

2 ± 1% (SE, $n = 29$). Colony partial mortality rates between sampling dates were calculated by dividing the change in partial mortality from one sampling date to the next by the number of days in the sampling interval expressed as a percentage of the colony area (% d^{-1}) and as mm^2 d^{-1}. The rate of variation in planar area between sampling dates was calculated by dividing the accumulated colony surface area from one sampling date to the next by the number of days in the sampling interval (cm^2 d^{-1}). The change in arithmetic mean diameter appears to be the most appropriate method to standardize linear growth rate data of coral colonies versus the initial size, particularly for encrusting species that tend to grow primarily in the horizontal plane and have circular areas (Pratchett et al. 2015), such as *O. patagonica* (Fig. 3). Then, to provide a size-independent measure of the linear extension rate (cm diameter d^{-1}), the planar area (A, cm^2) was translated to the arithmetic mean diameter (D, cm) using the formula $D = 2 * \sqrt{A/\pi}$. The mean annual linear extension rate was estimated for each study year by integrating the mean daily values of the different sampling intervals.

Environmental data

Global solar radiation (J m^{-2}) throughout the study period was recorded by the Ebre Observatory (located 50 m above sea level; Fig. 1). The daily photosynthetically active radiation (PAR, mol photons m^{-2} d^{-1}) at a depth of 5 m was obtained from global irradiance and light attenuation coefficient data (ESM Supplementary methods). The mean annual and monthly PAR were determined based on the daily values averaged over the study period.

ST was recorded hourly throughout the study period using onset HOBO pendant temperature data loggers (UA-002–64) placed at a depth of 5 m, and the mean annual and monthly STs were determined based on the averaged daily values. We also calculated the number of days in which the mean daily ST was above and below different thresholds (≥20 to ≥28 °C and ≤19 to ≤11 °C, respectively).

Statistical analysis

The individual and combined relationships between coral performance (partial mortality and linear extension rates) and environmental parameters (PAR and ST) were assessed by multiple regression using the mean PAR and ST calculated for each sampling interval. Cross-correlation analyses were used to establish relationships between the environmental parameters (PAR and ST) over time and to determine the relationship between *O. patagonica* performance and ST. One-way repeated-measures ANOVA was used to test the inter-annual differences in mean partial mortality and linear extension rates, combined with Tukey's test for post hoc comparison. A Chi-squared (χ^2) test was used to examine the inter-annual variability in ST thresholds. We used STATISTICA version 7.0 for the analyses, and the results are expressed as the mean ± SE.

Results

Environmental parameters

The mean annual PAR at L'Ampolla (5 m depth) during the study period was 19.5 ± 0.7 mol photons m^{-2} d^{-1} (2009–2011, $n = 3$) and ranged between 18.3 and 20.8 mol photons m^{-2} d^{-1} (Fig. 2a). The light regime was characterized by marked seasonality, with monthly mean PARs ranging from 6.1 mol photons m^{-2} d^{-1} in December 2009 to 36.6 mol photons m^{-2} d^{-1} in July 2010 (Fig. 2a; daily

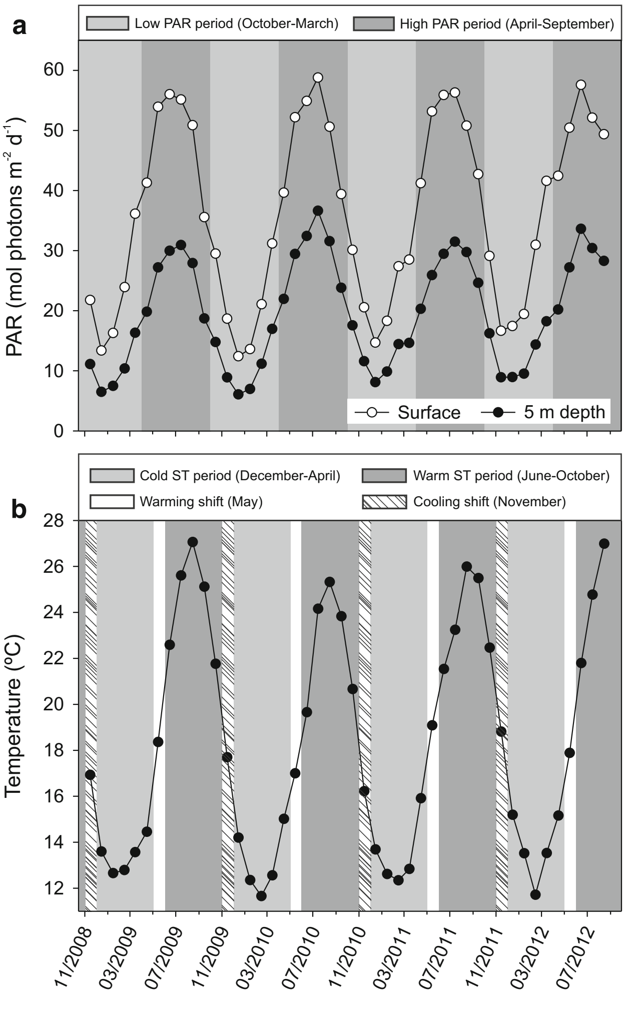

Fig. 2 **a** Monthly mean photosynthetically active radiation (PAR) at sea surface and 5 m depth at L'Ampolla. **b** Monthly mean seawater temperature (ST) at 5 m depth at L'Ampolla

mean PAR values are shown in ESM Fig. S1a). Two periods were distinguished based on the monthly mean PARs: (1) a high-radiation period from April to September (27.3 ± 1.0 mol photons m^{-2} d^{-1}, $n = 3$) and (2) a low-radiation period from October to March (12.1 ± 0.6 mol photons m^{-2} d^{-1}, $n = 3$; Fig. 2a).

The mean annual ST at L'Ampolla was 18.5 ± 0.4 °C (2009–2011, $n = 3$) and ranged between 17.7 and 18.9 °C (Fig. 2b). The thermal regime was characterized by marked seasonality with monthly mean STs ranging from 11.7 °C in February 2010 to 27.1 °C in August 2009 and a mean thermal amplitude of 13.9 ± 0.2 °C during the annual cycle. The minimum mean daily ST was observed in February 2010 (10.1 °C), and the maximum occurred in August 2009 (28.6 °C; ESM Fig. S1b). Based on the monthly mean STs, two periods were identified (each separated by a 1-month shift): (1) a cold period from December to April (13.5 ± 0.1 °C, $n = 4$) with a warming shift in May (18.1 ± 0.4 °C, $n = 4$) and (2) a warm period from June to October (23.6 ± 0.5 °C, $n = 3$) with a cooling shift in November (17.4 ± 0.6 °C, $n = 4$; Fig. 2b).

The PAR and thermal regimes exhibited similar seasonal trends but with a time delay (i.e., the maximum seasonal peaks in ST shifted to the right relative to the maximum peaks in PAR; Fig. 2). Based on the daily means, cross-correlation analysis revealed that the highest positive Pearson correlation coefficients were between the ST and the PAR measured 1–2 months earlier (the maximum correlation at −40-d lag, $r = 0.79$; ESM Fig. S1c). The wave-like form of the cross-correlation plot, with peaks separated by ∼6 months, reflected the seasonal nature of the changes in PAR and ST.

Annual cycle of coral partial mortality

The seasonal advent of partial mortality (i.e., tissue loss resulting in a denuded skeleton) and recovery in the *O. patagonica* colonies was the most predominant process and occurred each year throughout the four annual cycles examined at L'Ampolla (Fig. 3). The phenomenon of partial mortality began affecting small, unconnected parts of the coenosarc, exposing the denuded coenosteum in different (central and peripheral) but isolated parts of the colony (i.e., multifocal distribution; e.g., January in Fig. 3). In this first phase, partial mortality usually followed a progressive coalescence of the multifocal denuded skeleton that was conducive to the loss of nearly the entire coenosarc, but the remaining polyps remained healthy (alive and brown in color) and isolated within the calyx (e.g., April in Fig. 3). The phenomenon was rarely observed in the final phase, in which the isolated polyps disappeared from parts of the colony, leaving a completely denuded skeleton.

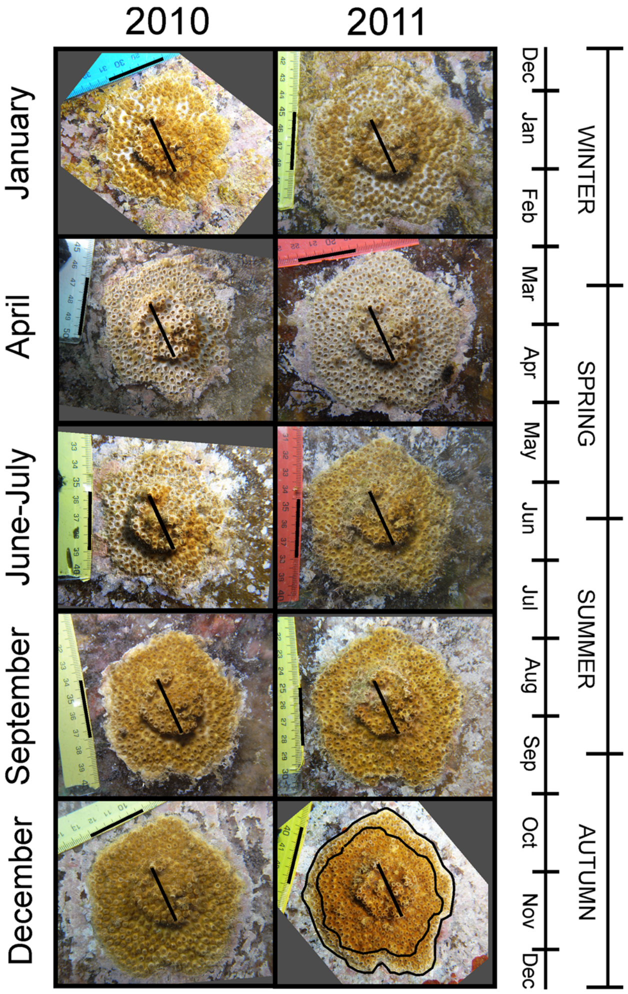

Fig. 3 Monitoring of a colony of *Oculina patagonica* from January 2010 to December 2011. Partial mortality occurred during winter and early spring, followed by recovery in late spring and linear extension during summer and autumn. The perimeter from January 2010 is superimposed on that from December 2011. *Scale bars* 3.40 cm

The first symptoms of denuded partial mortality were detected in December, and the symptoms increased until April of each year when the highest values were detected (49 ± 9%, 2009–2012, $n = 4$; Fig. 4a). The April peak in partial mortality resulted in the highest percentage of colonies with moderate and severe partial mortality (>15%, 75 ± 10%; ESM Fig. S2). The mean rate of partial mortality from December to April was 0.32 ± 0.08% d^{-1} ($n = 7$; Fig. 4b, c), which is equivalent to 10.0 ± 3.1 mm^2 d^{-1}. The colonies started to exhibit signs of recovery in May, when the tissue surrounding the denuded skeleton began to recover. The mean annual peak in the tissue regeneration rate from May to July was −0.35 ± 0.02% d^{-1} (2009–2012, $n = 4$; Fig. 4b, c), which is equivalent to −10.3 ± 2.7 mm^2 d^{-1}. By July, the mean extent of partial mortality was reduced to 24 ± 4% of the April peak each year (2009–2012, $n = 4$; Fig. 4a).

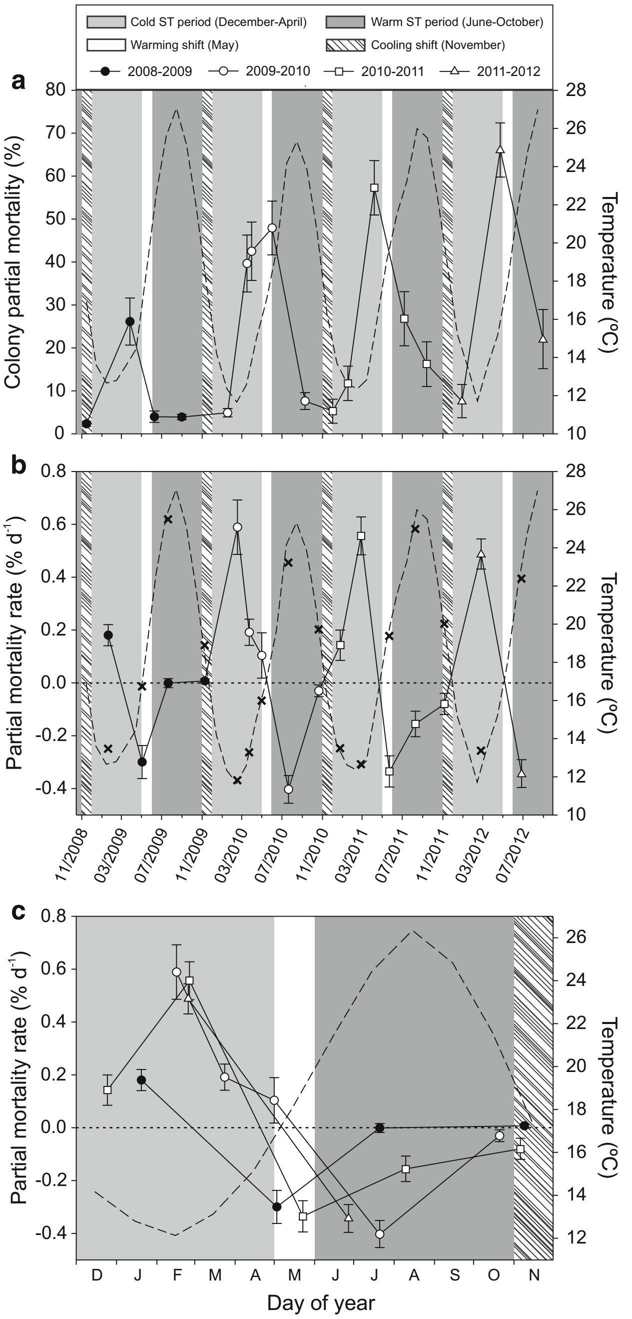

Fig. 4 Partial mortality of *Oculina patagonica* and seawater temperature (ST, *dashed lines* and *crosses*) at L'Ampolla. **a** Proportion of colony partial mortality on each sampling date ($n = 17$). Colony partial mortality rate **b** over the study period and **c** on an ordinal date for each sampling interval ($n = 16$). Values are mean ± SE

Some overgrowth of the denuded coral skeleton by filamentous and foliose algae and deposition of sediment particles occurred during the mortality and recovery periods (Fig. 3), so after this rapid recovery phase, tissue regeneration of the remaining areas of partial mortality continued at a slower pace from August to November ($-0.05 \pm 0.03\%$ d^{-1}, $n = 5$; Fig. 4b, c). Partial mortality rate values from this slow recovery phase were excluded in the regression analysis with environmental parameters, because lesion regeneration was already completed or affected by algae overgrowth. Overall, the regeneration process led to the lowest mean extent of partial mortality (4–8%, 2009–2011, $n = 3$) and the lowest percentage of colonies with mild partial mortality (<15%, 96 ± 2%) in November; these values remained low until the initiation of the subsequent partial mortality event in December (Fig. 4a; ESM Fig. S2). The occurrence of a recently denuded skeleton and/or visually apparent bleaching was not observed from May to November in any of the study years (Figs. 3, 4).

Annual cycle of coral growth

The mean size of the *O. patagonica* colonies increased from 10 ± 1 cm^2 in November 2008 to 60 ± 12 cm^2 in August 2012 at a mean linear extension rate of 13.27 ± 2.95 cm^2 yr^{-1} (Fig. 5a), which is equivalent to a mean increase in colony diameter of 1.27 ± 0.19 cm yr^{-1}. The maximum linear extension rate of an individual colony was 2.47 cm diameter yr^{-1}. Coral growth exhibited a marked pattern of seasonal variation that repeatedly occurred during the ~4-yr study period (Fig. 5). The mean linear extension rate reached a minimum during the 6 months from December to May (0.0016 ± 0.0007 cm diameter d^{-1}, $n = 9$; Fig. 5b, c), which coincided with a decrease in living colony size (i.e., the extent of the coral tissue, which is complementary to the proportion of partial mortality) between December and April (Fig. 5a). Despite this decline in live tissue, coral skeleton growth resumed in June following the rapid tissue regeneration that started in May (Fig. 5a). The mean linear extension rate during the ~6 months from June to November (growing period) was 0.0058 ± 0.0007 cm diameter d^{-1} ($n = 7$; Fig. 5b, c).

Coral mortality and growth in relation to environmental variables

The rate of *O. patagonica* partial mortality was negatively related to ST ($p = 0.0290$) but did not exhibit a significant relationship with PAR ($p = 0.64$) (multiple regression: $F_{2,8} = 15.79$, $r^2 = 0.80$, $p = 0.0017$, $n = 11$; values from the slow recovery phase were excluded). The proportion of colony partial mortality and ST displayed opposite trends but with a time delay (i.e., the maximum seasonal peaks in partial mortality shifted right relative to the minimum peaks in ST; Fig. 4a), and cross-correlation analysis indicated that ST and the proportion of partial mortality were negatively correlated and that the highest Pearson correlation coefficient was associated with a lag of –78 d ($r = -0.68$; ESM Fig. S3a). These results indicated that

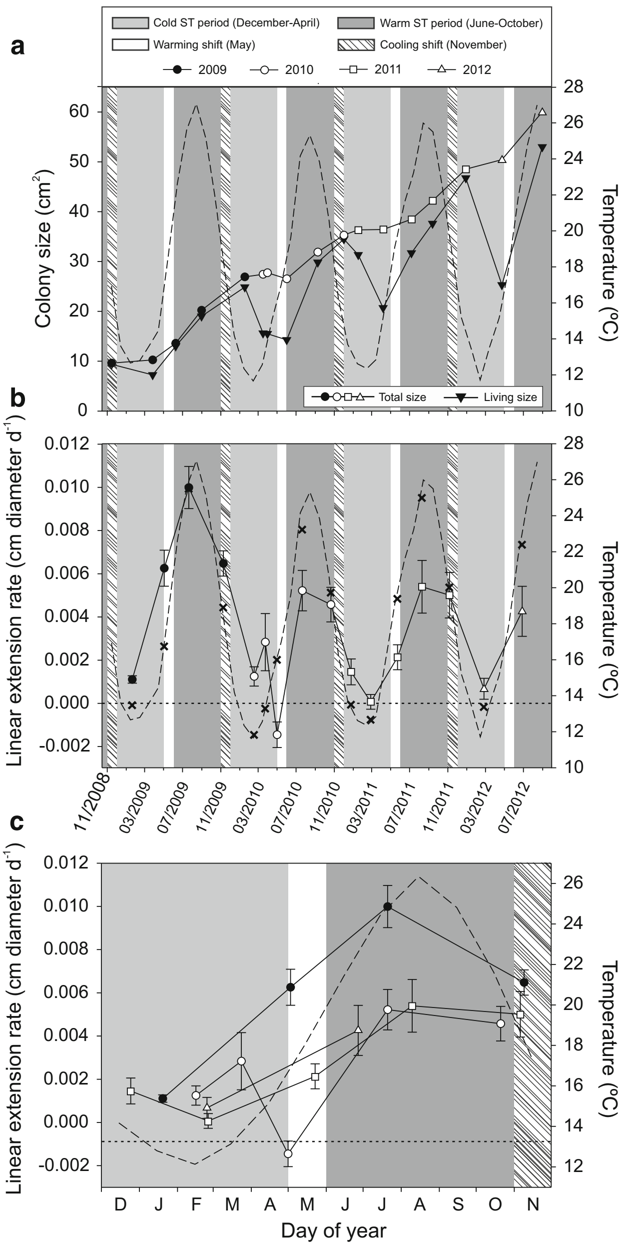

Fig. 5 Linear extension of *Oculina patagonica* and seawater temperature (ST, *dashed lines* and *crosses*) at L'Ampolla. **a** Total and living colony size on each sampling date ($n = 17$). Colony linear extension rate **b** over the study period and **c** on an ordinal date for each sampling interval ($n = 16$). Values are mean ± SE

the pattern of increased partial mortality was preceded by the minimum ST values 2–3 months earlier (i.e., the April peak in partial mortality was related to the lowest ST in January–February; Fig. 4a). The rate of partial mortality and ST exhibited opposite trends with no time delay (i.e., the maximum seasonal peaks in partial mortality rate coincided with the minimum peaks in ST; Fig. 4b; ESM Fig. S3b), and there was a negative relationship between the two variables ($r^2 = 0.79$, $p = 0.0002$, $n = 11$), indicating that the positive mortality rate values might be related to the <14 °C threshold that commonly occurred from December to April (Fig. 6a). These results suggest that cold STs are an important factor influencing *O. patagonica* partial mortality in the study area.

The linear extension rate of *O. patagonica* colonies was positively related to ST ($p = 0.0008$) but did not have a significant relationship with PAR ($p = 0.10$) (multiple regression: $F_{2,13} = 12.63$, $r^2 = 0.66$, $p = 0.0009$). The linear extension rate and ST exhibited similar trends with no time delay (i.e., the maximum peaks in the linear extension rate coincided with the maximum peaks in ST; Fig. 5b, ESM Fig. S3c), and there was a positive relationship between the two variables, with higher linear

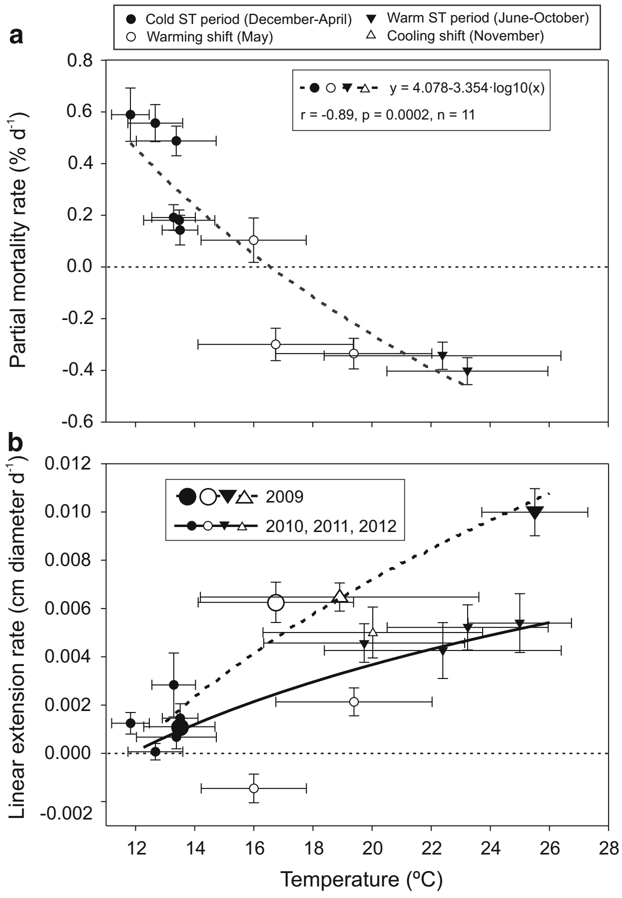

Fig. 6 Pearson product-moment correlations between *Oculina patagonica* performance and seawater temperature (ST) for each sampling interval. **a** Colony partial mortality rate. Values from the late warm ST and cooling shift periods were not included because lesion regeneration was already completed or was strongly affected by algal overgrowth. **b** Colony linear extension rate. Values are mean ± SE for coral performance and mean ± SD for ST. Two linear extension patterns depending on the severity of the annual event of denuded partial mortality are depicted: the pattern observed in 2009 (*dashed line*) and that observed in 2010, 2011 and 2012 (*solid line*). Data were fitted to logarithmic functions

extension rates related to the >16 °C threshold that commonly occurred from May to November (Fig. 6b). These results suggest that warm STs are an important factor increasing *O. patagonica* linear extension in the study area.

These results demonstrate that ST is related to both partial mortality and linear extension of the species. Consequently, a cross-correlation analysis was conducted to examine the potential trade-offs between the two processes. The highest negative correlation between colony partial mortality and linear extension rates occurred at a –48-d lag (ESM Fig. S3d), indicating that the high partial mortality rate from the previous 1–2 months negatively affected linear extension of the colonies.

Inter-annual variability in coral mortality and growth in relation to ST

The yearly peak in mean denuded partial mortality observed in April was always associated with similarly low values of partial mortality due to overgrowth in November (2–8%, 2008–2011), despite the fact that the April peak in 2009 (26%) was approximately half as large as those in 2010, 2011 and 2012 (48, 57 and 66%, respectively; Fig. 4a). Similarly, the percentage of colonies suffering from moderate to severe partial mortality (>15%) in April 2009 (45%) was 45–51% lower than those in 2010, 2011 and 2012 (83, 82 and 91%, respectively; ESM Fig. S2). The annual peak in the partial mortality rate was also lower in 2009 (0.18 ± 0.04% d^{-1}) than in 2010, 2011 and 2012 (0.54 ± 0.03% d^{-1}; one-way repeated-measures ANOVA, $F_{3,84} = 10.62$, $p < 0.0001$). The number of days that ST was ≤19 to ≤13 °C did not vary significantly among the cold periods studied (2008–2009 to 2011–2012, $n = 4$; χ^2, $p > 0.05$). However, the mean number of days that ST was ≤12 °C was 20 ± 4 d in 2009–2010, 2010–2011 and 2011–2012, a threshold that was not reached during the cold period of 2008–2009 (χ^2, $p < 0.05$; ESM Table S1). These results indicate that the occurrence of partial mortality was lower during the less severe cold period of 2008–2009 than during the other three more severe cold periods.

Generally, colony partial mortality occurred during the cold period (December–April) and was followed by tissue regeneration and linear extension. The annual peak in the regeneration rate was similar among the studied years (0.35 ± 0.02% d^{-1}, 2009–2012; one-way repeated-measures ANOVA, $F_{3,84} = 0.84$, $p > 0.05$). Hence, the time required for nearly complete regeneration of the tissue (i.e., when the lowest partial mortality values, of 4–8%, were first reached) appeared to be related to the severity of the annual partial mortality episodes (i.e., the time required for regeneration was longer in years showing high denuded partial mortality in April), which contributed to the inter-annual variation of the duration of the negative effect of partial mortality on the linear extension rate. As a result, the lower incidence of partial mortality in 2009 resulted in complete regeneration by June, but as the incidence of partial mortality increased in the following years (2010 and 2011), the regeneration time was longer (September and December, respectively; Fig. 4). This pattern is consistent with the higher linear extension rate observed in May 2009 (0.0063 ± 0.0008 cm diameter d^{-1}) compared to May 2010 and 2011 (0.0003 ± 0.0018 cm diameter d^{-1}, $n = 2$) and the twofold higher peak in the linear extension rate in July–August in 2009 (0.0100 ± 0.0010 cm diameter d^{-1}) compared with 2010 and 2011 (0.0053 ± 0.0001 cm diameter d^{-1}, $n = 2$; Fig. 5b, c). The mean annual linear extension rate of *O. patagonica* was twofold higher in 2009 (1.91 ± 0.25 cm diameter yr^{-1}) than in 2010 and 2011 (0.86 ± 0.22 and 1.03 ± 0.27 cm diameter yr^{-1}, respectively; one-way repeated-measures ANOVA, $F_{2,56} = 19.36$, $p < 0.0001$). These results indicate that ST may be exerting a direct effect on the growth dynamics of the species as well as an indirect effect through partial mortality. The number of days in which the ST was ≥20 to ≥24 °C did not vary significantly among the warm periods during the study (2009–2011, $n = 3$; χ^2, $p > 0.05$), whereas the ≥25 to ≥27 °C thresholds in the 2009 warm period were higher than those in 2010 and 2011 (χ^2, $p < 0.05$; ESM Table S1). For instance, the number of days in which the ST was ≥25 °C was 25 and 60% higher in 2009 than in 2010 and 2011, respectively. However, recently denuded skeletons and/or visually apparent bleaching were not observed during the summer and fall in any of the study years.

Discussion

Pattern of partial mortality and tissue regeneration

The yearly occurrence of denuded partial mortality in the *O. patagonica* colonies in winter (December–April) was the most distinctive process observed during the study. The denuded skeleton resulted from progressive tissue loss, which caused a loss of coloniality (i.e., dissociation of polyps from their connective coenosarc). The presence of colonies with brown, isolated polyps within the calyx distributed over a white coenosteum was a sign of the observed partial mortality, which we usually refer to as a Dalmatian mortality pattern (Fig. 7). The usual persistence of isolated brown polyps on the colonies distinguished the observed pattern of mortality from the pattern of tissue loss documented at the end of summer in colonies from Albissola, Monaco and Portman; although these colonies also exhibit areas of isolated brown polyps, they commonly

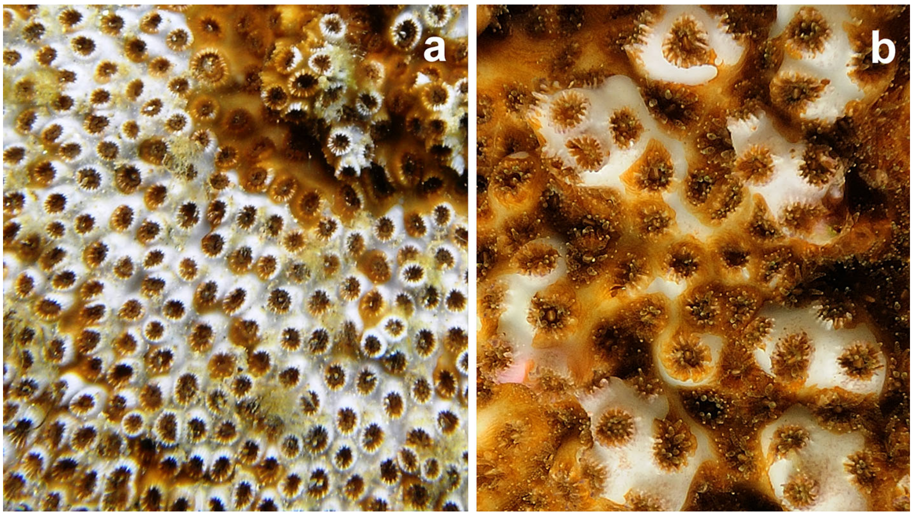

Fig. 7 Dalmatian mortality pattern in *Oculina patagonica*: **a** general view and **b** close-up view

display patches of completely denuded skeleton (i.e., the coenosteum and calyx; Rodolfo-Metalpa et al. 2008, 2014) that were rarely observed in our study. The process of denuded partial mortality that affected the colonies at our study site during winter resembled that observed in February 2006 in Monaco (Rodolfo-Metalpa et al. 2008). Colonies responded a similar way to reduced pH conditions in aquaria (Kvitt et al. 2015). The process observed in February 2006 did not appear to impact the dynamics of the species because the colonies completely regenerated by May, and the process was only observed during one year (Rodolfo-Metalpa et al. 2008). The dissociation of polyps from the coenosarc at low pH appears to be an essential mechanism mediated by apoptosis by which the species withstands acidification (Kvitt et al. 2015). Although addressing the mechanisms of tissue loss was outside the scope of this study, we did not observe any evidence of tissue necrosis that might have indicated that apoptosis was involved. As observed in other zooxanthellate coral species, the symptoms of the responses to different types of stress can be similar (e.g., Gates et al. 1992; Roth et al. 2012).

Lesion recovery is fundamental to coral survival, and during this 4-yr study, the *O. patagonica* colonies began to recover shortly (a few days) after the peak of partial mortality in April and were nearly fully recovered (down to 4–8%) from the yearly, recurrent partial mortality episodes. Over the ~4-yr study, the average regeneration rate was 10.3 $mm^2\ d^{-1}$, a rate that occurred in the absence of competition with other organisms (Fine and Loya 2003). This rate was 2.5-fold faster than the recovery rate of unbleached colonies documented in the Levant Sea (4.09 $mm^2\ d^{-1}$; Fine et al. 2002). Fine et al. (2002) observed that lesion regeneration in unbleached *O. patagonica* colonies resulted in intra-colonial translocation of resources toward recuperating lesions 4–5 cm away, whereas bleached colonies exhibited no lesion regeneration. These observations are consistent with tissue regeneration as an energetically costly process, as has been documented in other species (Oren et al. 2001). Thus, the more rapid regeneration rate at L'Ampolla might be attributable to the timing of the recovery of the lesions during the favorable growing season, whereas in the Levant Sea, recovery was examined during the unfavorable bleaching season (Fine et al. 2001, 2002). The denuded partial mortality of *O. patagonica*, which usually left polyps alive but isolated within the calyx, represents a characteristic pattern that may favor regeneration because (1) it increases the relationship between the wound perimeter and lesion size, which has been shown to positively correlate with the regeneration rate (Meesters et al. 1997), and (2) it rids the colony of energetically costly processes, such as calcification, and tissues (Kvitt et al. 2015). Moreover, the small polyp size and encrusting morphology of *O. patagonica* colonies may help to maintain mass transfer, which also favors lesion regeneration (e.g., van Woesik et al. 2012). The immediate initiation of regeneration at the end of the partial mortality event points to the prioritization of this life-preserving process that helps to reduce the detrimental effects of the settlement of algae and other organisms on the skeleton and the disruption of the physiological integration of the colony (Oren et al. 2001).

Potential causes of the observed pattern of partial mortality and growth

The complex interaction between ST and light on zooxanthellate corals (Lesser 1996) suggests that both factors are relevant to the seasonal dynamics of colony partial mortality in *O. patagonica*. However, although the loss of tissue in the coenosarc but not in the polyps might suggest a light effect, two sources of evidence suggest a secondary role of light in the observed pattern of partial mortality. First, the process of partial mortality started in December, the period with the lowest PAR levels. Second, the annual pattern of partial mortality exhibited a negative relationship with ST but not PAR.

The linear extension of *O. patagonica* colonies was positively related to ST but not to PAR, which also indicates that light might play a secondary role in the growth pattern of *O. patagonica*, in accordance with the results of previous studies (Shenkar et al. 2005; Rodolfo-Metalpa et al. 2008; Rubio-Portillo et al. 2014b). This finding is also consistent with the lack of a negative effect of turbidity on colony growth observed by Rubio-Portillo et al. (2014b), who observed that growth of the colonies did not differ between a harbor and a marine protected area, despite the much greater sedimentation in the harbor and the consequent reduction in light due to turbidity. This observation supports the hypothesis that *O. patagonica* may have a high capacity for photoacclimation to distinct and variable light regimes that may allow it to function as a facultative zooxanthellate and thrive in a wide range of light conditions, as has been observed (Fine et al. 2001; Rodolfo-Metalpa et al. 2014). Such characteristics would be consistent with the secondary role that light usually plays in promoting coral growth at high latitudes (Miller 1998; Rodolfo-Metalpa et al. 2008; Dimond et al. 2013). The absence of bleaching and/or mortality in the study area in summer might be related to the relatively low PAR levels caused by river runoff, which has also been suggested to contribute to the lack of partial mortality in response to warming in the laboratory (Rodolfo-Metalpa et al. 2014).

During the four annual cycles that were examined, the partial mortality episodes at L'Ampolla occurred during the cold periods, and thus we estimated the extent of exposure of this coral species to low ST based on data from this study and previous field studies to examine whether the intensity of the partial mortality episodes was related to the severity of the cold ST period. During the warmest winter at L'Ampolla, 2008–2009 (63 d ≤ 13 °C, 0 d ≤ 12 °C; ESM Table S1), the peak in partial mortality (26%) was similar to that reported during the winter of 2005–2006 in Monaco (5–20%) under similarly cold ST conditions (66 d ≤ 13 °C, 0 d ≤ 12 °C; Rodolfo-Metalpa et al. 2008). By contrast, the higher incidence of partial mortality (48–66%) during the more severe cold ST periods (2009–2010 to 2011–2012) at L'Ampolla could be related to exposure to the ≤12 °C threshold (15–29 d; ESM Table S1), suggesting that years with severely cold ST periods increased partial mortality in *O. patagonica*. The analysis of published data is consistent with this hypothesis because coral populations in the mid-Balearic Sea did not suffer from partial mortality and/or visually apparent bleaching during the winter of 2010–2011 (0 d ≤ 13 °C; Rubio-Portillo et al. 2014b) nor during the examined winters since 1993 in the Levant Sea (0 d ≤ 16 °C; e.g., Fine et al. 2001; Shenkar et al. 2005, 2006). Thus, the degree of exposure to cold ST appears to be related to the occurrence and severity of partial mortality events. However, although the cold thermal regimes at L'Ampolla were similar between 2010 and 2012, our results showed that the yearly peak in *O. patagonica* partial mortality gradually increased during this time period (Fig. 4a; ESM Table S1). As observed during consecutive extreme summers in *Porites astreoides* (Schoepf et al. 2015), we hypothesize that the cumulative impact of consecutive winter events of partial mortality may have affected the physiological status (energy budget) of the colonies, thus diminishing their recovery capacity.

The recurrent and severe partial mortality of the colonies in winter indicates that cold ST may be exerting both a direct effect on the linear extension dynamics of the species and an indirect effect via partial mortality, as the growth of the colonies did not resume until the colonies recovered from their lesions. Such direct and indirect effects are consistent with (1) the lower incidence of partial mortality during the warmest first winter period at L'Ampolla (2008–2009), which reduced the time needed for complete tissue regeneration, and (2) the twofold higher linear extension detected in 2009 compared to 2010 and 2011. Our interpretation is that the high linear extension observed in summer 2009 was not an isolated estimate that could be considered an outlier because compared to the other years, linear extension in that year was also higher in spring and fall. Although the colonies in 2009 were exposed to 27 °C during summer, the linear extension in fall suggested no detrimental effect on the colonies (probably due to the low PAR levels, see above). The lack of a detrimental effect may be related to the lower impact of partial mortality in winter 2008–2009, which permitted rapid recovery and an earlier onset of the linear extension period (Figs. 4, 5). These results suggest the occurrence of two linear extension patterns depending on the severity of the annual event of denuded partial mortality: the pattern observed in 2009, i.e., an increase with ST up to ~26 °C, and that observed in the other years, i.e., an increase with ST up to ~20 °C and then a plateau, which may be related to the cost of the regeneration process (Fig. 6b). Thus, cold STs may be playing an important role in constraining the growth dynamics of *O. patagonica* at the northern limit of its distribution, in contrast to the dynamics documented in the Levant Sea, where growth occurs during the cold period (16–26 °C, November–May) and bleaching recurrently affects the colonies in summer (>26–32 °C, June–October; Fine et al. 2002; Shenkar et al. 2005). The *O. patagonica* linear extension rate at L'Ampolla during the study period

(1.27 cm in diameter yr^{-1}) was 69–112% higher than those in natural populations from the Levant Sea (0.60–0.75 cm in diameter yr^{-1}; Fine et al. 2001), suggesting that the negative effects of high ST stress occurring at the Levant Sea are more harmful than the cold ST stress occurring at the north Balearic Sea. This conclusion is consistent with previous studies documenting the effect of cold STs on corals (Gates et al. 1992; Saxby et al. 2003; Hoegh-Guldberg et al. 2005; Colella et al. 2012) and the differential effect of low- and high-ST stress on *Acropora yongei* (Roth et al. 2012). However, the detrimental effect of competition on scleractinian corals (e.g., Fine and Loya 2003), which may diminish coral linear extension in natural populations, was excluded in our study.

Our results also indicate a trade-off between regeneration and linear extension that is consistent with the priority of energy allocation to recovery rather than to other biological processes. This trade-off is in agreement with previous studies from the Levant Sea, where bleaching and mortality events in *O. patagonica* during summer result in a low-energy state of the colonies that is responsible for the cessation of resource translocation and a reduction in gametogenesis and colony growth (Fine et al. 2001, 2002; Armoza-Zvuloni et al. 2011). The recurrent mortality events at L'Ampolla peaked in April and overlapped temporally with the gametogenesis of *O. patagonica* (March–September; Fine et al. 2001), suggesting that this energy shortage might also impair species reproduction and population growth.

The results of this study have demonstrated that *O. patagonica* at this northern limit of its distribution can survive and grow under wide seasonal variation in ST (monthly mean ranging from 11.7 to 27.1 °C). The coral exhibits a strong seasonal cycle that includes partial mortality and cessation of linear extension during winter (December to April), tissue regeneration starting in late spring (May) and linear extension during summer and fall (June to November), a cycle that appears to be primarily driven by ST. However, our data provide only correlational evidence, and causation of the observed pattern of denuded skeleton cannot be determined without additional experimental work. Partial mortality affected approximately half of the surface area and most of the colonies (~70%) and occurred repeatedly in all four years studied, indicating that partial mortality is a crucial process affecting the dynamics of the species, the relevance of which is comparable to that of the recurrence of summer bleaching in the Levant Sea (e.g., Fine et al. 2001).

Due to concerns regarding the threat of global warming to tropical coral reefs, understanding the resilience of zooxanthellate corals at high latitudes is crucial for predicting shifts in coral communities and their responses to climate change. The results of our experimental exclusion from competition indicate that the recurrent and severe pattern of denuded skeletons results from unfavorable environmental conditions that may constrain the population dynamics of the coral and affect the poleward expansion of the species. However, *O. patagonica* can withstand harsh environments because of its high regeneration capacity, which is among the highest reported for a coral species, particularly at high latitudes (Henry and Hart 2005). The stress response of polyp dissociation from the coenosarc appears to be a crucial pattern favoring the rapid regeneration of the species. The combination of the dissociation stress response and the rapid regeneration of the species appears to be a decisive biological characteristic that enables the species to withstand unfavorable environmental conditions affecting zooxanthellate coral species at high latitudes.

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