UNIVERSITAT DE BARCELONA

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Tesis Doctoral

UNIVERSITAT DE
BARCELONA

Facultat de Biologia, Universitat de Barcelona
Programa de Doctorat d'Ecologia, Ciències Ambientals i Fisiologia

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Història de vida, ecologia de poblacions i conservació dels boscos submergits del Mediterrani: el cas de l'alga longeva Cystoseira zosteroides

Memòria presentada per Pol Capdevila Lanzaco per obtar al Grau de Doctor per la Universitat de Barcelona

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Juliol de 2017

Director de tesi
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Al meu avi Ramon i a la meva àvia Bel,
als meus pares i família,
als meus amics,
als fons submarins que he explorat,
i als que em quedem per descobrir...

"The richness of form and function in the natural world is undoubtedly part of its fascination;
this intriguing variety is often the lure that draws one to the formal study of biology.
Large organisms and small organisms, long-lived and short-lived,
those that produce a single young at a time and those whose progeny are counted in terms of thousands -
is Nature simply a random assemblage of these traits or are they evolved adaptations to their environment?"
Southwood, Tactics, strategies and templets

"The challenge in understanding dynamic processes is that
these forces of nature are invisible to the glance,
and can remain unseen no matter how intently one looks."
James Estes, Serendipity

"Not until we are lost
do we begin to understand ourselves."
Henry David Thoreau

Agraïments

Encara recordo la primera vegada que em vaig ficar sota l'aigua amb un regulador. Va ser en una piscina de Sant Feliu quan tenia 15 anys recent complerts. Recordo la sensació de l'aire emplenant els meus pulmons. . . Tot envoltat d'un silenci tranquil·litzador... Recordo mirar-me les mans i resseguir cadascun dels plecs que formaven les arrugues dels meus dits. Crec que aquell instant va marcar un abans i un desprès. Des de llavors, la meva obsessió pel mar no ha parat de créixer, i m'ha portat a explorar moltíssim llocs. Més important, totes aquestes experiències m'han permès conèixer molta gent, que m'ha aportat moltíssim. Tot aquest cúmul d'experiències, d'aventures, emocions i d'amistats, m'ha portat avui a escriure aquestes paraules després de més de tres anys fent la tesi, i si sóc qui sóc, i si he arribat on he arribat, segurament és gràcies a molts dels que llegireu aquestes paraules (quelcom de la tesi també llegireu, no?). Probablement, si estàs llegint aquestes línies has contribuït d'una manera o altre a aquesta tesi, potser fent una cervesa o un cafè, potser acompanyant-me a casa desprès de la feina, potser amb dubtes d'R, potser escalant, potser simplement estan allà... Per això et dono les gràcies, i si no veus el teu nom en aquestes línies estigues tranquil/a, que si has compartit temps amb mi, segur que has contribuït.

Aquesta tesi no s'hagués fet si no fos pels dos grans directors que he tingut, el Bernat i na Cristina. He gaudit moltíssim al vostre costat, gràcies per dipositar la vostra confiança en mi. Gràcies per portar-me de campanya als llocs més bonics de la mediterrània que he conegut, merci per la vostra paciència i per la llibertat que m'heu donat durant la tesi. M'heu ensenyat moltes coses, tant a nivell laboral com personal. Bernat, gràcies per sempre estar disposat a tot, potser a última hora i corrents, però sempre has estat, a les dures i a les madures. T'agraeixo la teva força de voluntat per sempre tirar del carro quan ha calgut, gràcies per deixar-nos casa teva, el teu cotxe, equip de busseig, etc.... Cristina, ets una persona a qui admiro moltíssim, no sé com t'ho fas per compaginar-ho tot tant bé, tant de bo tingués un 10% de la teva capacitat organitzativa. T'agraeixo molt la teva guia, gràcies per posar-me els peus a terra quan tocava però també deixar-me volar quan ha calgut, i, sobretot, gràcies per aportar sempre una dosi de positivisme quan em feia falta. Gràcies també al Joseba, en especial per ajudar-me amb la portada! L'Asier i l'Ona tenen uns pares increïbles. També vull agrair al Joan Lluís, que com a tutor m'ha ajudat en moltes coses, sobretot guiant-me en el món de la programació amb R, corregint-me l'anglès i aportant uns coneixements extraordinaris d'estadística.

Gran part dels treballs realitzats aquí també s'han fet gràcies a l'ajuda de varis membres del grup MedRecover i altres investigadors afins. Gràcies Emma, per iniciar-me en el món del cultiu de les algues. Gràcies Diego, per deixar-me acompanyar-te en el que varen ser les meves primeres campanyes a Cap de Creus i, sobretot, a les illes Columbretes. Un agraïment molt especial és per l'Andrea i la Núria, per la vostre energia i felicitat, per ensenyar-me a fer gnocchis, per totes les cerveses al passadís i perquè sou collonuts! El Simone, com no, mereix una menció a part, gràcies per aportar un toc diferent i molt divertit al grup. A més, he tingut la sort de compartir moltes campanyes ja siguin de projectes o pel seguiment a Cabrera, Port-Cros, Columbretes, Medes o Cap de Creus amb molta gent, gràcies: Jana, Kike, Mikel, Quim, Emma, Xavi T., David, Anabel, Toni, Simone, Graciel·la, Tulasi, Eugeni, Clara... i segur que m'hen deixo.

A part, voldria destacar la facció més jove del grup, els MiniMedRecovers, que per sort ha anat creixent amb el temps. A vosaltres us dec molts bons moments, que sovint han anat acompanyats d'una bona cervesa al Tucan. Estic especialment agraït a l'Eneko, sense l'ajuda del qual aquesta tesi no seria el mateix (estaria feta en word). Perquè sí, amb tu he discutit en totes les situacions possibles, des del despatx a més de 40 metres de profunditat, i tot i això, m'has aportat molt. Gràcies per fer-me de germà gran, per sempre estar allà quan ha calgut, pels teus consells d'R i Latex, per les infinites cerveses i converses, per totes les immersions que hem fet junts i per les que ens queden. Gràcies Ignasi, per transmetre aquesta gana incansable de ciència i pels infinits debats que em tingut. Marta i Alba, a vosaltres vaig tenir la sort de veure com passàveu d'estudiants de màster a unes doctorandes exemplars, sabeu quant us aprecio, gràcies per les vostra dosis d'alegria que en el seu moment varen animar molt el grup. A la Jana, perquè ets una tia collonuda i perquè amb tu les cystos estan en bones mans. A les últimes incorporacions Dani, Maria i Jorge, esteu davant d'un camí molt llarg i dur, però teniu l'actitud i capacitats sobrades per fer unes grans tesis, molts ànims!

Estic molt agraït per tots els estudiants que he tingut la sort d'ajudar, però en especial vull destacar a la Graciel·la. Gràcies per convertir-te en molt més que una estudiant, i a pesar de que no sé encara si em tens respecte o no, penso que ets una de les persones més autèntiques que he conegut, espero veure't complir tots els teus propòsits. A l'Albert, tot i que hem tingut uns finals de tesi/TFG quasi solapats, hem trobat força temps per compartir, espero que trobis el teu camí. A la Tulasi, que no és estudiant meva però amb el poc temps que et conec he gaudit de molt bones converses, tot i fer-te de secretari! I com no, agrair al Marc Collell, que tot i que tampoc no vas ser el meu estudiant, vaig compartir molt bones estones amb tu al laboratori/aquaris, a part de múltiples immersions, ets un vivetis i ho saps.

I am also very thankful for the support that I received from Rob Salguero-Gómez and Maria Beger during my internship in Brisbane. Both of you have guided me through the difficult ways of science, boosting my analytical and writing skills. I am specially grateful to Rob, for your "fast" meetings personally or through Skype, for being an incredibly rigorous mentor and a great scientist.

La major part d'aquesta tesi s'ha desenvolupat en múltiples despatxos (4 en 3 anys de tesi, no esta mal) del departament d'ecologia i és aquí on he tingut la sort de trobar-me amb grans persones. Primer vull agrair a la Sílvia, perquè des de que vaig arribar fins als meus últims dies com a doctorand has fet el possible per fer-me sentir bé, ja sigui quan no coneixia a ningú fins a quan he estat més trist, gràcies per tot el que m'has donat que és MOLT! Al Pol 1 (si, 1), per ser un compi de pis excepcional i pels bons moments que ens esperen. A l'Astrid, per ser tant autèntica, per estar sempre disposada al que calgui, i sobretot, per ensenyar-me tant a escalar. A la Rebeca, por tus dosis de positivismo durante este tramo final de tesis, porque me has animado mucho más de lo que crees. A Yaiza, coreana!!! dejame vivir! por todas la sonrisas que me has arrancado en estos pocos días que llevo en vuestro despacho, claro que si guapi! A l'Aurora, xiqueta, per lo be que m'ho he passat en tu i per totes les conversacions existencials que hem tingut (algunes en Valencià xapurrini), si es que es de veres. A l'Anna, per tirar del carro de tantes coses i sempre estar a TOT. Al Lluís per introduir-me en el món de l'escalada. I a tots (que sinó no acabo avui) els membres del departament que hem format una gran família: Max, Carles, Pablo, Txell A., Vero, Neus, Daniel, Txell B., Ada, Pau, Núria C., José, Aida, Núria de C., Myrto, Dani, Eusebi, Lídia, Mari, Kele, Sandra (i a tots els que em deixo). Gràcies també al Jordi Boada, per l'ajuda en el congrés de Pisa i per tots els dubtes que m'has resolt de l'Endeavour, et dec vàries birres. També he pogut compartir assignatures amb grans professors d'aquesta facultat, com el Jofre, el Joan Lluís o el Javier.

Tinc la sort de tenir molts grups d'amics que m'han alegrat el dia a dia, i, sobretot, m'han donat les forces per tirar endavant. Als meus amics de tota la vida, Luis, Meri, Ferran, Jandro i Sandra, perquè les meves visites a Girona, sense vosaltres no són el mateix. Als "fantastic four", Jordi, Sergi i Gerard, perquè us dec tantes quedades que no sé ni per on començar! A les noies, Chantal, Ari, Ada, Irene i Laia, amb qui he rigut tant que crec estaré en deute amb vosaltres només pel que em debeu haver allargat la vida. Als meus companys de màster Roger, Sílvia, Marta i Anna, a vosaltres us dec molts bons moments a Barcelona i recentment a Girona, espero que seguim quedant i que aviat recuperem el temps perdut. Als membres del centre de busseig Piscis Diving, per introduir-me en el món del busseig, en especial a la Janine, Fran, Bru i Fede, i com no, a l'Albert i al Marc, per compartir amb mi tantes immersions. A tots els meus grups d'amics aquesta tesi ens ha robat molts moments que espero tornar-vos poquet a poquet. I finalment, a tu Marta Calamar, per tots els records que em vares donar, els quals guardo amb mi.

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Finalment, i amb el permís de tothom, aquesta tesi està dedicada al meu avi Ramón. A tu, que malauradament no m'has pogut veure acabar aquest somni que vàrem compartir junts durant tant de temps, et voldria dir tantes coses. Gràcies, per donar-me la força per creure en mi mateix, a pesar de totes les adversitats. Gràcies, per ensenyar-me a lluitar pel que m'estimo i perseguir els meus somnis, en contra de tota raó i lògica, com bé és aquesta tesi. Gràcies, per ensenyar-me que el més important a la vida, no és el càrrec que ocupi, sinó com he estat com persona. A tu et dec tant, que potser mereixeria una tesi sencera, ara que no hi ets a vegades em sento perdut, gràcies per aplanar prou el camí perquè pugui seguir endavant. Gràcies avi.

Barcelona, 17 de Juliol de 2017

Informe dels directors

El Dr. Bernat Hereu Fina i la Dra. Cristina Linares Prats, professors del Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals de la Universitat de Barcelona, directors de la Tesi Doctoral elaborada pel candidat Pol Capdevila i Lanzaco, i que porta per títol "Life history, population dynamics and conservation of underwater Mediterranean forests: insights from the long-lived alga *Cystoseira zosteroides*",

INFORMEN

Que els treballs de recerca duts a terme pel Sr. Pol Capdevila i Lanzaco com a part de la seva formació pre-doctoral i inclosos a la seva Tesi Doctoral han donat lloc a quatre capítols, dos dels quals ja estàn publicats, un està en procés de revisió i el darrer manuscrit està a punt per ser enviat a una revista d'àmbit internacional. A continuació es detalla la llista d'articles, així com els índex d'impacte (segons la ISI Web of Science) de les revistes on han estat publicats o bé s'han enviat els capítols.

1. Capdevila, P., Linares, C., Aspillaga, E., Navarro, L., Kersting, D. K. and Hereu, B. (2015) Recruitment patterns in the Mediterranean deep-water alga *Cystoseira zosteroides. Marine Biology*, 162: 1165–1174. `DOI10.1007/s00227-015-2658-0`

   L' índex d'impacte de la revista *Marine Biology* l'any 2015 va ser de 2.375. Aquesta revista està situada en el primer quartil de la categoria "Marine and Freshwater Biology". Aquesta categoria té una mediana d'índex d'impacte de 1.50 i inclou un total de 105 revistes. Tenint en compte l'índex d'impacte de *Marine Biology*, aquesta revista ocupa el 21è lloc de la seva categoria.

2. Capdevila, P., Linares, C., Aspillaga, E., Riera, J. L., Hereu, B. Effective dispersal and density-dependencen in mesophotic macroalgae forests. En revisió a la revista *Scientific Reports*.

L' índex d'impacte de la revista *Scientific Reports* l'any 2016 va ser de 4.259. Aquesta revista està situada en el primer quartil de la categoria "Multidisciplinary Sciences". Aquesta categoria té una mediana d'índex d'impacte de 0.956 i inclou un total de 64 revistes. Tenint en compte l'índex d'impacte de *Scientific Reports*, aquesta revista ocupa el 10è lloc de la seva categoria.

3. Capdevila, P., Hereu, B., Riera, J. L., Linares, C. (2016) Unravelling the natural dynamics and resilience patterns of underwater Mediterranean forests: insights from the demography of the brown alga *Cystoseira zosteroides*. *Journal of Ecology*, 104: 1799–1808. `DOI10.1111/1365-2745.12625`

   L' índex d'impacte de la revista *Journal of Ecology* l'any 2016 va ser de 6.180. Aquesta revista està situada en el primer quartil de la categoria "Plant Sciences" i "Ecology". La primera categoria té una mediana d'índex d'impacte de 1.335 i inclou un total de 211 revistes. La segona categoria té una mediana d'índex d'impacte de 1.897 i inclou un total de 153 revistes. Tenint en compte l'índex d'impacte de *Journal of Ecology*, aquesta revista ocupa el 15è i 11è lloc, respectivament, en aquestes categories.

4. Capdevila, P., Hereu, B., Salguero-Gómez, R., Rovira, G., Medrano, A., Cebrián, E., Garrabou, J., Kersting, D., Linares, C. Warming impacts on early life stages increases the vulnerability and delays the recovery ability of macroalgae populations. Preparat per enviar a la revista *Proceedings of The Royal Society B-Biological Sciences.*

   L' índex d'impacte de la revista *Proceedings of the Royal Society B-Biological Sciences* l'any 2016 va ser de 4.940. Aquesta revista està situada en el primer quartil de la categoria "Biology", "Ecology" i "Evolutionary Biology". Aquestes categories tenen una mediana d'índex d'impacte de 1.572, 1.897, 2.500 i inclouen un total de 84, 154 i 48 revistes, respectivament. Tenint en compte l'índex d'impacte de *Proceedings of the Royal Society B*, aquesta revista ocupa el 9è, 17è i 8è lloc de les respectives categories.

Alhora CERTIFIQUEN

Que el Sr. Pol Capdevila i Lanzaco ha participat activament en el desenvolupament del treball de recerca associat a cadascun d'aquests articles, així com en la seva elaboració. En concret, la seva participació en cadascun dels articles ha estat la següent:

- Plantejament dels objectius.
- Planificació i execució dels experiments, tant pel què fa a feina de camp com al laboratori.
- Processat i anàlisi de les mostres obtingudes, a més dels anàlisis de dades obtingudes.
- Redacció dels articles i seguiment del procés de revisió dels mateixos.

Finalment, certifiquen que cap dels coautors dels articles presentats a continuació i que formen part de la Tesi Doctoral d'en Pol Capdevila i Lanzaco utilitzarà implícitament o explícitament aquests treballs per a l'elaboració d'una Tesi Doctoral.

Director de tesi
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Abstract

Life history theory and population ecology have been especially neglectful of marine species, with most ecological principles developed from studies based on terrestrial species. This is especially true for macroalgae species, for which population dynamics and life history studies are still scarce. Given their fundamental role as habitat-forming species and primary producers in temperate seas worldwide, understanding the dynamics of macroalgae populations is fundamental, not only for their own conservation but also for their associated biodiversity and marine coastal ecosystems functioning. Therefore, the present dissertation aims to unravel some of the processes and mechanisms that shape the population dynamics of the deep-water, long-lived and habitat-forming macroalga, *Cystoseira zosteroides*. With this information, we aim to bolster our ability to predict the future of this species in a globally impacted world, as well as to develop management tools to improve their conservation status. Overall, we aim to improve our current comprehension about the population dynamics and life history of macroalgae.

The results obtained from our monitored populations show that *C. zosteroides* have slow population dynamics. By using comparative analyses, we observed contrasting life history strategies among macroalgae species. While other intertidal fucoid and kelp populations highly depend on reproductive processes and the growth of organisms, natural and undisturbed *C. zosteroides* populations are maintained by the high survival and long lifespan of adult individuals. We also demonstrated that the dispersal ability of brown macroalgae is very limited compared to other taxa, with kelps showing higher dispersal potential than fucoids.

Our findings showed that disturbances highly influence *C. zosteroides* population dynamics. After an extreme storm and the impact of a ghost fishing net, their populations displayed a high increase in recruitment rates, suggesting a negative density-dependence effect of adults on early stages. We observed that in recruitment plates located inside well-developed adult canopies post-settlement survival is lower than outside the adult canopy.

This evidence that adult *C. zosteroides* individuals establish a ceiling for the development of recruits. Thus, density-dependence plays a key role regulating *C. zosteroides* population dynamics, triggering their recovery after major disturbances. In contrast to natural populations, after major mortality events, their recovery and dynamics highly depend on the reproductive process. This is particularly worrying given the limited effective dispersal of this species.

Finally, despite the high ability of *C. zosteroides* to compensate morality pulses through density-dependence, their recovery can take decades, rendering their populations more vulnerable. Although isolated mortality events can be compensated, our demographic simulations showed that the combined effect of physical disturbances, compromise the viability of *C. zosteroides* populations. Furthermore, we demonstrated that warming has a high impact on the early life stages of this species. Decreased early survival and settlement rates due to rising temperatures delay the recovery of *C. zosteroides* and increase the vulnerability of their populations.

Overall, our findings do not only contribute to better comprehend macroalgae population dynamics, but also provide new insights for their effective management. With this dissertation we evidence the key role of population ecology and life history into understanding the dynamics of species, stressing how these disciplines may help us to better comprehend the future of coastal marine ecosystems.

Resum

La teoria sobre les història de vida i l'ecologia de poblacions desenvolupen principis ecològics basats principalments en estudis realitzats en espècies terrestres, sovint sense tenir en compte les espècies marines. Aquest fet és especialment cert en el cas de les macroalgues, un grup d'organismes dels quals, històricament, s'ha ignorat la seva dinàmica de poblacions i història de vida. Donat el seu paper fonamental com a espècies formadores d'hàbitat i com a productors primaris en els mars temperats de tot el món, entendre millor la seva dinàmica poblacional és fonamental, no només per a la seva pròpia conservació, sinó també per la seva biodiversitat associada i pel funcionament dels ecosistemes marins costaners. Per tant, la present tesi pretén descriure alguns dels processos i mecanismes que configuren la dinàmica poblacional de *Cystoseira zosteroides*, una macroalga longeva i formadora d'hàbitat, que habita en aigües profundes del Mediterrani Nord-Occidental. Amb aquesta informació volem incrementar la nostra capacitat per predir el futur d'aquesta espècie en un món globalment alterat, així com per desenvolupar eines de gestió que permetin millorar el seu estat de conservació. En un context més ampli, amb aquesta tesi també es pretén augmentar la nostra comprensió actual sobre la dinàmica poblacional i la història de vida de les macroalgues.

Els resultats obtinguts de les nostres poblacions monitoritzades mostren que *C. zosteroides* presenta una dinàmica poblacional molt lenta. Mitjançant l'ús d'anàlisis comparatives, es van observar diverses estratègies de vida entre les espècies de macroalgues. Mentre que altres poblacions de Fucals i de Kelps d'hàbitats somers depenen molt dels processos reproductius i del creixement dels organismes, les poblacions naturals i no pertorbades de *C. zosteroides* es mantenen gràcies a l'elevada supervivència i la llarga esperança de vida dels individus adults. També demostrem que la capacitat de dispersió de les macroalgues brunes és molt limitada en comparació amb altres taxons, tot i que els Kelps presenten un major potencial de dispersió que les Fucals.

Els nostres resultats varen mostrar que les pertorbacions tenen una

gran influència en la dinàmica poblacional de *C. zosteroides*. Després d'una tempesta extrema i de l'impacte d'una xarxa de pesca fantasma, les seves poblacions varen mostrar un increment de les taxes de reclutament, suggerint un efecte de denso-dependència negativa per part dels adults a les primeres etapes de vida d'aquesta espècie. Vàrem observar que en col·lectors de reclutes situats a l'interior de boscos de *C. zosteroides* la supervivència post-assentament és inferior que fora d'aquests. Això evidenciava que els individus adults de *C. zosteroides* estableixen un sostre pel desenvolupament dels reclutes. D'aquesta manera, la denso-dependència juga un paper clau regulant la dinàmica poblacional de *C. zosteroides*, ja que pot impulsar la seva recuperació després de grans pertorbacions. A diferència de les poblacions no alterades, després de grans esdeveniments de mortalitat, la recuperació i dinàmica de les poblacions de *C. zosteroides* depèn molt dels processos reproductius. Això és especialment preocupant donada la limitada dispersió efectiva d'aquesta espècie.

Finalment, tot i la gran capacitat de *C. zosteroides* per compensar esdeveniments de mortalitat a través de la denso-dependència, la seva recuperació pot trigar dècades, fent que les seves poblacions siguin més vulnerables. En aquesta tesi, vàrem observar que els esdeveniments de mortalitat aïllats es poden compensar amb polsos de reclutament. Tanmateix, les nostres simulacions demogràfiques demostren que l'efecte combinat dels pertorbacions físiques, com les tempestes i les xarxes de pesca abandonades, comprometen la viabilitat de les poblacions de *C. zosteroides*. A més, hem demostrat que l'escalfament té un gran impacte en les primeres etapes de vida d'aquesta espècie. La disminució de la supervivència primerenca i de l'assentament retarden la capacitat de recuperació de *C. zosteroides*, fet que augmenta la vulnerabilitat d'aquesta espècie.

En general, els nostres resultats no només contribueixen a comprendre millor la dinàmica poblacional de les macroalgues, sinó que també proporcionen noves perspectives per desenvolupar eines de gestió eficaç. A més, a través d'aquesta tesi, es demostra el paper clau de l'ecologia de poblacions i la història de la vida en la comprensió de la dinàmica de les espècies i destaca com aquestes disciplines poden ajudar-nos a entendre millor el futur dels ecosistemes marins costaners.

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Chapter 1

General Introduction

1.1 Elucidating the natural dynamics of species

1.1.1 Population ecology and demography

Natural systems are highly complex and, as such, often prove puzzling to comprehend; however, it is the main objective of ecologists to be able to understand and predict their dynamics. Ecological questions scale up from the relative simplicity of individuals to the complexity of interactions between organisms and their environments, ecompassing a considerable range of scales across space, time and biological organizations (Levin, 1992). The implications of such knowledge stretch beyond natural systems into society challenges through conservation and management.

Population ecology is a branch of ecology which explores the drivers of changes in the abundance of individuals over time and space, tries to relate this variation to the underlying vital rates (survival, growth, and reproduction) and seeks to unveil the ways in which demographic processes are influenced by environmental factors (Begon et al., 2006). In an academic sense, a population can be defined as a group of individuals of the same species living and interbreeding within a given area (Tarsi and Tuff, 2012). Its members often rely on the same resources, are subject to similar environmental constraints and depend on the presence of other members to persist over time. Some authors consider the study of the underlying vital rates or demographic processes to describe population dynamics as a parallel disciple, known as demography (Lebreton et al., 1992).

This thesis is encapsulated within the discipline of population ecology. This discipline provides the ideal framework to study biological systems at scales that, to some extent, are apparent and measurable for researchers, which are also ecologically relevant. Many of the processes affecting populations take place over multiple years or decades, rather than across hours, weeks or months (Clutton-Brock and Sheldon, 2010), accordingly to the life history of the species (Stearns, 1992). On the other hand, the propagation of genes, traits and individuals within and between populations highly depends on the survival, fertility, and dispersal of organisms at each age/stage of their life cycle. That is, natural selection operates within populations, favoring those individuals whose demographic contributions over their lifespans are greatest (Metcalf and Pavard 2007; Lowe et al. 2017). Furthermore, population-level changes scale up to community-level responses, for example, determining the strength of interaction between species (Lowe et al., 2017). Overall, this enables to link evolutionary questions and fundamental research with more applied disciplines such as conservation biology.

1.1.2 Life history theory

Population ecology cannot be studied without taking into account the evolutionary context. The concepts that we introduce in the following lines are key for the comprehension and interpretation of our results, but we did not address them directly throughout this dissertation.

Species present different dynamics according to their life histories. Life history theory is the discipline that tries to explain how natural selection and other evolutionary forces have shaped organisms to optimize their demographic schedules, in face of ecological challenges posed by the environment (Stearns 1999). Thus, life history theory links population dynamics to evolutionary processes (Saccheri and Hanski 2006; Lowe et al. 2017).

Almost all organisms are born, survive and develop to advanced/older stages/ages, reproduce and one day they die (Figure 1.1). The schedule of these key demographic events during an individual life cycle results in the so-called life history strategies (Stearns, 1992). Nevertheless, there are some constraints on the combination of tactics available for a given species (Figure 1.2). Some are determined intrinsically by the potential of the genome which will vary from taxon to taxon (i.e. evolutionary history/phylogenetic inertia), while others are restricted extrinsically by the environment (i.e. environmental filtering), filtering out those strategies that are not viable (Southwood, 1988; Stearns, 1992). This has resulted in a tremendous variety of life histories, fine-tuned to Earths' harsh and varied

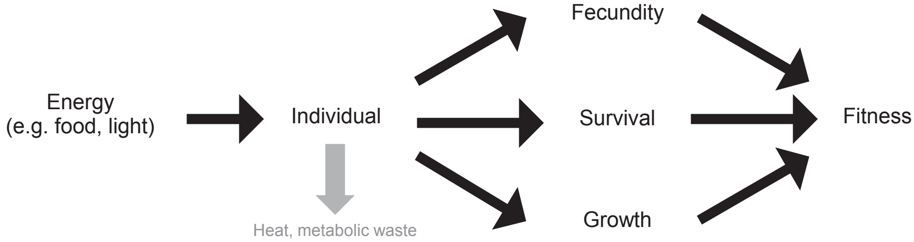


Figure 1.1: A schematic model representing the different paths by which individuals can invest their energy into demographic processes that may lead to greater fitness. Growth, survival and fecundity investments contribute to overall population dynamics what in turn determines the fitness, which is highly influenced by the environment.

All this is unfolded within other limiting forces tightly related with evolutionary constraints, the so-called trade-offs. This concept is rooted in the principle of allocation developed by Cody (1966). Given that time and resources to expend are finite, there exists a budgetary compromise on allocating more in one biological function than in others (Stearns, 1992). In other words, all the components of life history cannot be maximized (Figure 1.1).

1.2 Changing the rules: global change and the birth of conservation biology

The human footprint in ecosystems is now so pervasive and profound that have pushed Earth into a new era, the Anthropocene (Steffen et al., 2015). From the early 1950s to 2000s human populations have experienced a dramatic increase, what has been coupled with its technological development and the inevitable increase of natural resources exploitation, the so called Great Acceleration (Steffen et al., 2011). Many anthropogenic pressures on ecosystems have increased rapidly over the last century, from nitrogen deposition to stocking rate of livestock, suppression, and atmospheric CO_2 concentrations (Steffen et al., 2015).

Perhaps, the most apparent signal of the contemporary human civi-

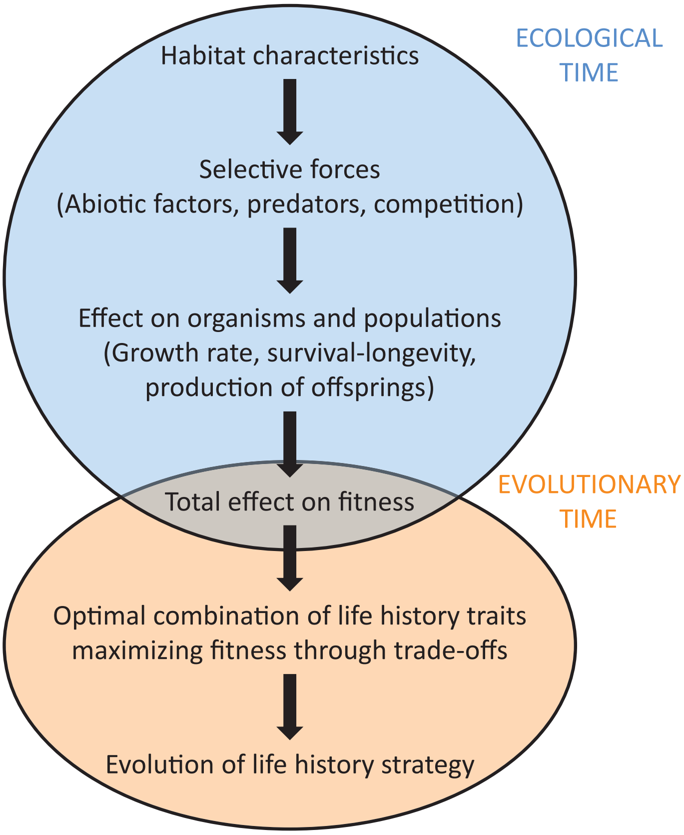


Figure 1.2: Development of life history strategies modified from Southwood (1988). The blue coloured bubble represents the environmental filtering, whereby the surrounding environment favours certain strategies but not others. For example, adaptations to adverse physical conditions have costs that can be a disadvantage if these organisms live in less adverse conditions, where they may be in competition with other organisms. The orange coloured bubble represents phylogenetic inertia, whereby species are prisoners of their evolutionary history, limiting the repertoire of available choices. There are intrinsic connections between demographic/life history traits determined by the species ancestry, what ensures that all traits are not simultaneously available.

lization influence to the environment is climate change (Figure 1.3). The increased emission of long-lived, heat-trapping greenhouse gasses (CO_2, CH_4, N_2O, tropospheric ozone, and chlorofluorocarbons; Figure 1.3a) warms the planet's surface globally (Figure 1.3b; Cox et al., 2000). Although oceans have absorbed >80% of the heat added to the global climate system, the ocean's thermal capacity has led to surface waters warming three times slower than air temperatures over land (Figure 1.3b; IPCC, 2013). Nevertheless, areas of high marine biodiversity often have greater velocities of climate change and seasonal shifts (Burrows et al., 2011). Climatic variability has increased, with extreme events becoming more frequent and intense, such as heavy rainfalls (Figure 1.3c), droughts, storms or heat waves (IPCC, 2013). In marine ecosystems, there are additional threats, such as ocean acidification (Figure 1.3d), which is caused by the uptake of anthropogenic CO_2 by the oceans (Hoegh-Guldberg and Bruno, 2010).

The consequences of this global change have already echoed into the biosphere, transgressing almost all levels of organization in biological systems and extending to a wide range of spatial and temporal scales (Parmesan 2006; Bellard et al. 2012; Scheffers et al. 2016). Evidence scale up from the physiology of species (Mota et al., 2015) to the fate of populations (McCauley et al., 2015), driving changes in species distributions (Smale and Wernberg, 2013), altering community interactions and composition (Vergés et al., 2016; Wernberg et al., 2016a), with their associated socio-economic consequences to the mankind (Pecl et al., 2017).

Within the global change context, it is necessary not only to understand the natural dynamics of systems, but also to predict how they will respond to global change. Therefore understanding and predicting how these changes on Earth will affect ecological and evolutionary processes is urgently needed, to design and support robust and successful management strategies.

1.2.1 Linking conservation biology, global change and population ecology

All these alterations, increasing at an unprecedented rate, were not followed by an increase of a serious social awareness about the ability of biological systems to absorb multiple disturbances. In fact, it was not before the 1980s,

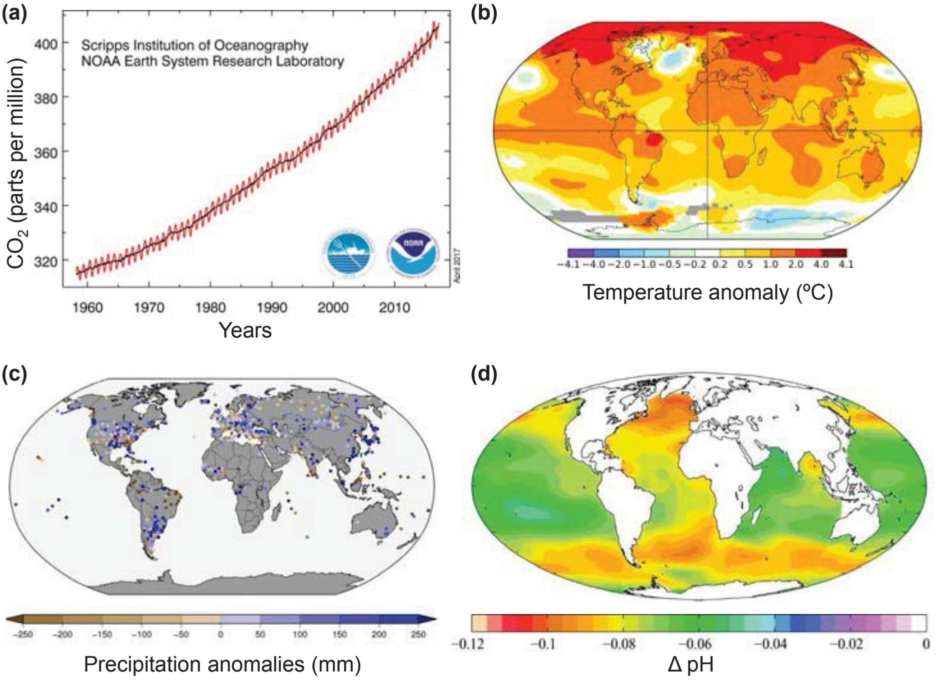


Figure 1.3: Examples of global climatic changes on Earth: (a) CO$_2$ concentration changes over the years since 1960, the red line represents the monthly mean values, centered on the middle of each month, the black line represents the same, after correction for the average seasonal cycle; (b) Surface temperature anomaly during the year 2016 relative to the mean for 1951–1980; (c) Land only precipitation anomalies in 2016 with respect to a 1961-1990; (d) Estimated change in annual mean sea surface pH between the pre-industrial period (1700s) and the 1990s. [Credits: (a) and (c) NOAA National Center for Environmental Information, (b) NASA Goddard Institute for Space Studies, and (d) Global Ocean Data Analysis Project]

that conservation biology emerged as a discipline, through the influential texts of Otto Frenkel and Michaels Soulé (Frankel and Soulé, 1981).

Conservation biology combines several branches of biology, such as ecology, taxonomy, genetics, to policy and social sciences, with the general aims of (1) evaluating the anthropogenic impacts on biological diversity and (2) developing useful tools to prevent the extinction of species (Mills, 2012).

Therefore, as a discipline, conservation biology poses questions about the real world in an ecological context. Linking principles developed by natural sciences, such as population ecology, to manage species, developing conservation plants or habitat restoration, with the purpose to somehow benefit society and nature itself (Mills, 2012). Answering such issues is important to alert scientists and decision makers about potential future conservation risks, to provide means to bolster attribution of biological changes to climate change and to support the development of proactive strategies to reduce global change impacts on biodiversity (Parmesan et al., 2011).

In this context, population ecology offers ideal means to nourish conservation biology. Global change impacts on populations can be distilled into abiotic and biotic factors, both influencing directly and indirectly the number of births, deaths, and immigrants in a population (Figure 1.4). Once quantified the impact of these factors on the demographic processes of populations, it is possible to predict their future responses to climate change (Jenouvrier et al., 2014) or assess the vulnerability of species according to their life history (Box 1), and can be integrated with other modelling techniques to improve their mechanistic basis (Keith et al., 2008).

Abiotic factors are influenced by global change through the modification of habitat conditions (Figure 1.4). These alterations can directly influence the physiology and behaviour of species (Sentis et al., 2017), what generate effects on the demographic parameters by changing the flow of individuals within (through birth and death) and among (through immigration, emigration and/or dispersal) populations. On the other hand, environmental variation interplays with density-dependence, as increasing or decreasing the number of individuals can modify the vital rates (Benton et al., 2006; Gamelon et al., 2017). Eventually, all of these changes (due to a/biotic factors) can result in extinction/colonization processes which determine the species' range of distributions (Smale and Wernberg, 2013). Furthermore, changes in the distribution of species reshuffle ecological communities. This has the potential to alter interactions among species that have co-occurred for centuries and generates novel interactions between species whose ranges previously did not overlap (Vergés et al., 2016)

What we want to illustrate with all the aforementioned concepts and information is that we can only understand the effecs of global change, and anticipate its consequences through a profound understanding of many population-level processes. However, quantifying all these processes is not an easy task and it is usually necessary to measure them separately. In this thesis we will try to unravel some of these processes and mechanisms, to improve our comprehension about the population dynamics of a deep-water and habitat-forming macroalga. With this information, we will trigger our ability to predict the future of this species in a globally changed world, as well as to develop management tools to improve their conservation status. Although we will focus on a very particular system that we will introduce in the following sections, we believe that our approach could be used as a

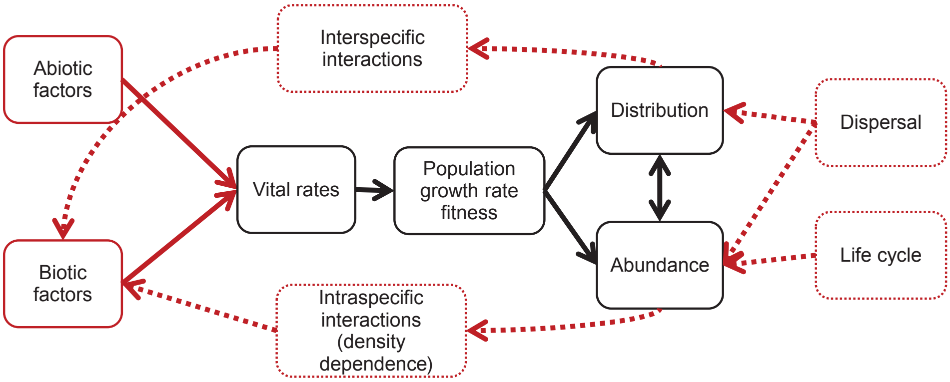
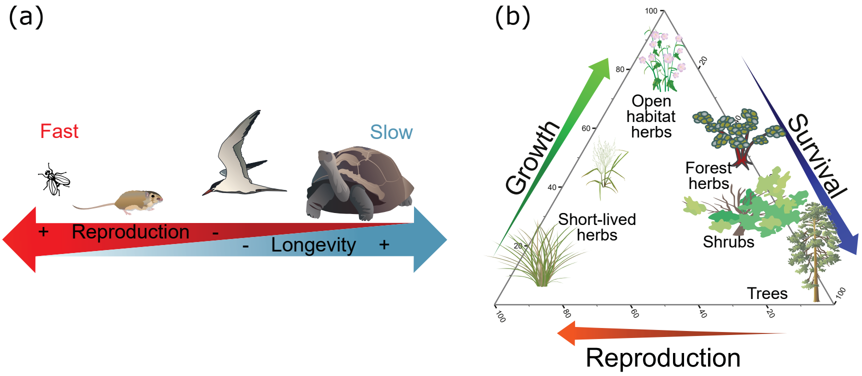


Figure 1.4: Underlying processes shaping vital rates, population growth rates, abundance and distribution of species. Red color boxes represent all processes altered by global change, black boxes are the ultimate outcomes.

Box 1: Can we anticipate global changes through life history theory?

Life history theory hypothesizes that the diversity of traits displayed by species is highly structured, and can be organized along major axes of variation (a and b). Those axes of variation conform different life history strategies, which may display divergent responses to the same stressors. Thus, life history frameworks aim to create predictable "types of species" that, in a certain way, can predict the consequences of global change and guide conservation and management (e.g. Darling et al., 2013).



Classically, animal ecologists classified species between r- or K-strategists (Pianka, 1970), and later on in a continuum between fast-slow ends (a; Stearns, 1992). Organisms could life fast, being highly-reproductive but short-lived; or life slow, being low-reproductive but long-lived, or anything in between both extremes. Under unpredictable environments (i.e. high mortality risk), species tend to live faster, as a way to reproduce early in life before dying (Cohen, 1967), while at stable environments species tend to life slower.

Instead, plant ecologists considered that three principal axes define life history strategies (b; Grime, 1977). Under stable and productive habitats species invest resources in continued vegetative growth and rapid attainment of large size (open-habitat herbs and forest herbs); in stable but resource-poor environments, species maximize survival by investing mainly in capacity to retain resources and repair cellular components in persistent tissues (shrubs and trees); and in environments with periodic biomass destruction, species invest a large proportion of resources in propagules from which the population can regenerate quickly (short-lived herbs and open-habitat herbs).

1.3 The ecology of algae: a long road to wander

Population ecology and life history theory disciplines have been especially neglectful of marine species (Figure 1.5). Marine and terrestrial biomes strongly differ in the spatial and temporal variability of biological, physical and chemical processes (Webb, 2012), as well as on the threats at which they are exposed (e.g. ocean acidification, sea level rise; Burrows et al. 2011; Sunday et al. 2012; Poloczanska et al. 2013). Rescuing the concepts introduced in Section 1.1, if we take into account that marine species are composed by very differing taxa with distinct evolutionary history; and that they have evolved in very different physical environments (i.e. distinct environmental filtering), it suggests that there are no reasons to believe that life history principles developed on terrestrial organisms should apply to marine ecosystems.

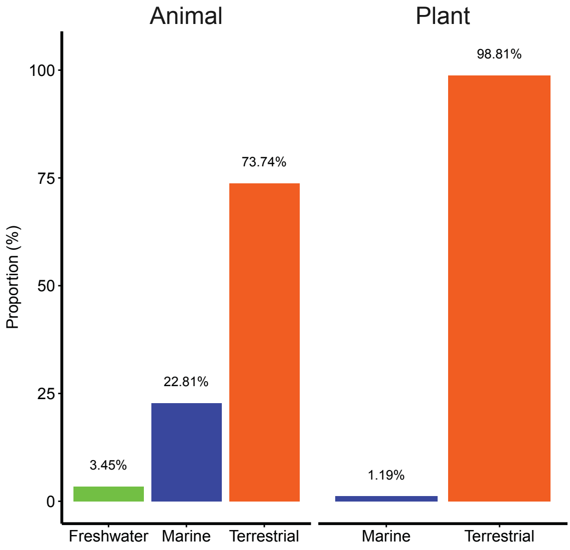


Figure 1.5: Proportion of freshwater, marine and terrestrial demographic studies of sessile species from the public databases COMPADRE (Plants) and COMADRE (Animals) (`http://www.compadre-db.org/`; accessed 20/04/2017).

This is especially true for algae, a highly heterogeneous group with very different evolutionary history. Despite their worldwide distribution, high abundance and, environmental and economic importance; still, we have a very limited knowledge about their population dynamics and life histories. Different research traditions between ecologists and phycologists may have prevented our perception of macroalgae population dynamics (Schiel and Foster, 2006). Much focus of ecologist research has centered in trophic and community dynamics, while phycologists focused on taxonomy, biology, and physiology. In addition, their complex life histories, combining microscopic and macroscopic life stages, may have added additional layers of complexity to study their dynamics.

1.3.1 Macroalgae: what are they?

Algae are represented by a heterogenic group of organisms, aquatic, oxygen-evolving photosynthetic autotrophs which are unicellular, colonial or constructed by filaments or composed by simple tissues (Graham et al., 2009; Guiry, 2012). This definition encompasses three evolutionarily distinct clades (Graham et al., 2009): Rhodophyta (red algae), Chlorophyta (green algae) and Phaeophyceae (brown algae). The Phaeophyceae are of a lower taxonomic rank than the other two clades; however, like the Rhodophyta and Chlorophyta, they constitute a monophyletic clade (Guiry, 2012). There also exists a gross distinction between microalgae and macroalgae; with the former group being those that are only visible with a microscope (e.g. plankton), while macroalgae (also named seaweeds) are visible to the unaided eye (Graham et al., 2009). This classification has an important ecological meaning, given that the dynamics and ecological roles of micro- and macroalgae are very different, as it is the methodological approach for their study. For the purpose of this thesis, we will focus on macroalgae.

1.3.2 Why macroalgae? Their ecological role

Because of their diverse and ancient origins, macroalgae exhibit an astonishing diversity of forms and functions, ranging from tiny unicellular to giant multicellular individuals, with a huge disparity of life cycles (Graham et al., 2009). Consequently, they have developed the ability to live in a wide range of environmental conditions (Lüning, 1990; Santelices et al., 2009). They are present in almost all the oceans around the globe, although being more diverse in the temperate regions than in the tropics (Lüning 1990; Keith et al. 2014).

Macroalgae are particularly important as primary producers, contributing to the carbon cycle, and as habitat-forming species. Besides, they also contribute to nitrogen fixation and nutrient retention (e.g. green algae; Heil et al., 2004), reef construction by deposition of calcium carbonate (e.g. crustose calcareous algae such as *Peyssonnelia*; Littler and Littler, 1984) or facilitating coral settlement in tropical ecosystems (Doropoulos et al., 2016).

Recent studies suggest that macroalgae are among the most productive macrophytes, with estimates of a global net primary production (NPP) of 1,020–1,960 TgC/year (Krause-Jensen and Duarte, 2016). This biomass can be retained within the macroalgae forest, consumed directly by herbivorous (fish and invertebrates), or exported to adjacent (sometimes distant) and deeper habitats. It can be exported as particulate organic matter (POM) or dissolved organic matter (DOM) (Graham et al., 2009; Krumhansl and Scheibling, 2012), nourishing filter feeders (Figure 1.6). Most of the NPP of macroalgae contributes to carbon sequestration (mainly in the deep sea), with estimates similar or even greater than for the carbon buried in angiosperm-based coastal habitats (Krause-Jensen and Duarte, 2016).

Additionally to their fundamental role in the carbon cycle, macroalgae are considered engineering species (*sensu* Jones et al., 1994). Perhaps, the most emblematic habitat-forming macroalgae species in temperate seas are canopy-forming seaweeds of the orders Laminariales and Tilopteridales (kelps), and Fucales (fucoids). These brown algae generate three-dimensional structure, providing food and shelter to many associated species (Steneck et al. 2002; Schiel and Foster 2006). The canopy of those macroalgae is also home of rich understory assemblages formed by other algae and animals. Some other algae species (mainly Rhodophytes) are well adapted to the scarce light that arrives beneath macroalgae canopies, as their pigmentation is fine-tuned to low light intensities. Sessile and mobile animals can be abundant as well, increasing biodiversity and contributing to the ecosystems functioning as herbivores, detritus feeders, suspension feeders, predators, etc. (Ballesteros, 2006; Boudouresque et al., 2016). Furthermore, the structural biomass of macroalgae has a nursery function for early stages of many invertebrates, fish and shellfish species, providing shelter from predation and food (Graham 2004; Cheminée et al. 2013).

The loss of canopy-forming macroalgae is usually driven by major disturbances, such as outbreaks of herbivores (Ling et al., 2014), heat waves (Wernberg et al., 2016a) or storms (Dayton and Tegner, 1984). When this takes place, it is frequent to observe a transition from structurally complex ecosystems to alternative states, dominated by opportunistic species (e.g. turf, ephemeral, filamentous or invasive algae; Filbee-Dexter and Scheibling, 2014; Ling et al., 2014). These changes reduce the primary production and habitat complexity (Filbee-Dexter and Scheibling, 2014; Ling et al., 2014), with the consequent biodiversity loss and the alteration of ecosystem functioning (Estes et al., 1989; Steneck et al., 2002). For example, the decline of macroalgae forest can echoes into society through the loss of catches in local fisheries (Ling et al., 2009). However, chronic stressors such as global warming may drive a transition into novel ecosystem, resulting in the tropicalization of temperate seas (Vergés et al., 2014; Wernberg et al., 2016a).

1.3.3 Mediterranean *Cystoseira* underwater forests

The Mediterranean Sea is considered a hotspot of biodiversity, and algae are the main responsible. Although it only represents a 0.82% of the world ocean area and the 0.3% of its volume, more than 17,000 marine species has been described in the Mediterranean Sea, representing a 4–18% of the world marine species, with a remarkable 25% of endemisms (Coll et al., 2010). The number of described algae species are close to 1,120, a 10.9% of their counterparts worldwide (Figueroa et al., 2014). Of these species, about 190 are green algae, 700 red algae and 227 brown algae, representing a 7.6%, 10.6% and 17.3% of the global estimates respectively (Coll et al., 2010).

Because of its particular environmental conditions, the main habitat-forming species worldwide are not present in the Mediterranean Sea (Zabala and Ballesteros, 1989). The low nutrient concentrations limit the development of kelps (with some exceptions), while the marked seasonality (with relatively cold periods) prevent the development of hermatypic corals (Zabala and Ballesteros, 1989). In contrast, these conditions favoured the speciation of fucoids of the genus *Cystoseira*, which are the major habitat-forming species in the Mediterranean Sea (within the photic zone).

The genus *Cystoseira* C. Agardh was described in 1820, and it is currently constituted by 51 species. Although they are distributed through most of the Mediterranean climatic regions worldwide (Figure 1.7), 36 *Cystoseira* species are present in the Mediterranean Sea and 30 are endemic (Oliveras-Plá and Gómez-Garreta, 1989). It has been suggested that they were originated in the Tethys Ocean during the Mesozoic, and afterwards, some species remained in the Indo-Pacific Ocean while others may have entered into the Mediterranean Sea from the Atlantic Ocean during the Cenozoic,

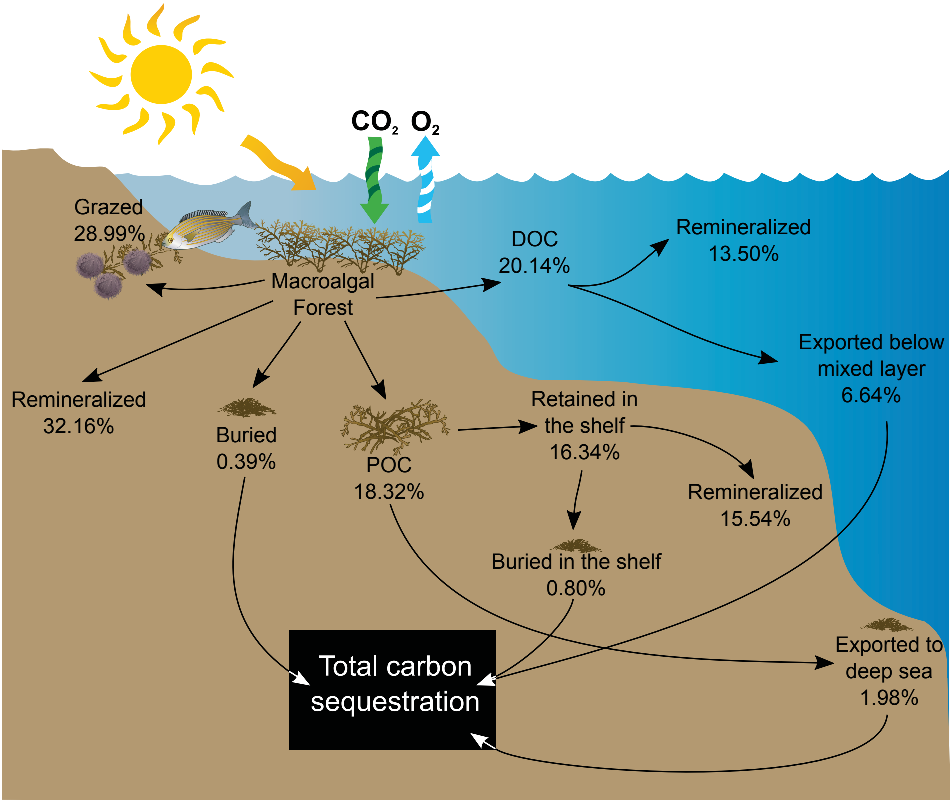


Figure 1.6: Conceptual diagram about the possible fate of fixed carbon from macroalgae to the carbon sequestration in coastal ecosystems. Each step and estimates of the carbon flow are based on Krause-Jensen and Duarte (2016) review. Symbols have been taken from the IAN, University of Maryland, Center for Environmental Science (`ian.umces.edu/imagelibrary/`).

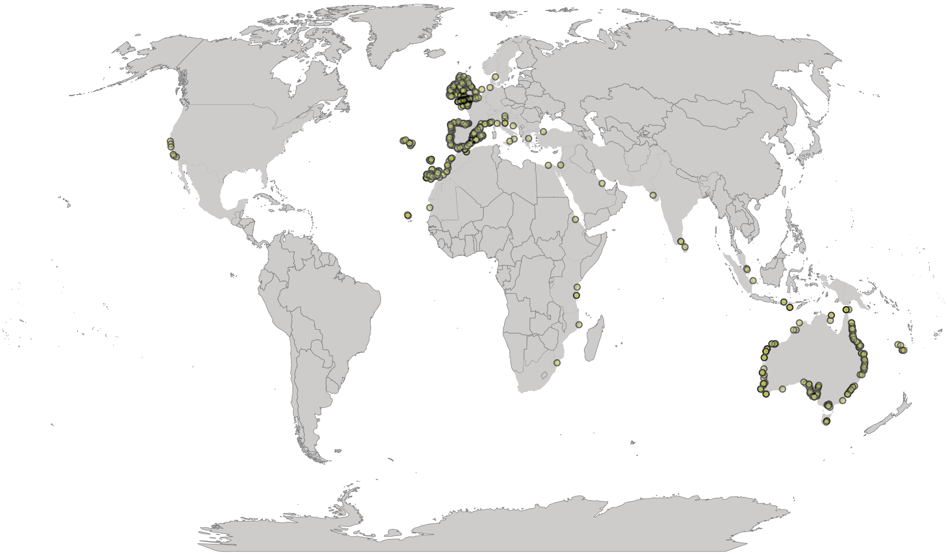


Figure 1.7: Global distribution of *Cystoseira* species worldwide, based on occurrence data from the public data base GBIF (accessed 20/04/2017).

starting a speciation process that continues nowadays (Oliveras-Plá and Gómez-Garreta 1989; Amico 1995).

Cystoseira species are characterized by a single or several primary axes attached to the substratum, usually perennial and no longer than 1 m (depending on the species), which can be ramified in branches that conform dense canopies (Box 2; Gómez-Garreta et al., 2001). Their canopy provides habitat for a considerable number of other algae and invertebrate species (Figure 1.8), and range among the most productive communities in the Mediterranean (Giaccone 1973; Ballesteros et al. 2009). Habitats dominated by *Cystoseira* species are considered late successional stages and they tend to dominate in the best preserved Mediterranean benthic ecosystems (Figure 1.8; Sala et al., 2012).

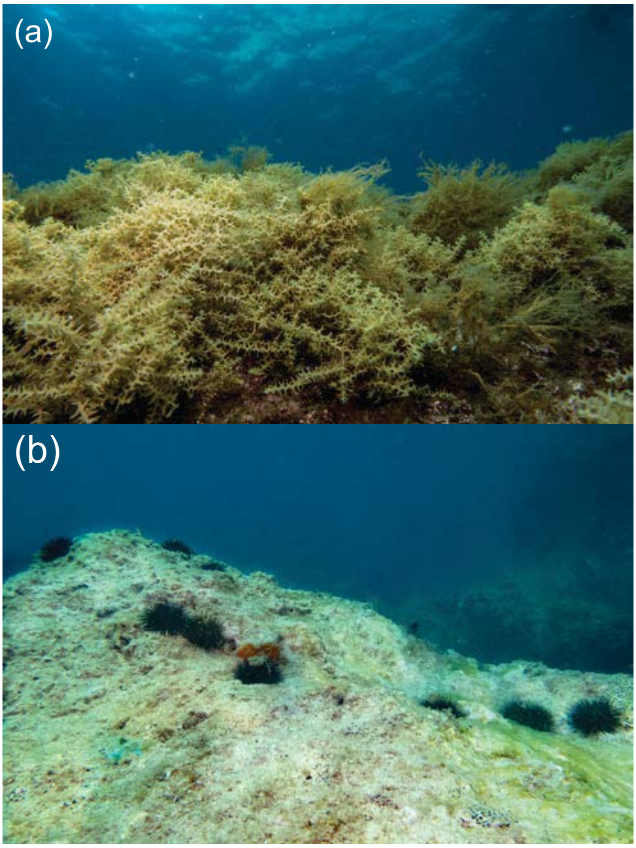


Figure 1.8: Examples of a *Cystoseira*-dominated macroalgae in Medes Islands (a) and a degraded rocky bottoms in Montgrí coast where *Cystoseira* canopy has been substituted for extensive barrens and turf algae (b).

1.3.4 Deep-water *Cystoseira* forests

Deep-water macroalgae assemblages are invaluable because of their uniqueness and associated biodiversity. Unfortunately, due to the logistical difficulties of studying in deep-water environments, quantitative data on these assemblages is still scant. Given that major physical limiting factors vary predictably with depth, it can be considered a stress gradient (Figure 1.9). Shallow communities are exposed to high irradiation, high hydrodynamics and receive more nutrients. On the contrary, deep environments are more restricting; with low light and nutrient levels highly depend on bottom currents. Deeper communities tend to be less productive, they present slow dynamics but with a high structural complexity (Garrabou et al., 2002).

The speciation of *Cystoseira* becomes evident with their bathymetric distribution in the Mediterranean (Figure 1.9). Although most *Cystoseira* species inhabit in shallow waters, there are several species that can be found deeper than 50 m (Figure 1.9; Giaccone 1973; Ballesteros 1990; Hereu et al. 2008a). Deep-water macroalgal communities are usually dominated by the species *C. zosteroides* C. Agardh in the Mediterranean Sea (Figure 1.9 and Box 2), which can occur in monospecific stands or together with other *Cystoseira* species, such as *C. spinosa* v. *compressa* and *C. funkii* (Giaccone 1973; Ballesteros 1990; Hereu et al. 2008a). Because of their deep distribution these assemblages live under relatively constant environmental conditions, with almost no herbivory pressure (Vergés et al., 2009). They develop highly structured communities, with much associated biodiversity (72–121 species) of plants and animals (Ballesteros 1990; Serio 1994; Ballesteros et al. 2009). At such deep environments these species are close to the limits of their physiological light compensation point for growth (Markager and Sand-Jensen, 1992), what results in low community dynamics, with low individual growth rates, long lifespans and low recruitment rates (Ballesteros 1990; Ballesteros et al. 1998; Garrabou et al. 2002).

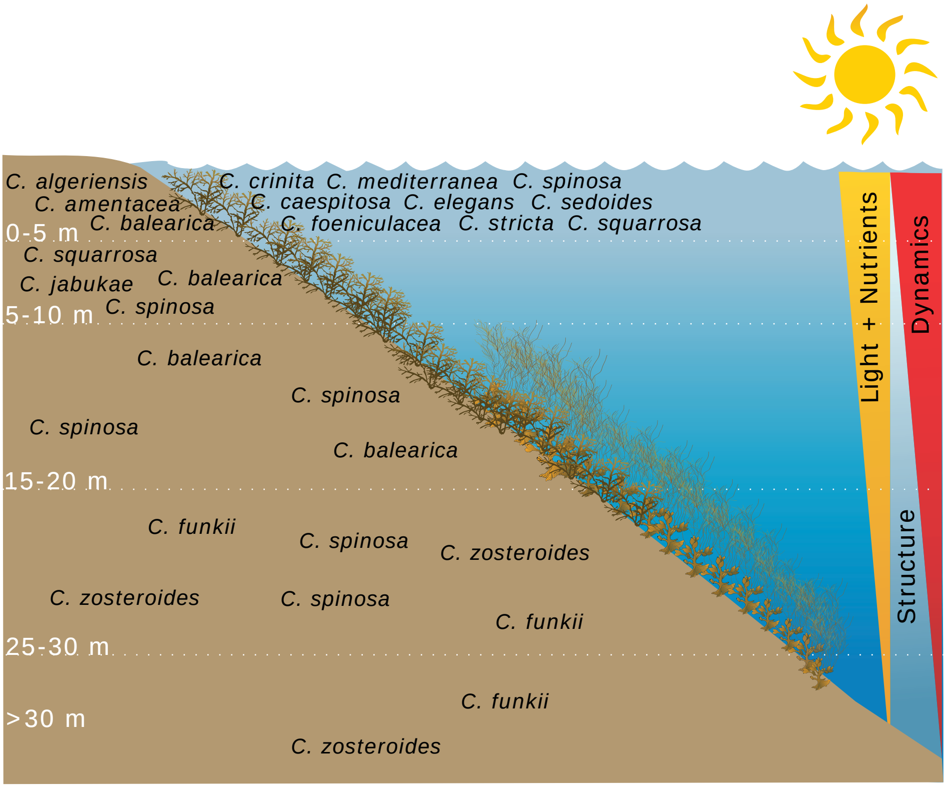


Figure 1.9: Vertical distribution of Mediterranean endemic *Cystoseira* species (Rodríguez-Prieto et al., 2013). Symbols from the IAN, University of Maryland, Center for Environmental Science (`ian.umces.edu/imagelibrary/`) and own design.

Box 2: *Cystoseira zosteroides* (C. Agardh, 1820) natural history

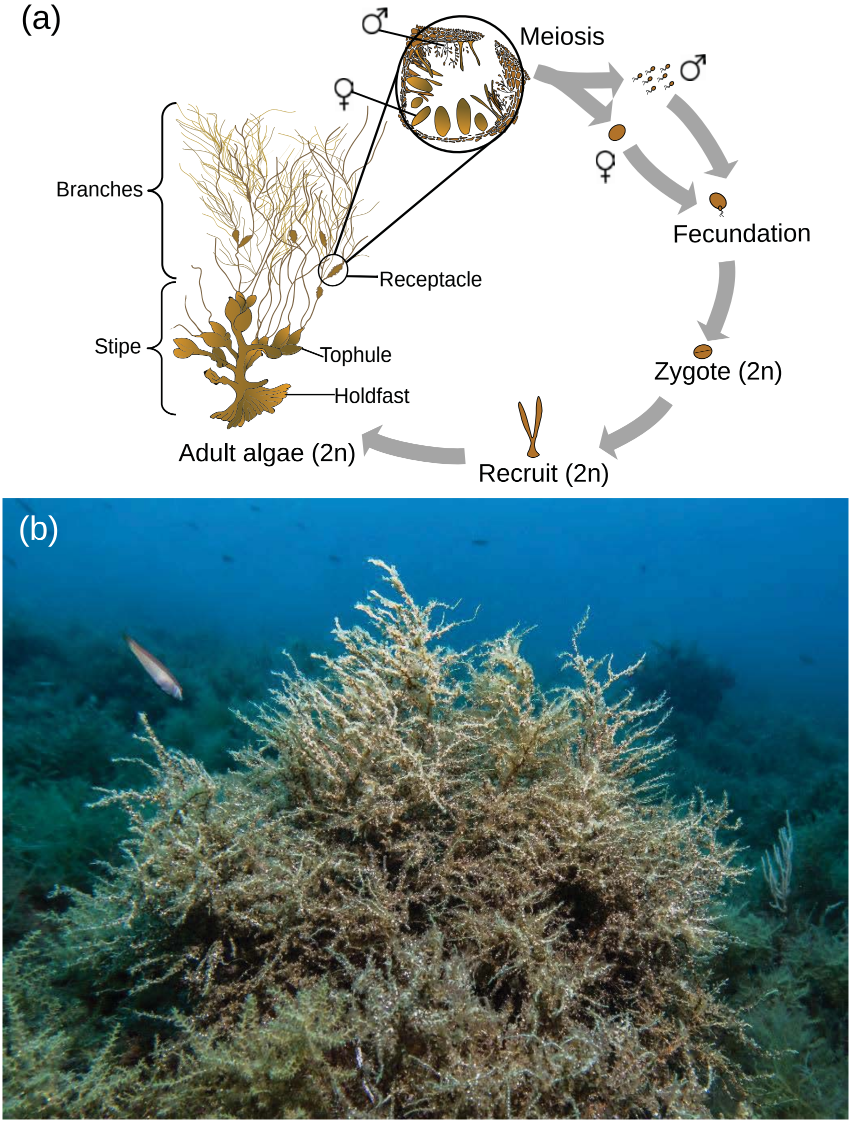
Distribution: *Cystoseira zosteroides* is a Mediterranean endemic species distributed throughout the western basin with the exception of the Alboran Sea and surrounding areas (Giaccone, 1973). This species usually thrive in rocky bottoms, between 15 to 50 m depth (depending on the water clarity), exposed to strong unidirectional currents and with light levels ranging between 1% and 0.3% of surface irradiance (Giaccone, 1973).

Morphology: *Cystoseira zosteroides* is a perennial species with an erect thallus monopodically organized. The holdfast is attached to the substratum by a basal disc, which lead to a perennial stipe with a maximum height of 20 cm (a and b). It is characterized by the presence of reservoir vesicles named tophules, which are smooth, spaced and lobulated, located at the top of the perennial axis (a). Annually primary branches are formed from the tophules and can be ramified into secondary, tertiary and quaternary branches (a). Primary branches led to reproductive structures named receptacles (sometimes secondary branches, but all close to the perennial axis), which are aggregations of specialized cavities named conceptacles, opened by a small ostiole, where male and female gametangia are developed (a).

Life cycle and reproduction: They have a diploid monophasic life cycle (a), so most of the cycle corresponds to a diploid sporophyte (2n), with the haploid phase only represented by the gametes (Rodríguez-Prieto et al., 2013). As in most of fucoids, meiosis results in gametes, which are liberated through the ostioles. Reproduction is oogamy (i.e. larger female gametes), with external fertilization. After the fertilization the free-living zygote fall into the bottom encapsulated in a protector membrane, followed by the segmentation of the zygote (Gómez-Garreta et al., 2001). Then, rhizoidal cells appear, enabling the fixation to the substrate after the loss of the protective membrane. Individuals can be either, monoecious or dioecious. The reproductive period spans from the end of May to the end of June (pers. obs.).

Population biology and ecology: Despite their perennial nature, this species shows a marked seasonal development. Branches are formed at the beginning of February, what coincides with the period of highest nitrate concentration values (Ballesteros, 1990). The deciduous branches keep growing until September-October, although the nitrate concentrations are usually low during this period. This is promoted by the mobilization of photosynthetates produced during the summer and stored in tophules (Ballesteros, 1990). This enables *C.*

zosteroides to inhabit in habitats where high irradiances do not coincide at the same time with nutrient availability. Their population structure and dynamics is highly variable among the few studied populations (Hereu et al. 2008a; Ballesteros et al. 2009; Navarro et al. 2011). In well preserved environments (such as Scandola Marine Reserve), *C. zosteroides* populations show high survival rates (close to 99%), with slow growth rates (0.5 cm/year), scarce recruitment rates and high longevities (more than 50 years; Ballesteros et al., 2009).



1.3.5 *Cystoseira* forests under siege

There is a global decline of habitat-forming organisms worldwide (Butchart et al. 2010; Ellis 2011). A recent review showed that 32% of kelp forest are in regression (Krumhansl et al., 2016), and fucales have considerably regressed in most Atlantic and Mediterranean coasts (Airoldi and Beck, 2007). *Cystoseira* species are not an exemption to this global decline, with already documented local extinctions during the last decades (Thibaut et al. 2005: Airoldi and Beck 2007). Consequently, five *Cystoseira* species (*C. amentacea*, *C. mediterranea*, *C. sedoides*, *C. spinosa* and *C. zosteroides*) are protected by the Berne Convention (Annex I 1979), and all the Mediterranean species, except *C. compressa*, have been listed under Annex II of the Barcelona convention (2010).

Nevertheless, the causes and consequences of *Cystoseira* decline are still poorly understood. Because they are usually late successional species, they are believed to be “slow” species (see Box 1), although still few quantitative evidences exist. Indeed, some studies in the NW Mediterranean suggest that the recovery of *Cystoseira* canopies takes longer than for fish assemblages (Thibaut et al. 2005; Sala et al. 2012). Hence, they are highly sensible to multiple human-induced disturbances such as water quality (Sales et al., 2011), coastal development (Ferrario et al., 2016), sea urchin grazing (Bulleri et al., 2002), fishing pressure (Sala et al., 1998) or lost fishing gears (references in Thibaut et al., 2005). Although, the most probable causes of their decline came through the interactive effects of local threats with global stressors (Strain et al., 2014). In regions where major disturbances are removed through a strong regulation of human activities and high water quality, macroalgae forest remain well preserved (Thibaut et al., 2014). Thus, there is evidence that *Cystoseira* are affected by multiple disturbances, and determining the main drivers of their disappearance is key for their conservation.

1.3.6 What do we know about *Cystoseira* populations ecology?

Despite the paramount role of *Cystoseira* species in the Mediterranean, it is surprising how limited is our comprehension about their population dynamics and life history. By searching in the ISI Web of Science *Cystoseira* related studies until the start of this thesis (2014), we found that most of them were pharmaceutical/chemical or biochemical (Figure 1.10a), probably because of their usage as a source of alginates. On the other hand, ecological studies are mostly based on community composition, with population-related remaining scant (Figure 1.10a). The first *Cystoseira* studies date back to the beginning of the past century (Figure 1.10b), which were basically taxonomic, carried out by Camille F. Sauvageau, a French phycologist. Although the number of studies in many other topics has progressively increased, the number of population studies remains very scant (Figure 1.10b).

The biases of *Cystoseira*-related studies are also common in macroalgae research (Schiel and Foster, 2006). Ecological studies based on macroalgae species have historically focused in their trophic and community dynamics, while population dynamics, demography and life history traits are often passed by without a glance (Schiel and Foster, 2006). The first demographic analysis of a fucoid population date back to early 80s (Gunnill, 1980). At that time, most of macroalgae population-related studies were focused on recruitment and settlement (Vadas et al., 1992). This was because the first step to understand the demographic schedule of a species, is to determine the reproductive patterns of populations (*sensu* Ang, 1991). These studies lead to the first demographic modelling analyses using life-table approaches, which didn't gained much popularity, because of the difficulty of determining the age of individuals and its poor predictive value in the demography of sessile organisms. Then, Ang Jr and De Wreede (1990) pioneered the use of matrix population models to explore the dynamics of macroalgae. Åberg (1992a,b) described the population dynamics of *Ascophyllum nodosum* at the west coast of Sweden and explored their response to winter ice disturbances, these studies mastered the use of matrix modelling in macroalgae. Aside from its general interest during early 80s to date, still very few studies have explored the life history of macroalgae or used population modelling tools

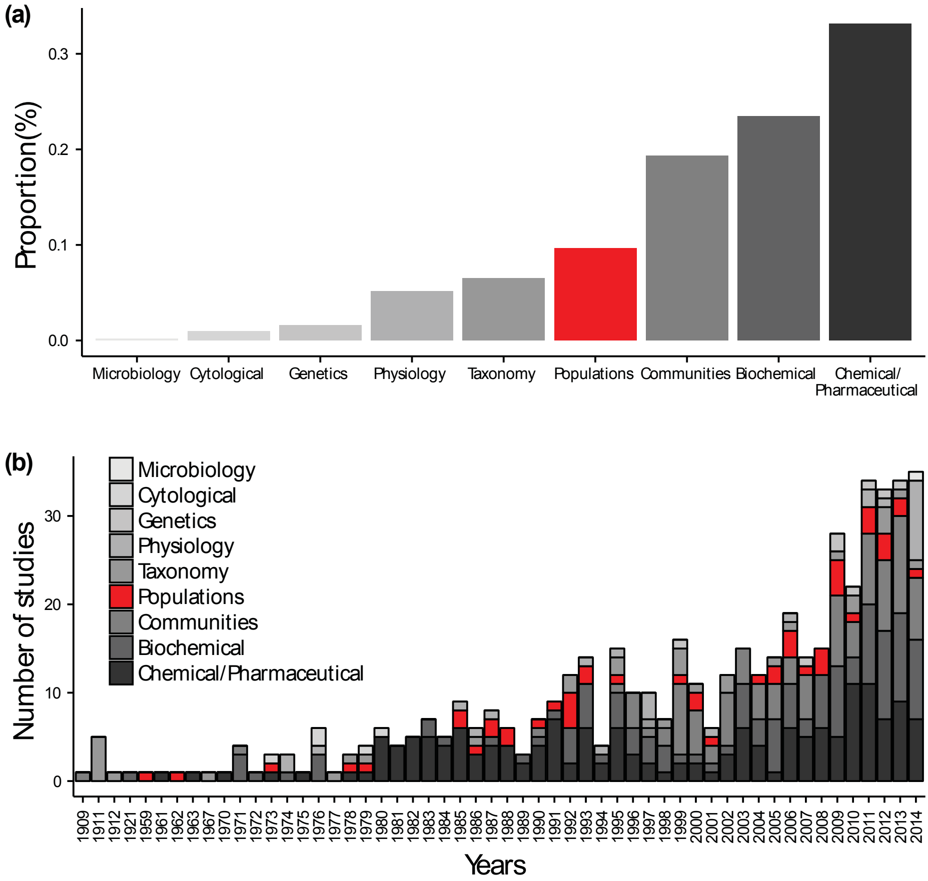


Figure 1.10: Number of studies about *Cystoseira* until 2014. (a) Proportion of all studies related to 9 categories considered here. (b) Number of *Cystoseira* related studies *vs* time, separated by 9 major topics. [Information from ISI Web of Science, accessed 20/04/2016].

to predict their future (Åberg, 1992b; Engelen and Santos, 2009; Engelen et al., 2005).

Indeed, the only predictive model about the dynamics of Mediterranean macroalgae, was formulated by Ballesteros (1991), but it was at the community level. According to Ballesteros' model, phytobenthic assemblages tend to occupy a specific region under a space defined by production-diversification and biomass-heterogeneity axes (for further details Ballesteros 1991). Because of the predictive variation of environmental factors with depth in benthic Mediterranean communities (Zabala and Ballesteros 1989; Garrabou et al. 2002), we would expect that deep-water communities should be highly structured, with slow population dynamics and with low resistance to disturbances (Zabala and Ballesteros 1989; Ballesteros 1991; Garrabou et al. 2002).

Other attempts to characterize macroalgal communities have focused into group macroalgae species accordingly to their morphological and/or functional traits (Littler 1979; Littler and Littler 1980; Steneck and Dethier 1994). Then, these groups were linked to abiotic factors, to predict community composition in a given environment, according to the levels of disturbances or/and productivity. The generalizations of these classifications often had a low predictive power when applied to other systems (e.g. Phillips et al. 1997; Hereu et al. 2008b). At the same time, it was noticed that life histories of macroalgae were highly determined by environmental conditions (Hereu et al., 2008b), bringing up the importance of studying the population ecology of these organisms.

Still, much research is focused on documenting the decline of *Cystoseira* populations (Thibaut et al., 2005), rather than exploring their population-level recovery mechanisms. Indeed, studies documenting the responses of macroalgae to disturbances are mostly based on kelp or fucoid species of intertidal environments (Dayton et al. 1992; Åberg 1992a; Engelen et al. 2005). Consequently, our understanding of macroalgae population studies is still skewed towards this systems, neglecting the existence of different life histories. Furthermore, the life history of macroalgae is framed under plant-related studies, without taking into account their considerable ecological and evolutionary differences. This may hinder the assessment of macroalgae conservation status, as well as the design of management or restoration tools.

1.4 Objectives

The objectives and research questions of this thesis are encapsulated in the disciplines of population ecology, life history theory, and conservation biology. Overall, this thesis aims to contribute to improving our comprehension of the population dynamics and life history of macroalgae. Our results will increase our knowledge about the dynamics of macroalgae, and will provide new tools to assess their conservation status and design effective management tools.

As a study system, we choose the deep-water macroalgae *Cystoseira zosteroides* for several reasons. First, the interest of this species relies on their adaptations to a very constraining environment such as deep-water rocky beds, what result in assemblages with a unique composition. It is an endemic species from the NW Mediterranean, but it is currently regressing (Thibaut et al., 2005). Yet, the causes and consequences of this decline are still poorly understood. In addition, as for many other *Cystoseira* species, almost nothing is known about the population dynamics of *C. zosteroides*, and their responses to disturbances are poorly understood.

Several monitoring programs targeted *C. zosteroides* populations in the NW Mediterranean, specifically in Cap de Creus Natural Park (2010-2012), Montgrí, Medes and Baix Ter Natural Park (2008-2010), and Columbretes Islands Marine Reserve (2010-2012). Furthermore, unfortunately in December 2008 there was an extraordinary storm that impacted several *C. zosteroides* populations that were monitored in the NW Mediterranean. Later on, in 2009 a ghost fishing net impacted another of our monitored populations in Medes Islands. This enabled us to quantify the impacts of a major disturbance in *C. zosteroides* populations (Navarro et al., 2011). All this information settled the basis for this thesis, and most of the questions that we aim to answer serendipitously arose from field observations during the monitoring programs.

This thesis is structured in four chapters which focus on different processes of the population dynamics and life history of *C. zosteroides.* The first two chapters (2 and 3) are focused on the recruitment and dispersal of *C. zosteroides*, while the lasts (4 and 5) are a more in-depth exploration of its life history, population dynamics, and disturbance responses. The chapters combine field studies (2, 4 and 5), field manipulative experiments (3), controlled experiments in the laboratory (5) and population modelling techniques (4 and 5). The specific objectives of each chapter are:

- Chapter 2: We study *C. zosteroides* population structure and dynamics under disturbed and non-disturbed conditions, with the main focus on understanding their recruitment dynamics. Particularly we test the hypothesis that recruitment in natural populations is subject to density-dependence (Ballesteros et al., 2009; Navarro et al., 2011).

- Chapter 3: Given the importance of recruitment for the recovery of threatened populations, observed in Chapter 2, in this chapter we experimentally determine the effective dispersal of *C. zosteroides* at small-scale. We also assess the survival of early stages during their first year, and test if it is subject to density-dependence by comparing it inside and outside the canopy. Finally, to put this in a broader context, we review all available scientific literature about brown macroalgae dispersal and compare it with our results.

- Chapter 4: Using demographic modelling tools we investigate the population dynamics of *C. zosteroides* and compare it with other brown algae and with several terrestrial plant species. With this, we aim to test the validity of a terrestrial life history framework in macroalgae, as well as to contextualize the life history strategy of *C. zosteroides*. Furthermore, given the increasing number of disturbances, and the need to understand their combined effects, we modelled the potential response of *C. zosteroides* populations to an increase in the recurrence of large, low-frequency disturbance events, such as storms; and local impacts, such as a lost fishing gear.

- Chapter 5: Complementary to the previous chapter, in this one we explore the population-level consequences of warming and its combined effect with the previous assessed physical disturbances (storms and ghost fishing nets). We experimentally assessed the impact of warming in their early life stages. These results were coupled with full life cycle demographic models to forecast the population consequences of warming, and how this will affect to their recovery dynamics and viability with the combined impact of other physical disturbances.

Chapter 2

Recruitment patterns in the Mediterranean deep-water alga *Cystoseria zosteroides*

2.1 Abstract

Although recruitment is considered an essential process regulating populations of many marine species, there is still a lack of knowledge about the ultimate factors that influence it. This is especially true for seaweeds, where population dynamics studies are also lacking. The main objective of this study was to investigate the main mechanisms driving the recruitment patterns of an emblematic deep-water alga in the NW Mediterranean, *Cystoseria zosteroides*, and its influence on their population dynamics. Five *C. zosteroides* populations were monitored annually at different sites along the coast of Spain by using permanent transects over three to four years. Some of these populations suffered mass mortality events from natural or anthropogenic disturbances, allowing us to study the influence of such events. Our findings agreed with the expected results for a long-lived species. Under low frequency of disturbances, *C. zosteroides* populations displayed few fluctuations over time given the longevity of the adults, and they were poorly influenced by the dynamics of early life stages because of negative density-dependent control of conspecifics. Moreover, disturbances had a great influence on population dynamics because the removal of adults decreased the effects of density-dependent processes, and enhanced the recruitment. Nonetheless, a high mortality was found for early life stages ($\sim$50% yr^{-1}), contrasting with the high survival of adults ($\sim$90% yr^{-1}). This study confirmed the slow population dynamics of these deep assemblages, demonstrated the influence of intraspecific interactions in the *C. zosteroides* population dynamics and highlighted their vulnerability to the increase of natural and human-induced disturbances.

2.2 Introduction

Knowledge about key demographic processes is required to understand and predict the response of populations to environmental change (Caswell, 2001; Smallegange and Coulson, 2013). Recruitment is an essential process regulating population abundance and dynamics (Caley et al., 1996; Hughes and Tanner, 2000; Wright and Steinberg, 2001). Nevertheless, factors controlling recruitment success are still poorly understood for most of marine organisms, mainly because of their small size during early life-history stages (Caley et al., 1996; Schiel and Foster, 2006). Given the cumulative stressors to which marine ecosystems are exposed (Jackson et al. 2001; Harley et al. 2006; Halpern et al. 2008), understanding the dynamics of the early life-history stages of species is of great importance to assess their resistance and recover capacity.

Long-lived organisms often play an important role as foundation species creating unique habitats, providing biomass, producing biogenic structures, and enhancing biodiversity (Jones et al., 1994). These organisms usually exhibit low recruitment rates and their populations are maintained by the long life span of the individuals (Åberg, 1992a). Thus, the slow dynamics of these species make them very vulnerable to the increase of perturbations. After disturbances their recovery rate depends on both the supply of propagules to the disturbed site and their ability to colonize upon arrival (Dayton et al., 1992; Hughes and Tanner, 2000; Reed et al., 2000). Macroalgae are important habitat-forming species in temperate rocky ecosystems (Schiel and Foster, 2006); however, there are still few studies about population structure and dynamics on algae (Ang Jr and De Wreede 1990; Åberg 1992a; Chapman 1993; Wright and Steinberg 2001), and this is especially true for deep-water algal species (Flores-Moya et al. 1993; Spalding et al. 2003, Graham et al. 2007, Leichter et al. 2008).

Over the last decades some efforts have been made to understand the drivers of early life stage dynamics in algae populations (reviewed in Vadas et al. 1992; Schiel and Foster 2006). From settlement until the juvenile stage, algae are likely to experience substantial mortality (Brawley and Johnson 1991; Dudgeon and Petraitis 2005; Schiel and Foster 2006). Density-dependent processes, such as intra- or interspecific competition, can play an important role in mediating settlement and recruitment success, with both positive and negative effects being possible (Reed 1990a; Reed et al. 1991; Ang and de Wreede 1992; Steen and Scrosati 2004). Furthermore, early survival can be influenced by density-independent factors, such as light (Reed et al., 1991), microhabitat characteristics (Brawley and Johnson 1991; Benedetti-Cecchi and Cinelli 1992), sedimentation (Airoldi and Cinelli 1997; Irving et al. 2009), and herbivory (Dudgeon and Petraitis 2005; Araújo et al. 2012). Nevertheless, most studies of algal recruitment have been based on laboratory or *in situ* manipulative experiments, and few have been based on the observation of natural perturbations (Dayton et al., 1992).

In the Mediterranean Sea, the brown algae of the genus *Cystoseira* are important habitat-forming species. Because of their perennial thallus and canopy, they structure several Mediterranean benthic communities, as they increase three-dimensional complexity, provide refuge and food for many species and harbour a high biodiversity of associated sessile invertebrates and algae (Ballesteros 1990; Ballesteros et al. 2009; Cheminée et al. 2013; Gianni et al. 2013). Nevertheless, some studies have shown evidence of *Cystoseira* assemblages decline over the last decades (Giaccone and Bruni 1973; Thibaut et al. 2005; Serio et al. 2006). Although the ultimate causes of this decline are not fully understood, several reasons have been proposed, including pollution (Sales et al., 2011), water turbidity (Cormaci and Furnari, 1999), plucking from the bottom by fishing nets (Feldmann, 1937; Thibaut et al., 2005), and episodic events, such as exceptional storms (Navarro et al., 2011).

Cystoseria zosteroides is an endemic and one of the most representative species of Mediterranean deep-water *Cystoseira* assemblages (Giaccone 1973; Ballesteros 1990; Ballesteros et al. 2009). Previous studies that focused on *C. zosteroides* populations showed that they were generally dominated by large organisms (which can be more than 50 years old), that displayed low recruitment and slow growth rates (0.5 cm/year) and they were highly vulnerable to perturbations (Hereu et al. 2008a; Ballesteros et al. 2009; Navarro et al. 2011). Given the limited information about the dynamics of this emblematic species and the paramount role of recruitment facing to increasing disturbances, the main objective of the present study was to assess the dynamics of the early life stages of this species and their influence on the population dynamics under disturbed and non-disturbed conditions.

2.3 Material and methods

2.3.1 Study sites

Our study was performed on five *C. zosteroides* populations located at four localities in the NW Mediterranean Sea: Medes Islands Marine Reserve (Catalunya, Spain); Montgrí coast (Catalunya, Spain); Cap de Creus Natural Park (Catalunya, Spain) and two populations in Columbretes Islands Marine Reserve (Valencia, Spain) (Figure 2.1, Table A.1).

2.3.2 Sampling design

Permanent transects were installed in the summer of 2008 at Montgrí Coast and Medes Islands where 209 and 181 individuals were mapped, respectively. In addition, in May 2010 permanent transects were installed in Cap de Creus and in Columbretes (I and II), mapping 175, 124, and 130 individuals, respectively. Transects were monitored yearly during 4 years in Montgrí and Medes and during 3 years in Columbretes and Cap de Creus. Each transect was 1 m wide and 3 to 10 m long, depending on the morphology of each sampling zone (see Table A.1 for details), and was partitioned using 50 x 50 cm square quadrats. Transects were placed between 20 and 28 m depth.

C. zosteroides is a perennial species with an erect thallus monopodically organized. The perennial part is the main axis (the stipe), and the tophules are reservoir vesicles which are situated at the top of stipe. In a previous study Ballesteros et al. (2009) determined that the main axis was the best morphometric measurement to carry out underwater for size structure studies. Thus, here we used the length of the main axis, as the distance between the apical part of the last tophule and the base of the axis insertion as the morphometric indicator. We did not measure the primary branches because of their deciduous character, they are formed annually at the beginning of spring (Ballesteros, 1990). At each quadrat, all individuals were mapped, and the length of main axis was measured using a caliper with

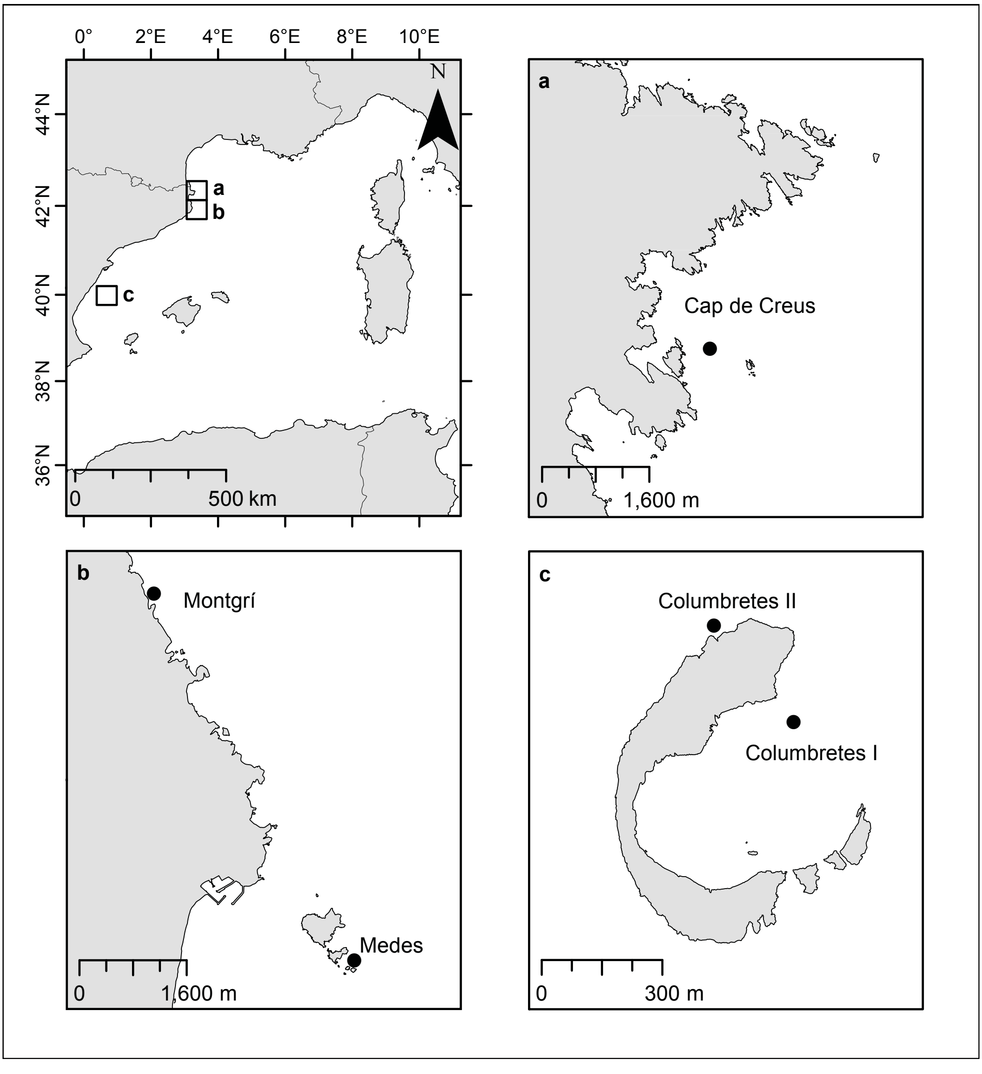


Figure 2.1: Location of the study sites in the NW Mediterranean Sea. a. Cap de Creus Natural Park (Catalunya, Spain). b. Medes Islands Marine Reserve and Montgrí coast (Catalunya, Spain). c. Columbretes Islands Marine Reserve (Valencia, Spain).

1 mm accuracy. Recruits were identified as the new individuals appearing in the quadrats. During the first year of the census, recruits were considered those individuals with main axis length equal to or less than 0.5 cm long, based on our observations during the subsequent years of the study. Sampling was always performed by SCUBA diving at the beginning of the summer, between July and August, when *C. zosteroides* attain the highest seasonal biomass (Ballesteros, 1990).

An unusual extreme easterly storm hit the Catalan coast (NW Mediterranean, Spain) on 26-27th December 2008 (Mateo and Garcia-Rubies, 2012). This event was the largest recorded in the area and probably the most virulent one during the last decades. The most detrimental effect of the storm was the substrate movement which abraded and buried severely many shallow and deep benthic communities (Hereu et al. 2012; Sanchez-Vidal et al. 2012; Pagès et al. 2013). Damage on species depended on the exposure to wave action (latitude, orientation and depth), the type of surrounding substrate (continuous rock, boulders, sand) and the morphological traits of the organisms. The most affected region was the northern part of the Catalan coast (Costa Brava, NW Mediterranean), with winds of 20 m/s, maximum wave heights of 14 m and wave periods of 14 s (Jiménez, 2012). Three of the studied *C. zosteroides* populations were situated in this northern region: Medes and Montgrí populations were observed to present 80% and 50% mortality respectively (Navarro et al., 2011); Cap de Creus population, situated at the northern part of the Catalan coast (Fig. 2.1), was probably also affected by the storm, though it was not previously reported. The virulence of the storm progressively diminished as it moved to the southern part of the Catalan coast, where the wave power was only one third of the recorded in the northernmost region (Jiménez, 2012). Thus, there is no evidence that it affected to Columbretes populations situated 200 miles far from Medes Islands one of the most affected location by the storm (Figure 2.1). In addition, in 2009 an abandoned fishing net was found affecting the Montgrí population by eroding the bottom and plucking several *C. zosteroides* stands.

2.3.3 Data analysis

Population size structure was calculated by pooling individuals in size classes of 1 cm. Differences among populations and years in size-frequency distribution were tested using the non-parametric two-sample Kolmogorov-Smirnov test (K-S test; Legendre and Legendre, 1998). Furthermore, Spearman's correlation (Wilcox, 2003) was calculated between the number of recruits and adults per quadrat, and the number of recruits per quadrat and the mean size (length) of individuals inside the quadrat.

Generalized Linear Models (GLMs) were applied to explore the effect of different factors on the vital rates (recruitment and survival). Here GLMs were used because they are mathematical extensions of linear models that do no force data into unnatural scales, and thereby they enable to test differences between factors or explore relation between variables without assuming a normal error distribution or non-constant variance (McCullagh and Nelder, 1989). A GLM with a binomial distribution and a logit link function was used to test the differences in survival (explanatory variable) between stages (adult/recruit), populations and years (factors). To explore the density-dependence we used a GLM with a negative binomial error distribution and a logit link function, because of the over-dispersion of the data. Number of recruits per quadrat was the explanatory variable, and factors were adult abundance per quadrat, site and years. For parameter selection in this case we have tested different models with all different factors, we tested the fitted-model factors using the Rao's score test in the survival test and the recruit model, because it is a good approximation when dealing with binomial or over-dispersed data (Lovison, 2005). All statistical analyses and the construction of the models was performed by using R software (R Development Core Team, 2011)

2.4 Results

2.4.1 Size distribution

A shift to small individuals was observed in Medes population when it was affected by the 2008 storm (two-sample Kolmogorov-Smirnov test, $P<0.001$,

Table A.2, Figure 2.2) and in Montgrí population after the effect of the fishing net in 2009 (two-sample Kolmogorov-Smirnov test, P<0.001, Table A.2, Figure 2.2). Conversely, the Columbretes I and Columbretes II populations were mostly dominated by large individuals without showing significant differences between consecutive years (Table A.2, Figure 2.2). In Cap de Creus a greater proportion of small-sized individuals were observed, with a lower abundance of large individuals and no significant differences between years (Table A.2, Figure 2.2).

2.4.2 Density of individuals through time

Medes and Montgrí populations showed a decrease in density after the storm, in 2009; however, both populations showed contrasting recruitment dynamics. The Medes population displayed a high increase in recruit density in the years following the storm. In contrast, the density in Montgrí population notably decreased but not reaching the low density values observed in Medes, with no recruitment pulse; however, after the additional impact of an abandoned fishing net, density continued decreasing and recruit density increased slightly in 2010. On the other hand, Columbretes I and Columbretes II populations showed different dynamics, with almost no recruitment and a high density of non-recruit individuals with mild fluctuations over the years of study. Finally, the Cap de Creus population displayed intermediate values of adult density, with mild fluctuations and relatively high recruit density (Figure 2.3). The number of recruits per quadrat was negatively correlated with the number of adults per quadrat (Spearman correlation: ρ= -0.52, N= 997, $P < 0.001$, Figure 2.4a), and with the mean size of individuals inside the quadrat (Spearman correlation: ρ= -0.82, N= 997, $P < 0.001$, Figure 2.4b). Mean size and adult density were positively correlated (Spearman correlation: ρ= 0.61, N= 997, $P < 0.001$). Thus, to test the influence of adult density on recruitment patterns across time and space, we applied a set of GLMs for the factors adult density, populations and years. The Rao's score test showed that the only significant factors were adult density ($S_1 = 249.25$, P<0.001) and population ($S_5 = 953.72$, P<0.001) but not years ($S_4 = 2.95$, P = 0.566), indicating a great variability on the recruitment between the studied places but not between overall years. The increase of adult

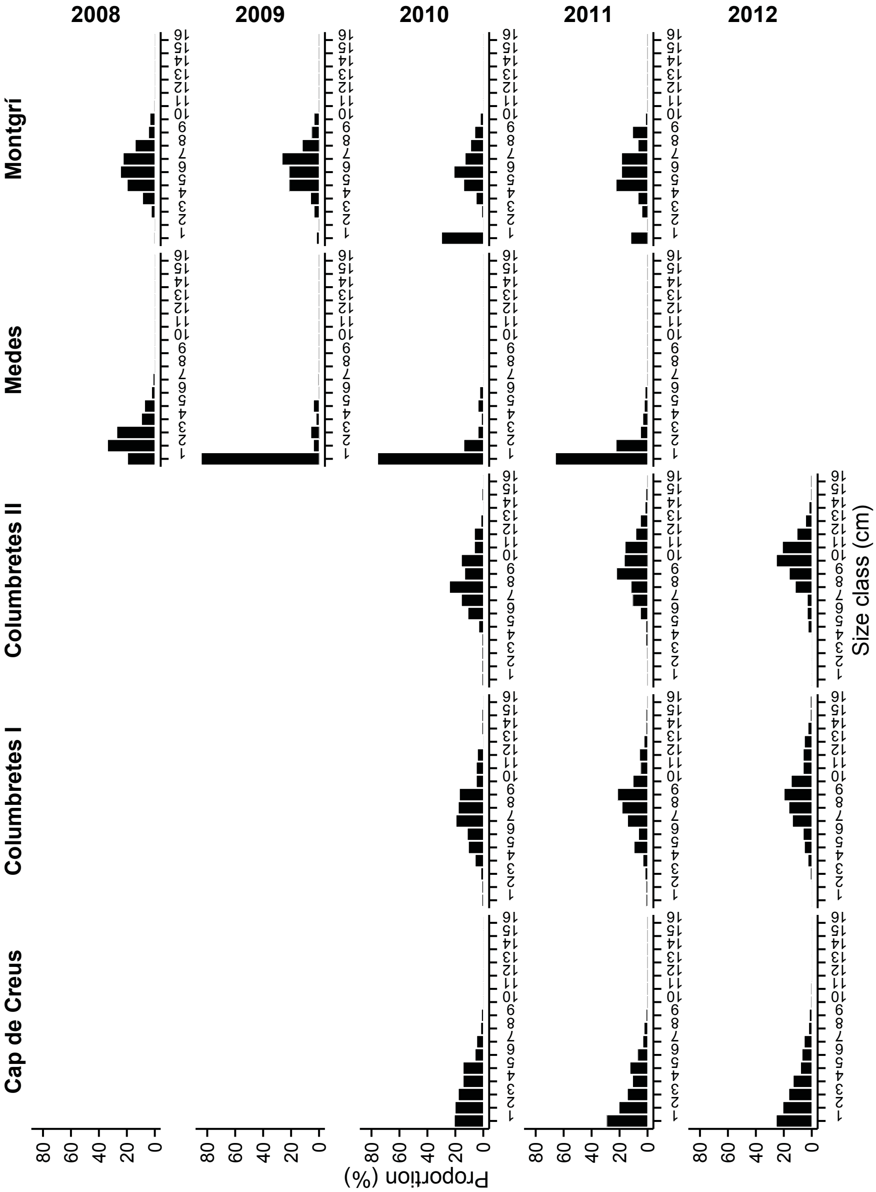


Figure 2.2: Temporal evolution of size-frequency distribution of the length of the main axis (cm) for each studied population.

density was negatively related to recruit abundance (b=-0.205, P<0.001).

2.4.3 Temporal and spatial survival of recruits and adults

Survival was significantly higher for adults than for recruits (S_1=10.49, P = 0.001), although a great variation between years (S_4 = 403.3, P < 0.001) and populations (S_5 = 96.52, P < 0.01) was observed. Mean adult survival (± standard error) was 75.25 ± 1.13% yr^{-1} for adults and for recruits was 45.34 ± 2.29% yr^{-1}, but removing the years which populations were affected by disturbances mean survival values increased to 90.02 ± 0.97% yr^{-1} for adults and 55.21 ± 3.10% yr^{-1} for recruits. During the year of the storm adult survival rates were lower than for other years; however, there were differences between impacted populations. Adult survival rates were lower in Medes (20.55 ± 3.35% yr^{-1}) in comparison to the Montgrí's population (56.25 ± 3.45% yr^{-1}). Both populations, Montgrí and Medes, showed an increase of the mean adult survival after the storm (Figure 2.5), but in Montgrí population this increase was less evident due to the impact of a fishing net (62.93 ± 4.50% yr^{-1}). In contrast, populations of Cap de Creus,

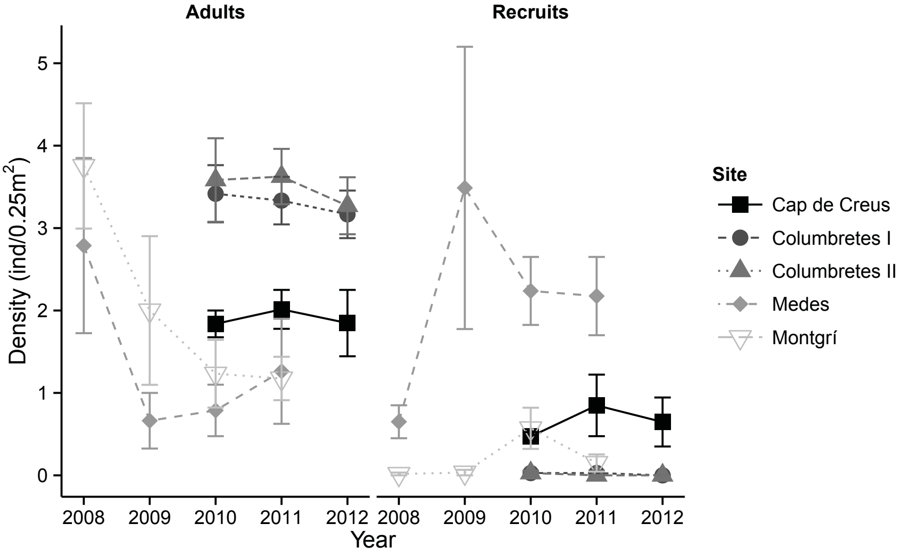


Figure 2.3: Density of recruits and adults (mean ± SE) over years for each studied population.

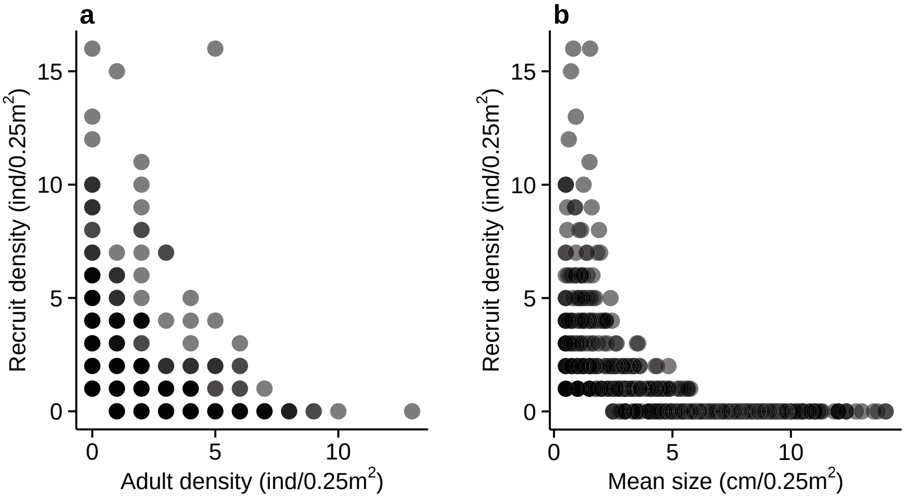


Figure 2.4: Correlation between; a. The number of recruits and the number of adults per quadrat (50x50 cm^2), b. The number of recruits and the mean size of individuals at each quadrat. Grey intensity of dots is proportional to the number of quadrats.

Columbretes I and II showed higher adult survival rates, close to 90% yr^{-1} during the study period (Figure 2.5). Recruit survival was highly variable among populations. In Cap de Creus and Medes, the populations with a higher abundance of recruits (Figure 2.3), recruits showed survival values close to 50% yr^{-1}. In Medes, an increase in the survival of recruits in the following years after the storm was observed, as occurred for adults (Figure 2.5). In contrast, recruit survival in Cap de Creus was very stable between the two years of study.

2.5 Discussion

Despite the paramount role of the genus *Cystoseira* as a habitat-forming species for Mediterranean communities, little attention has been paid to the population dynamics of these species and this is especially true for deep-water species such as *C. zosteroides* (but see Hereu et al. 2008a; Ballesteros et al. 2009; Navarro et al. 2011). To our knowledge this is the first study regarding the dynamics of the early life stages of this species. Our

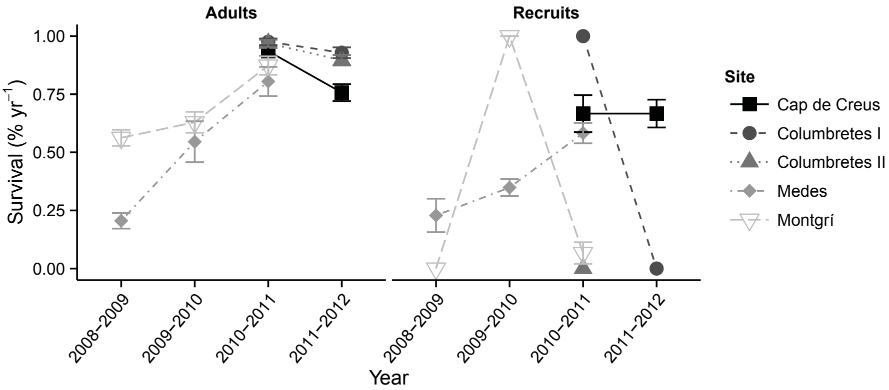


Figure 2.5: Survival rates (mean ± SE) of recruits and adults estimated at each studied population and year.

studied populations displayed more contrasting size-frequency distributions than previously reported (Hereu et al. 2008a; Ballesteros et al. 2009). It was observed a continuum of situations between populations dominated mainly by small individuals to others mainly dominated by large individuals with no recruits, showing a negative correlation between adult and recruit densities. Large disturbances seem to be the main factor explaining the contrasting dynamics of the studied populations. The impact of the storm in Medes and the fishing net in Montgrí caused an increase of recruitment rates, as a consequence of adult density reduction. In addition, Cap de Creus population, which was probably affected by the same storm, showed higher recruitment rates and lower adult density that the non-disturbed populations (Columbretes I and II). Hence, the contrasting size structure and recruitment dynamics suggested that this species was strongly influenced by density-driven responses, with adult canopy having a negative effect on the recruitment success.

Due to the scarcity of recruits in most of our studied populations general survival patterns were difficult to observe. However, our results suggest that, on average, recruit survival was lower than for adults. In non-disturbed populations adult survival was very close to 90% yr^{-1}, with similar values (98%yr^{-1}) that those reported by Ballesteros et al. (2009) for *C. zosteroides* populations from the Natural Reserve of Scandola (Corsica, France). Although, adult survival rates in disturbed populations were notably lower during the impacted year, they showed a tendency to increase from the disturbed year to the subsequent years. This suggests some delayed effects of these disturbances years after their impact. The investment of *C. zosteroides* in perennial thallus and reservoir vesicles (tophules) enhance their survival through years and enable them to persist during un-favourable seasons (Ballesteros, 1990). Recruits do not have perennial thallus and tophules, and then are probably more vulnerable than adults, which may explain their lower survival rates. This is commonly found in many perennial algal species, which display high mortality rates during their earlier stages (e.g. *Fucus disctichus*, Ang Jr and De Wreede 1990; *Ascophyllum nodosum*, Åberg 1992a; *Laminaria digitata*, Chapman 1993; *Delisea pulchra*, Wright and Steinberg 2001), and it is also observed in other long-lived invertebrate species (Garrabou et al. 2002, Linares et al. 2007, Teixidó et al. 2011, Kersting et al. 2014).

Previous authors observed no recruitment and low densities of small-sized individuals in *C. zosteroides* populations over long-time periods (Hereu et al. 2008a; Ballesteros et al. 2009). Although we found higher recruitment rates in some *C. zosteroides* populations than previous studies, they are still much lower than the reported for other shallow *Cystoseira* species such as *C. barbata* (Perkol-Finkel and Airoldi, 2010), *C. amantacea* and *C. compressa* (Mangialajo et al., 2012). This is probably because of the paucity of the deep-water algae. Nonetheless, comparisons are difficult because most of studies about *Cystoseira* recruitment are based on manipulative or laboratory experiments rather than in natural rates (Benedetti-Cecchi and Cinelli 1992; Irving et al. 2009; Perkol-Finkel and Airoldi 2010; Mangialajo et al. 2012; Perkol-Finkel et al. 2012). Previous studies suggested that *C. zosteroides* is subjected to recruitment pulses promoted by occasional disturbances (Hereu et al. 2008a; Ballesteros et al. 2009). Navarro et al. (2011) supported this hypothesis, as they found a pulse of recruitment after an extreme storm that caused mass mortality. Accordingly, we found that recruitment had little influence on the dynamic of populations under non-disturbed conditions. When adult densities decreased, due to mortality events (in our case), recruit densities increased rapidly. The recruit density was also negatively correlated with the mean size of individuals in the quadrat, as adult density was positively correlated with the mean size of individuals in the quadrat. This suggests that at high adult densities recruitment success is more limited due to intraspecific competition. In addition, due to the paucity of this species, the changes on the population dynamics remained several years after perturbations, as showed in Medes or in Cap de Creus two and four years after the storm (respectively).

Density-dependent processes influencing algal population structure have been very controversial, with studies showing both positive and negative effects (reviewd in Scrosati, 2005). On one hand, some reproductive individuals are needed to provide new recruits (Dudgeon et al., 2001). Furthermore, in some species it has been observed that adults can also provide protection against physical stress (Brawley and Johnson, 1991) or grazing (Jenkins et al., 1999). Nonetheless, our results indicate that density of adults may have a strong negative influence on recruitment success in *C. zosteroides* populations, probably through intraspecific competition. Some studies suggest that dense algae stands can inhibit the survival of newly settled individuals in different ways, including by sweeping them (Vadas et al., 1992) or limiting light availability (Reed, 1990a). For example, experiments carried out by Cervin et al. (2005) showed that the shade effect of large canopies lowered the growth rate of *Ascophyllum* and *Fucus* recruits and prevented the development of mature plants. Light availability has a strong influence on the *Cystoseria* recruits development (Irving et al., 2009). Thus light inhibition by adults could be a plausible explanation in our case, because of its scarcity under deep-water environments where *C. zosteroides* inhabits; however, data on light availability for the different study populations are not available.

Although most brown macroalgae species have a great reproductive potential, they greatest mortality occurs during microscopic stages (Schiel and Foster, 2006), so very few eggs become settlers, and even less become visible recruits (Ang, 1991; Chapman, 1995). Nevertheless, the processes influencing the step from spores to recruits are not fully understood for most of the algae species (the so called “black box”, Schiel and Foster, 2006). Many environmental factors have been suggested to influence recruitment patterns, such as sediment accumulation (Airoldi and Cinelli, 1997; Irving et al., 2009), predation by herbivores (Dudgeon and Petraitis 2005; Araújo et al. 2012), habitat characteristics (Brawley and Johnson 1991; Benedetti-Cecchi and Cinelli 1992) or competition with other species (Blanchette, 1996). *C. zosteroides* populations have been observed to present a high variability at small spatial scales (Hereu et al., 2008a; Navarro et al., 2011), so the differences observed between our populations suggests that environmental factors may also have influenced recruitment success. For example, the limited recruitment observed in the population of Montgrí after disturbances could be related to their isolation in relation to other *C. zosteroides* populations (Hereu et al., 2008a) and due to the limited dispersion ability of *Cystoseira* species (Gianni et al., 2013). Differences in the response to the disturbances may also be explained by the type of substrate. Medes population was more affected by the storm than Montgrí, as the bottom of the former is formed by boulders, which were easily displaced by the effect of waves, generating more free space available for recruits. In contrast, Montgrí population was less affected by the storm as it thrives above hard rocky bottom, being a more stable substrate. Therefore, although our results suggest that conspecific density is an important factor determining recruitment success, the variability of environmental factors observed among populations point to that recruitment is influenced by several factors acting together.

2.6 Conclusions

Overall, our findings suggested that the scarcity of recruits in previously studied *C. zosteroides* populations (Hereu et al. 2008a; Ballesteros et al. 2009) is related to post-settlement mortality and to negative effects of conspecifics on the recruitment success. During the absence of disturbances, *C. zosteroides* populations displayed few fluctuations over time because they are poorly influenced by the dynamic of early life stages, as observed in most long-lived plants (Åberg 1992a; Adler et al. 2014). This stability was produced by the survival and longevity of large individuals, which established a ceiling for the smaller individuals through intraspecific competition. Disturbances acting at local or regional scales could alter the population dynamics of the species, decreasing the effects of density-dependent processes through the elimination of large individuals and through enhancing recruitment rates (Åberg 1992a; Dayton et al. 1992; Engelen et al. 2005). These results suggested that these populations, similar to many other long-lived species, are conformed by intense pulses of recruitment, which produce cohorts that survive over long time periods (Hughes and Tanner 2000; Ballesteros et al. 2009). Nonetheless, the high natural mortality during early life stages (as observed in this study) may limit the recovery capacity of this species facing the increase of natural and human-related perturbations.

Because of the high endangerment of deep-water *Cystoseira* assemblages throughout the Mediterranean (Thibaut et al. 2005; Serio et al. 2006), more efforts should be addressed to better understand their dynamics and the key processes shaping their populations. Our results have provided important knowledge about the population ecology of *C. zosteroides*, which is poorly understood for most of the deep-water algae species. This information helps to improve the predictive power of demographic models about future trends of these populations. In addition, a better understanding of demographic parameters, such as recruitment dynamics, may improve conservation initiatives (Perkol-Finkel et al. 2012; Gianni et al. 2013); however, there is still a need for more studies focused on the reproduction, the ecology of microscopic early life stages, and the dispersal ability of deep-water algae, what still remains an open question.

2.7 Acknowledgments

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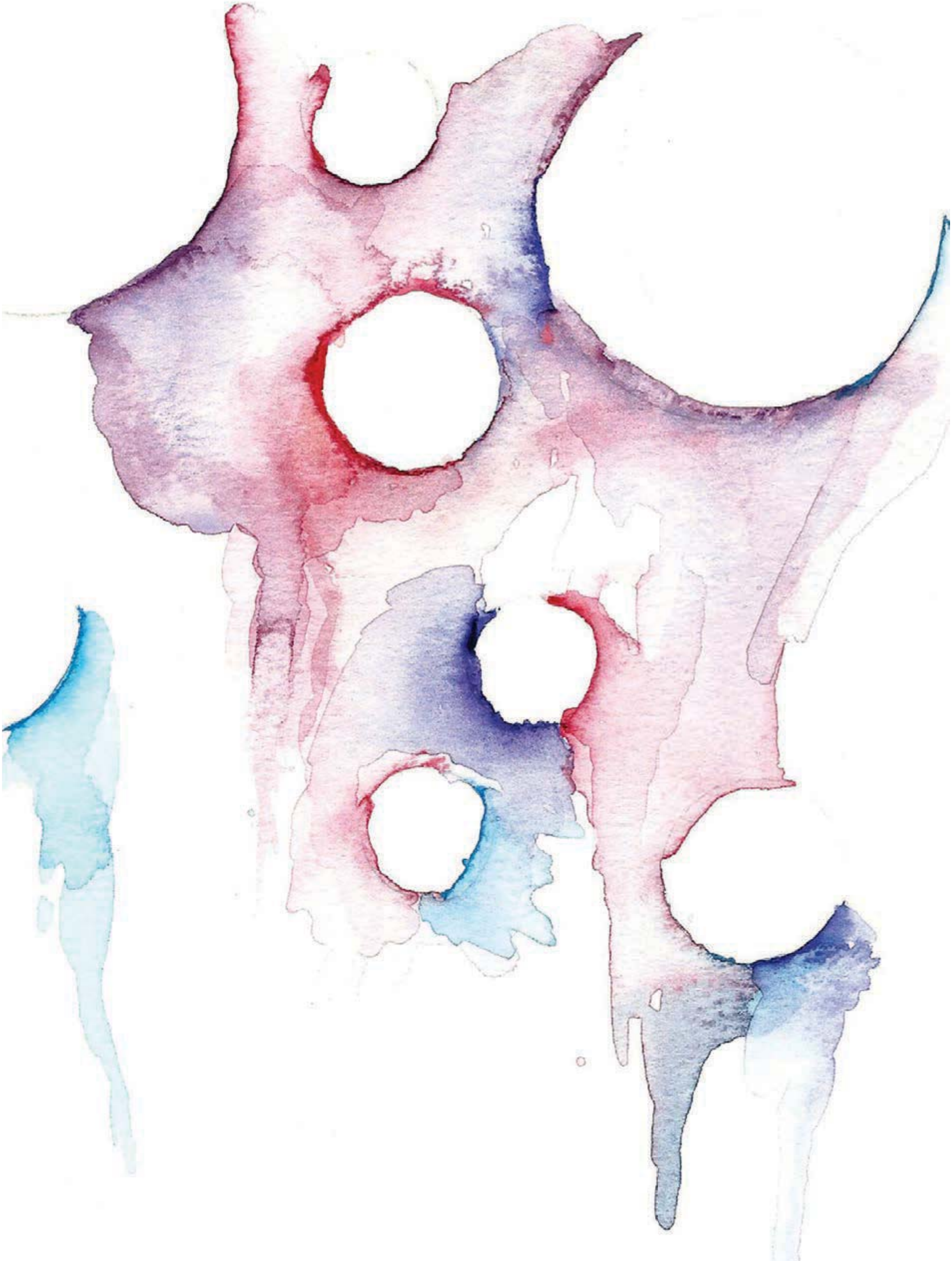

Chapter 3

Effective dispersal and density-dependence in mesophotic macroalgal forests

3.1 Abstract

Dispersal and recruitment are fundamental processes for population recovery following disturbances. While both are well understood for many habitat-forming species, they still remain relatively unknown for macroalgae species. Here we experimentally investigated the effective dispersal and the post-settlement survival of a mesophotic Mediterranean fucoid, *Cystoseira zosteroides*. In three isolated populations, four sets of recruitment collectors were placed at increasing distances (from 0 to 10 m) and different orientations (North, South, East and West). We found that dispersal was better fitted to a Weibull distribution, with an average of 6.43 m and a tail of 13.33 m, suggesting that *C. zosteroides* effective dispersal was restricted to populations' vicinity. During their first year of life survival was up to 50%, but it was lower underneath the adult canopy, suggesting a negative density-dependence. To put our results in a broader context we compared the effective dispersal of other fucoid and kelp species, which highlights the low dispersal ability of brown algae, in particular for fucoids, with an effective dispersal of few meters. Given the importance of recruitment for the persistence and recovery of populations after disturbances, these results underline the vulnerability of *C. zosteroides* and other fucoid species to escalating threats.

3.2 Introduction

The increase of human-induced disturbances has driven the loss of key habitat-forming organisms, such as terrestrial plants, corals, and algae, rendering their populations more fragmented, isolated and vulnerable to further sources of disturbance (Hughes et al. 1999; Nathan and Muller-Landau 2000; Wernberg et al. 2010; Lloret et al. 2012). In this context, dispersal and recruitment play a crucial role in maintaining the resilience and ensuring the long-term population stability of habitat-forming species (Hughes et al. 1999; Wernberg et al. 2010; Lloret et al. 2012). At the local scale, dispersal and successful recruitment determine population dynamics and structure, also driving their recovery after disturbances; while at larger scales these processes ensure population connectivity, gene flow and the colonization of new locations (Nathan and Muller-Landau 2000; Levin et al. 2003; Coulson et al. 2011). Thus, understanding the dispersal ability as well as recruitment dynamics of habitat-forming species is fundamental for appropriate management and restoration plans.

Nonetheless, the wealth of dispersal ecology studies in terrestrial plants (Clark et al. 1999; Bullock et al. 2006) contrasts with the relative poor mechanistic understanding about the dispersal of other habitat-forming species like macroalgae. Canopy-forming macroalgae, particularly large brown algae of the orders Laminariales (kelps) and Fucales (fucoids), play a key ecological role as habitat-forming species in temperate marine ecosystems (Schiel and Foster 2006; Cheminée et al. 2013; Mineur et al. 2015). Nevertheless, their dispersal is likely a very passive process, as it occurs through the release of non-motile (or with limited mobility) propagules (spores or zygotes) in the water column(Norton 1992; Chapman 1995). Consequently, macroalgae are located at the lowest end of the range of dispersal distances reported for the marine realm (Kinlan and Gaines 2003; Shanks et al. 2003; Kinlan et al. 2005). However, their early stages are microscopic and elusive to study, so their dispersal scales are still poorly understood.

In the Mediterranean Sea, *Cystoseira* spp. are late successional species which conform important forest-like assemblages from the intertidal to sublittoral zone (in some cases deeper than 50 m) (Ballesteros et al., 2009; Mineur et al., 2015). During the last decades, a widespread decline of these assemblages has been documented in many regions (Thibaut et al. 2005; Airoldi and Beck 2007). The multiple anthropogenic stressors to which they are exposed, as well as the paucity of their populations (in comparison to other algal species, see Chapter 4), have been argued to be the main consequences of their decline (Chapter 4; Gianni et al., 2013; Mineur et al., 2015). Nevertheless, little is known about their dispersal abilities and population dynamics. Hence, understanding the dispersal of these species may be crucial to predict their ability to respond to local and global stressors, as well as to assess the scale at which management strategies may be effective (Carr et al. 2003; Shanks et al. 2003; Durrant et al. 2014).

Cystoseira species are often assumed to present low dispersal distances (Gianni et al., 2013), given that their zygotes develop closely attached to the thallus of adult stands, although quantitative data regarding this topic are scant (Mangialajo et al., 2012). Genetic tools have brought the opportunity to unravel large-scale connectivity patterns, but there are very few genetic studies dealing with *Cystoseira* species (but see Susini et al. 2007; Buonomo et al. 2017). In contrast to genetic studies, classical experiments have provided important insights in short- to medium-distance dispersal for other algae and terrestrial plant species (Dudgeon et al., 2001; Gaylord et al., 2006). Thus, when no genetic tools are available experimental studies can provide useful information about effective dispersal of species (Gaylord et al., 2006).

Here we have experimentally determined the effective dispersal at small-scale of *Cystoseira zosteroides* C. Agradh (Fucales, Ocrophyta), a canopy-forming macroalga, which thrives in mesophotic Mediterranean rocky bottoms. Given previous studies on *Cystoseira* species, we expected that *C. zosteroides* would exhibit limited dispersal ability. Density-dependent survival of recruits was also expected, because of the intraspecific competition with adults (Chapter 2). Finally, in order to find general patterns among the main canopy-forming algae (kelps and fucoids), we reviewed all available scientific literature about macroalgal dispersal. The final aim of this study was to shed light on the dispersal and recruitment dynamics of macroalgae, discussing how important these outcomes are for conservation actions and habitat restoration plans.

3.3 Material and methods

3.3.1 Study species

Cystoseira zosteroides is one of the few species of this genus with a deep distribution, inhabiting bedrocks between 15 to 50 m depth. It is a long-lived species (about 50 years) and is very vulnerable to disturbances (Ballesteros, 1990; Ballesteros et al., 2009). *C. zosteroides* has a perennial thallus with reservoir vesicles (tophules) at the top. Tophules are formed annually and constitute the origin of primary branches, which emerge during the productive season (early spring) until late summer or early autumn (Ballesteros, 1990). *C. zosteroides* is considered monoecious with a diplontic and iteroparous life cycle. Gametes are enveloped on parenchymatic walls forming “small bags” named conceptacles, often aggregated into groups of 5 to 8 conceptacles on the basis of primary deciduous branches named receptacles. Their reproduction starts between late March and early April, and lasts until late June-early July (pers. obs.). Male gametes are released before females, which are fertilized externally but attached to the external part of the receptacles. There is no planktonic stage, zygotes are non-motile, and this species does not present clonal reproduction.

3.4 Study site and experimental design

Experiments were conducted at three well-developed *C. zosteroides* populations on Medes Islands Marine Reserve (Catalonia, Spain; Site 1: N 42°2′53.272” E 3°12′50.943”; Site 2: N 42°2′54.38”E 3°12′49.546”; Site 3: N 42°2′53.873” E 3°12′53.928”; Figure 3.1a). These populations were selected because they showed densities (2-4 individuals/0.25m^2), size structures (dominated by mature individuals) similar to other mature populations studied at the same location (Navarro et al., 2011) and with similar extension. All the three populations were found on isolated rocks surrounded by sand at a depth range of 20-28 m, separated between 50 and 100 meters from each other. For this reason, we assumed that the exchange of individuals among these populations and during the period of study was unlikely. The particular conditions of our studied populations enabled us to place four sets of recruitment collectors on the surrounding sandy bottom at a distance of 1, 2, 3, 4, 5, 7.5 and 10 m from the edge of the *C. zosteroides* populations, following a cross in N, E, S and W directions (Figure 3.1b). This resulted in a total of 31 collectors placed at each site. They were made by irregular calcareous tiles, with the same composition as the rocks of the area to simulate the natural recruitment substrate of this species (Figure 3.1c). Inside the populations, recruitment collectors were fixed to the bottom by epoxy putty; while outside the populations, we used a metal bar crossing a drilled hole in the center of the tile and nailed into the sand to immobilize them. To prevent collectors from being buried by sand, they were laid on a brick keeping them about 15 cm above the bottom (Figure 3.1c). The area of each tile was estimated by photography, comparing the number of pixels occupied by the tile with a reference surface of a known area with the software Photoshop version CS5.

Collectors were placed at Site 1 in February 2014 and at Sites 2 and 3 in February 2015, before the reproductive period of *C. zosteroides*. In preliminary studies, we had observed that the reproductive period of *C. zosteroides* spans from the beginning of April to late July and recruits were visually distinguishable in July. For this reason, we first estimated recruitment abundance at all collectors in July and again after 60, 120 and 365 days (Figure B.1), although we only considered here the annual survival.

3.4.1 Dispersal kernel fitting

Dispersal kernels represent the statistical distributions of dispersal distances in a population (Clobert et al., 2012), or the probability density functions describing the distribution of the post-dispersal locations from a source point. To estimate the dispersal ability of *C. zosteroides*, we fitted seven commonly used dispersal models (Tufto 1997; Clobert et al. 2012) to the field data: (i) Power Exponential, (ii) Negative Exponential, (iii) Gaussian, (iv) inverse Gaussian, (v) log-normal, (vi) Weibull and (vii) 2Dt (Table 3.1). The functions selected here are dispersal location kernels (Clobert et al., 2012), projected in a two-dimensional space, so they consider the

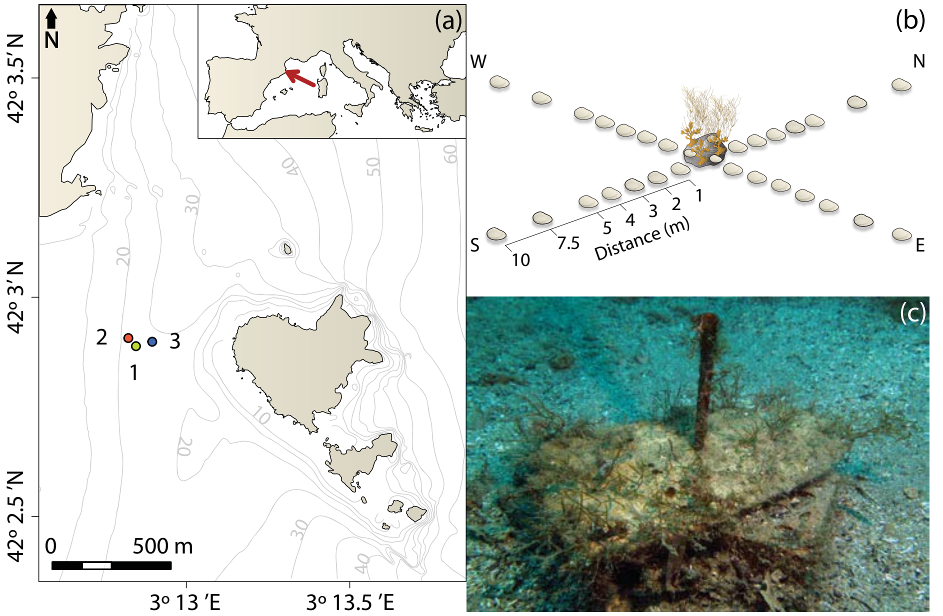

Figure 3.1: . (a). Map of the study area. Black dots represent the sites where the experiments were installed. Map was created using R software (R Development Core Team, 2014). The topographic base map (1:5.000), coastal limit and bathymetry are freely accessible through the Cartographic and Geologic Institute of Catalonia (`www.icgc.cat`) under Creative Commons Attribution License (CC BY 4.0). (b). Scheme of the experimental design, with a population of *C. zosteroides* surrounded by sand and collectors placed at different distances (from 0 to 10 m). (c). Picture of a recruit collector after one year of being installed.

increasing area of the circle when increasing distance from source (Tufto 1997; Clobert et al. 2012). Then, we fitted the empirical models expressed in term of counts rather than densities (Bullock and Clarke, 2000; Skarpaas et al., 2004). We multiplied these functions by another fitted parameter Q, which represents the number of propagules dispersed, and A, the total area sampled by the recruit collectors at distance r. Then, the recruit counts (c) were estimated as:

$$c = A \times Q \times f(r) \tag{3.1}$$

The respective parameters of the dispersal kernels in Table 3.1 and Q were fitted to our data by a maximum-likelihood approach using the function “mle2” in the package “bbmle”(Bolker and R Development Core

Table 3.1: Dispersal functions fitted to the four cardinal directions (N,S, W and E) obtained from (Tufto 1997; Clobert et al. 2012). In all cases, a is a scale parameter, b is a shape parameter and r is the radial distance from the recruit source.

Function	**Equation**
2Dt	$\frac{(b-1)}{\pi a^2}(1+\frac{r^2}{a^2})$
Negative Exponential	$\frac{1}{2\pi a^2}\exp(-\frac{r}{a})$
Power Exponential	$\frac{1b}{2\pi a^2\Gamma(\frac{2}{b})}\exp(-\frac{r^b}{a^b})$
Gaussian	$\frac{1}{\pi a^2}\exp(-\frac{r^2}{a^2})$
Inverse Gaussian	$\frac{\sqrt{b}}{\sqrt{8\pi^3 r^2}}\exp(-\frac{b(r-a)^2}{2a^2 r})$
Log-normal	$\frac{1}{(2\pi)^{\frac{2}{3}} b r^2}\exp(-\frac{\log(\frac{r}{a})^2}{2b^2})$
Weibull	$\frac{b}{2\pi a^b}\exp(-(\frac{r}{a})^2)$

Team, 2016) of the R software (R Development Core Team, 2014). To evaluate goodness-of-fit of the models and select the best-fitted models to our data we used the Akaike Information Criterion (AIC; Akaike, 1974):

$$AIC_i = -2\log L_i + 2V_i \tag{3.2}$$

where L_i is the maximum likelihood for the candidate model i, is determined by adjusting the V_i free parameters in such a way as to maximize the probability that the candidate model has generated the observed data. To select the best candidate model, we also computed the differences in AIC, with respect to the best one (with the minimum AIC value; Burnham and Anderson 2002):

$$\Delta AIC_i = AIC_i - min(AIC) \tag{3.3}$$

Finally, to estimate the probability that the selected model was the best one given our data and the set of candidate models, we estimated the Akaike weights $w_i(AIC)$(Burnham and Anderson, 2002):

$$w_i(AIC) = \frac{\exp(-\frac{1}{2}\Delta(AIC_i))}{\sum_{k=1}^{k}(-\frac{1}{2}\Delta(AIC_k))} \tag{3.4}$$

where K is the number of fitted models.

Dispersal studies usually assume that dispersal is isotropic (i.e. is the same in all directions; Bullock et al. 2017), so they usually don't split the data according to the direction (but see Bullock and Clarke 2000). Here, before making such assumption, we fitted individual models, splitting the data by direction and site, to account for a potential anisotropy. Once we obtained the best-fitted models, we selected the most frequent best-fitting function across sites and directions (Bullock et al., 2017). This enabled us to find the most representative model for our studied populations at a fine scale. In addition, dispersal distances estimated from different models depend much on the selected models and on the dispersal system (Hirsch et al., 2012). For this reason, to accurately predict and compare the dispersal distances between sites and directions we selected the best-fitting function as a general description of our system. Finally, at each direction and site, we estimated the mean and the tail of the dispersal distance as the median and the 95th percentile distances (m) respectively, formulated as the integral of the best-fitted dispersal kernel (Clobert et al., 2012).

3.4.2 Recruit survival

Recruit survival was estimated as the difference in the abundance between censuses, considering the starting point when recruits were visible to the unaided eye (July), which almost coincides with the end of the reproductive season. We tested for differences in yearly recruit survival inside and outside the *C. zosteroides* canopy. To compensate for the unbalanced design of the number of recruitment plates inside and outside the canopy we only used the dispersed individuals at the 0 m and 1 m distance. We fitted a generalized linear model (GLM), with a binomial error distribution and a logit link function. To test the null hypothesis of no effect of the scaling parameter in both models (sites and inside/outside canopy respectively) we used a Wald χ^2 test. All analyses were performed using the package "lme4" (Bates et al., 2014) of the R software (R Development Core Team, 2014). The normality of residuals and overall model performance was visually inspected by observing the residual distributions and quantile–quantile plots (Figures B.2 and B.3).

3.4.3 Comparative study

Dispersal estimates for macroalgal species were obtained from two published reviews (Kinlan and Gaines, 2003; Shanks et al., 2003) and our own literature survey. A total of 42 studies were found but only direct or experimental estimates measuring the settlement or recruitment at different distances from a propagule source were used, leading a total 17 studies (Table B.4). We did not consider genetic studies in order to avoid potential biases due to different methodologies and approaches. Due to the scarcity of data for several macroalgae orders, comparisons were performed only between the orders Laminariales and Fucales, which were the ones with the highest number of studies (7 and 10, respectively). We tested the differences between mean dispersal distances of the macroalgae orders using a Mann-Whitney test given the non-normal distributed data (Mann and Whitney, 1947), over 1000 bootstrapped samples of the data, to deal with the reduced sample abundance.

3.5 Results

3.5.1 Dispersal distances

A total of 727, 791 and 494 recruits were found at Sites 1, 2 and 3 respectively during the first census. Although some recruit collectors yielded no recruits, when considering all together, recruits were found at all distances and directions. For the Site 3 the directions North and East contained very low recruit densities, so we did not fit the individual distributions to avoid misleading dispersal estimates. At all sites, 95% of recruits fell within 7.5 m from the algal stand edge. The zygote abundance at 0 m was very variable.

The shape of the fitted dispersal kernels for all *C. zosteroides* populations and directions suggests a leptokurtic distribution, with many propagules deposited close to the source and a rapid decline in recruit densities with increasing distances (Figure 3.2). Of the 7 functions used to model the dispersal with distance, the Weibull function generally provided the best fit for all four cardinal directions and the three sites (Tables B.2 and B.3). The median and 95th quantile dispersal distances calculated from the Weibull dispersal kernels were very similar among sites and directions (Table 3.2). The 50th quantile of the dispersion values ranged from 4.65 to 8.31 m, with a mean value of 6.43 m, while the 95th quantile values ranged from 8.61 to 16.39 m, with a mean value of 13.33 m.

Table 3.2: Fitted maximum-likelihood Weibull function values of $\log(Q)$, a and b, for each site and orientation. All the parameters showed were significantly different to 0, see Table B.1. In addition, the median and 95th dispersal distances (in meters) are presented as measures of the average dispersal distance and its tail, respectively.

Site	**Orientation**	**Log(Q)**	***a***	***b***	**Median**	**95th**
1	E	10.654	8.563	1.802	6.99	15.76
1	N	11.816	5.520	2.121	4.65	9.27
1	W	10.398	8.560	1.756	6.95	16.00
1	S	12.480	9.936	2.046	8.31	16.99
2	E	11.680	8.954	1.817	7.32	16.39
2	N	12.016	8.162	1.897	6.73	14.58
2	W	12.020	8.208	1.904	6.77	14.62
2	S	11.576	5.751	1.940	4.76	10.14
3	E	-	-	-	-	-
3	N	-	-	-	-	-
3	W	11.870	6.229	1.948	5.16	10.95
3	S	5.469	7.050	5.491	6.59	8.61

3.5.2 First year of survival and density-dependence

In agreement with our expectations, we found that recruit survival was significantly lower inside than outside the *C. zosteroides* canopy ($\chi^2 = 107.35$, df = 1, P < 0.01; Figure 3.3), indicating negative density-dependence on post-settlement survival. There were significant differences in the survival between sites ($\chi^2 = 8.37$, df = 2, P < 0.05) and the interaction between factors was significant ($\chi^2 = 6.12$, df = 2, P < 0.05).

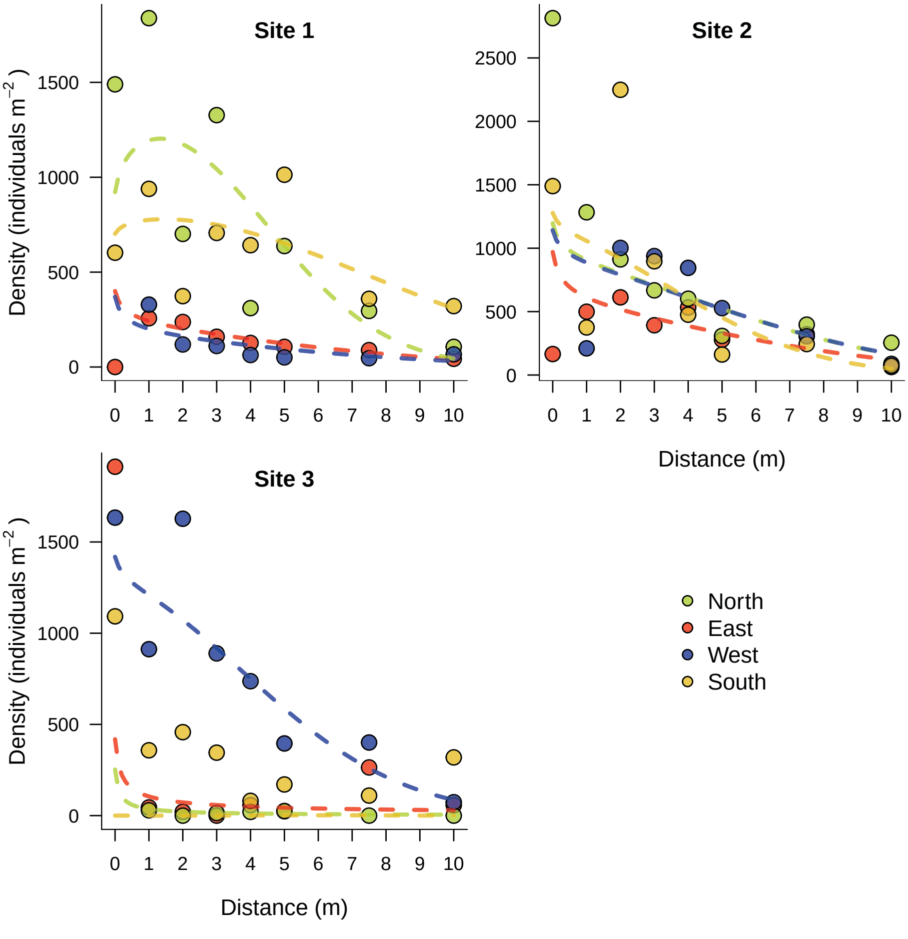

Figure 3.2: Density of *Cystoseira zosteroides* recruits at different distances from the source population. Lines indicate the predictions from Weibull model fit to the data. Panels contain the different studied sites, and colors indicate the different orientations.

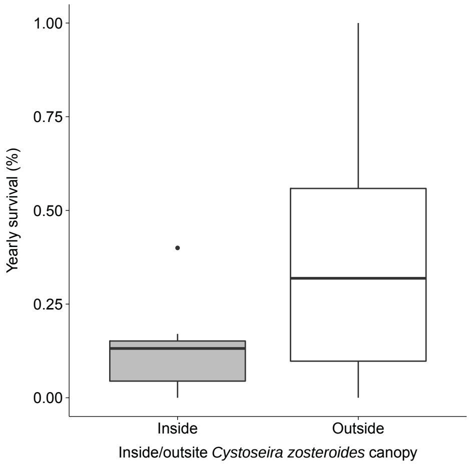

Figure 3.3: Annual recruit survival inside and outside the canopy. Boxes represent the interquartile range, the horizontal line represents the median, vertical line represents the upper and lower extreme values.

3.5.3 Comparative analyses

Mean dispersal distance was significantly higher (Mann-Whitney test, W = 18593000, $P < 0.01$; Figure 3.4) for kelps ($\widetilde{X}$= 105.50 m, SE = 71.18) than for fucoids ($\widetilde{X}$ = 1.58 m, SE = 0.63). The maximum reported mean dispersal distance was for *Pterygophora californica*, dispersing as far as 500 m (Table B.4). However, another kelp species displayed the lowest dispersal distance reported, *Undaria pinnatifida* dispersing only 17.5 cm. On the other hand, the maximum mean dispersal reported for a fucoid species was for *C. zosteroides* (this study, 6.4 m) and *Sargassum horneri* (6.3 m), while *C. compressa* and *C. amantacea* showed the lowest, only 20 cm (Table B.4).

3.6 Discussion

Few studies have examined effective dispersal for macroalgal species at small spatial scales (Dudgeon et al., 2001; Kinlan and Gaines, 2003) and very few have fitted dispersal kernels (Gaylord et al., 2006). Our results suggest that *C. zosteroides* effective recruitment is limited to the vicinity of their populations. However, comparing it with other fucoid species *C. zosteroides* shows the highest mean dispersal reported, according to our

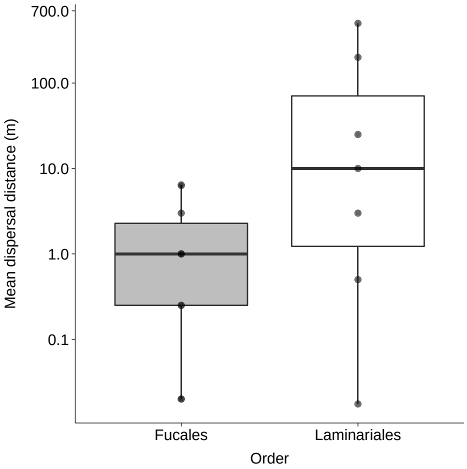

Figure 3.4: Mean dispersal distances of the different Fucoid and Laminariales species. Note that y-axis is on log10 scale. Boxes represent the interquartile range, the horizontal line represents the median, vertical line represents the upper and lower extreme values. Black dots are the observed values.

literature survey. In addition, their recruits displayed a high mortality (>50%), which contrasts with the high survival of adults (more than 90%; Ballesteros et al. 2009). Our findings reveal that first life stages are critical for the demography of this species and that the recovery capacity of their populations after disturbances may also be very limited.

Cystoseira zosteroides recruit abundance declined with distance from the source populations, slowly at the beginning, and more rapidly beyond the first meters following a Weibull distribution. This dispersal kernel is commonly used in terrestrial ecology (Clark et al., 1999; Clobert et al., 2012), although is usually outperformed by other fat-tailed kernels such as the log-normal or the 2Dt (Clobert et al., 2012). Estimates of the median and the tail of the dispersal were very similar among sites and directions. Given the similar environmental conditions between the populations analysed here, we could expect higher dispersal distance in some directions, what would indicate anisotropy in the movement of propagules. However, the influence of major currents is difficult to detect with experimental approaches which usually underestimate large-scale dispersal (Nathan and Muller-Landau, 2000). Moreover, *C. zosteroides* populations usually inhabit at rocky bottoms deeper than 20 m, with less hydrodynamics than in shallower waters

(Garrabou et al., 2002). Genetic studies (Coleman et al., 2011b) or experimental designs including larger scales and *in situ* physical measures (Gaylord et al., 2006) are more likely to be able to detect directionality on the dispersal patterns. Furthermore, dispersal patterns were quite variable among the three studied sites, supporting the notion that dispersal variability tends to be large at very small spatial scales (Dudgeon et al., 2001).

There was a low recruit survival, what is not surprising given that many macroalgal (Vadas et al. 1992; Wright and Steinberg 2001;Dudgeon and Petraitis 2005) and other sessile and long-lived species, both marine (Hughes and Tanner 2000; Doropoulos et al. 2016) and terrestrial (Forbis and Doak, 2004), experience high mortality rates during their early stages. It is worth noting that here we missed a substantial proportion of this mortality, which happens during settlement phases when individuals are not visually distinguishable (Schiel and Foster, 2006). Although recruitment was high inside *C. zosteroides* populations, recruit survival was lower than outside the adult canopy, suggesting a negative density-dependence on the recruit survival of this species (Chapter 2; Ballesteros et al., 2009; Navarro et al., 2011). These results explain the recruitment limitation observed in natural *C. zosteroides* populations (Chapter 2; Ballesteros et al., 2009) and likely apply to many other subtidal macroalgae (Schiel and Foster, 2006).

The low survival of recruits and the low dispersal ability of *C. zosteroides* highlights their poor ability to respond to disturbances (Ballesteros et al., 2009; Navarro et al., 2011). Here we show that their effective dispersal is very limited, supporting the high genetic differentiation observed among other *Cystoseira* species (Susini et al. 2007; Buonomo et al. 2017). Given the stable environments to which *C. zosteroides* is adapted (Ballesteros, 1990), it is not surprising that they show a relatively low dispersal capacity. However, rare successful migration events through drifting thallus or dislocated fertile algae have been suggested to enhance connectivity among distant *Cystoseira* populations (Buonomo et al., 2017). Yet, given the low survival of recruits, these rare events may not be enough to recover entire extensions of *C. zosteroides* populations at short-time scales, what may arguably explain local extinctions (Chapter 4; Thibaut et al. 2005, 2015).

To date, the scarcity of information about the biology and ecology of macroalgal species has hindered our understanding of their life history strategies (but see Chapter 4; Steneck and Dethier, 1994). As previously suggested (Kinlan and Gaines, 2003; Schiel and Foster, 2006), our comparative analysis illustrates that canopy-forming algae display very limited dispersal abilities, with fucoids showing the lowest values. Nonetheless, algae have come from very different evolutionary paths (Keeling, 2013), so even closely related taxons, like fucoids and kelps, can display very different biological and ecological traits. Fucoid species usually have external fertilization, followed by the production of passive and non-motile (or with limited mobility) zygotes, which have negative buoyancy (Norton 1992; Chapman 1995; Schiel and Foster 2006). As a consequence, zygotes spend little time in the water column, settling to the bottom shortly after reproduction, limiting their dispersal to few meters from the source. In contrast, the primary dispersal propagules of kelps are spores, which tend to have smaller sizes than fucoid zygotes (Chapman, 1995; Schiel and Foster, 2006). For this reason, our literature survey shows that kelps have the potential to disperse at scales of hundreds of meters (e.g. 200 m, *Laminaria hyperborean*; 500 m, *Pterygophora californica*), while fucoids tend to disperse at the scale of few meters or less (e.g. 3 m, *Sargassum muticum*; 20 cm, *Cystoseira compressa*).

Divergences among kelp and fucoid scales of dispersal are likely to translate into the different population and recovery dynamics, so they must be incorporated in management strategies. Some kelp forests can be very ephemeral; they can be eliminated within a year but are able to recover as quickly as they have disappeared (Tegner et al. 1997; Steneck et al. 2002). This may result from a combination of high productivity and great dispersal ability of some species. Thus, a better understanding of local hydrodynamics, together with the protection of potential “source” populations, may be sufficient to enhance the recovery of macroalgal forests constituted by large dispersing species (such as some kelps; Coleman et al. 2011b). In contrast, the recovery of fucoid populations can take decades (Underwood 1999; Jenkins et al. 2004), probably due to their poor dispersal ability and the paucity of some of their populations (Gianni et al., 2013; Mineur et al., 2015). This suggest that fucoid populations and those of low dispersing kelps may be favoured by further protection, and their recovery may need restoration actions. Adult transplantation (Campbell et al., 2014) or seeding techniques (Hernández-Carmona et al., 2000) are promising lines of management that need further exploration and optimization. Despite this potential differences, it is worth noting that the scarcity of data presented here prevents to generalize our results. Indeed, fucoid species can be also very dynamic while kelps can be very long-lived (Schiel and Foster, 2006). Thus, digging deeper on their life histories will probably help to improve management actions.

There are key differences between the biology of kelps and fucoids dispersive phases that could obscure our results. Fucoid zygotes are diploid (2n) and are capable of becoming adult individuals, while spores are haploid (1n) which become gametophytes (1n) and need to find another gametophyte of the opposite sex for fertilization success (Schiel and Foster, 2006). Furthermore, the progressive dilution of spores in the water column as they disperse reduces fertilization success, so early studies suggested that kelps had also a very restricted dispersal (Schiel and Foster 1986; Santelices 1990). However, kelps have evolved several mechanisms to compensate for dilution effects associated with longer distance dispersal and extend the distance over which spore dispersal leads to successful colonization (e.g. Reed et al., 1997). This would explain the observation of significant spore settlement in kelps at the scale of kilometres from the nearest populations (Gaylord et al., 2006). This is further supported by experimental and genetic studies (Durrant et al., 2014). For instance, a previous study, investigating the genetic connectivity of two kelps (*Ecklonia radiata* and *Phyllospora comosa*) and one fucoid species (*Hormosira banksii*), found that kelp species did not show any clear patterns of genetic structuring with geographic distance, while connectivity was low and with a strong pattern of isolation by distance for the fucoid species (Coleman et al., 2011a).

Our results illustrate that the effective dispersal of the deep-water macroalga *C. zosteroides*, as well as for other fucoid species, is limited to few meters. The patchiness and uncertainty of the spatial distribution of *C. zosteroides* populations across the Mediterranean, coupled with the lack of genetic markers, prevented us from studying the connectivity of this species at a wider scale. Furthermore, their deep distribution challenges more exhaustive studies that could help us to clear up the underlying dispersal mechanisms. Nevertheless, our approach enabled us to have an estimate of their short-scale dispersal, as well as their survival during their macroscopic recruit stage. Although it was the fucoid species with the highest propagule dispersal ability, their effective dispersal is still much lower than for other marine species (Kinlan and Gaines, 2003; Kinlan et al., 2005). This suggests that the loss of this species in fragmented areas would be hardly reversible even by restoration actions, as limited dispersal would not allow recolonization at short time scales. We also showed here that the scales of dispersal in macroalgae can variate from few meters to kilometres, so making generalizations from local studies can mislead conservation strategies. Previous studies already noted the different patterns of dispersal between fucoids and kelps (Schiel and Foster, 2006), but to our knowledge this study is the first quantitative assessment. Overall, we emphasize that given the increase in local and global stressors, ensuring the connectivity of macroalgal populations should be a conservation priority in temperate seas, but it requires a clear comprehension of dispersal mechanisms and life history of targeted species.

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Chapter 4

Unraveling the natural dynamics and resilience patterns of underwater Mediterranean forests

4.1 Abstract

Despite being among the most important habitat-forming organisms in temperate seas almost nothing is known about the demography of many algal species. This limits our ability to understand the effects of global and local stressors and to predict future trends under the ongoing environmental change, which in turn hinders conservation actions. Here we investigated the natural population dynamics and resilience patterns of a deep-water brown and canopy-forming macroalga, *Cystoseira zosteroides*. We used density-dependent and stochastic matrix models to estimate its basic life history and compare it with other relevant habitat-forming marine (brown algae) and terrestrial (plants) species. We also evaluated the consequences of increasing the disturbances caused by storms and the impact of lost fishing gear, and their interaction, on *C. zosteroides* population dynamics. The population dynamics of *C. zosteroides* showed similar patterns to terrestrial long-lived species such as shrubs and trees, with high survival due to their investment in structural biomass. Our data and models suggest that this species is able to buffer mortality pulses by increasing the number of recruits (and probably recruit survival) due to the new space liberated and, therefore, lower intraspecific competition. Nevertheless, when storm disturbances were more frequent than once every 50 years, their populations collapsed, and this effect worsened when several stressors acted simultaneously. Our results improve our understanding about the demography of algal forests, and highlight the fact that increases in local and global stressors may erode the resilience of macroalgae, resulting in a loss of structural complexity in the benthic communities of temperate seas.

4.2 Introduction

Understanding the relative importance of the demographic processes shaping populations is essential to answer relevant ecological and evolutionary questions (Metcalf and Pavard, 2007) as well as to predict the response of species to ongoing environmental change (Smallegange and Coulson, 2013). Despite the increased availability of demographic data (e.g. Salguero-Gómez et al., 2015), important biases exist towards studying terrestrial organisms over marine ones (Linares et al., 2007; Ripley and Caswell, 2008). This is particularly worrying because coastal ecosystems are among the most ecologically and socio-economically significant on the planet (Costanza et al., 1997; Harley et al., 2006).

Canopy-forming macroalgae, particularly large brown algae of the orders Laminariales, Tilopteridales and Fucales, have been historically considered the trees of marine temperate rocky ecosystems (Darwin, 1972; Dayton, 1985). Brown canopy-forming macroalgae are usually late successional species (with some exceptions, e.g. *Pleurophycus gardneri*; Spalding et al., 2003), which increase the structural complexity where they live, providing shelter and food for many associated species (Steneck et al. 2002; Schiel and Foster 2006). Macroalgae can form important forests that extend from the littoral fringe (0 m depth) to deeper than 100 m (Ballesteros 1990; Graham et al. 2007; Marzinelli et al. 2015), and make important contributions to the benthic carbon cycle (Duarte and Cebrian, 1996). Hence, the loss and/or reduction of canopy-forming algae has negative effects on the composition, structure and biodiversity of benthic assemblages (Steneck et al. 2002; Ling et al. 2014), which may impact the entire ecosystem functioning (Lotze et al. 2006; Worm et al. 2006; Smale et al. 2013).

Large natural disturbances (such as storms) play a major role in structuring macroalgal populations and communities (Steneck et al. 2002; Schiel and Foster 2006). These episodes can produce high mortality pulses, and macroalgal species are sometimes able to offset them through recruitment pulses (e.g. Dayton et al., 1992). Yet, the loss of dominant macroalgae can cause changes on the structure and dynamics of the community that can last for many years (Underwood 1999; Jenkins et al. 2004). Regrettably, human-induced perturbations (e.g. fishing, lost fishing gear, eutrophication) are increasing in coastal areas (Halpern et al., 2008) and climate change is expected to augment the frequency and intensity of storms in marine environments (Harley et al., 2006; IPCC, 2007; Kerr, 2011). The increase in the recurrence of these stressors, or their combined effect, is suggested to be the main driver of canopy algae decline in temperate seas worldwide (Airoldi and Beck 2007; Strain et al. 2014; Mineur et al. 2015). However, a sound understanding of the demographic processes shaping macroalgal populations is still lacking, and this limits our ability to predict how they respond to disturbances (Åberg, 1992a,b; Engelen et al., 2005; Svensson et al., 2009), and hinders conservation actions (Perkol-Finkel et al. 2012; Campbell et al. 2014). Thus, understanding the population dynamics of these habitat-forming organisms and determining the population-level effects of changing disturbance regimes are crucial for preservation of the biodiversity that they harbor.

Due to the complexity of algal life cycles and the logistical challenges of tagging individuals in marine environments, demographic studies have generally neglected macroalgae (Schiel and Foster, 2006). Most of the published studies are focused on easily accessible species located in shallow waters (Ang Jr and De Wreede, 1990; Engel et al., 2001, ; but see Spalding et al. 2003; Ballesteros et al. 2009), and assume that they are representative of other algal species. Nevertheless, community complexity (i.e. diversity and species richness) increases with depth, and community dynamics (i.e. productivity, turnover and growth rates) decrease (e.g. Ballesteros, 1990; Garrabou et al., 2002), as a consequence of the stabilization of physical restricting factors and light limitation. In addition, very few authors have modeled the effects of environmental stochasticity (but see Engelen et al. 2005; Engelen and Santos 2009; Svensson et al. 2009) and, to our knowledge, none has included density-dependence, despite the fact that these are important drivers of algal population dynamics (Schiel and Foster, 2006).

In this study we used high-resolution demographic data to build stochastic and density-dependent matrix models (Tuljapurkar and Caswell 1996; Caswell 2001) to study the population dynamics of a brown macroalga. As a model species we used the Mediterranean alga *Cystoseira zosteroides* C. Agradh (Fucales, Ocrophyta; Figure 4.1). This species is among the most long-lived macroalgae described to date, with a lifespan of up to 50 years (Ballesteros et al., 2009), and its populations are subjected to negative density-dependence on recruitment (i.e. the negative effect of conspecifics on the recruitment success; Chapter 2). Recent studies suggest that the distribution of *Cystoseira* spp. in the Mediterranean is shrinking mainly due to human disturbances including pollution (Sales et al., 2011), water turbidity (Cormaci and Furnari, 1999), plucking from the bottom by lost fishing gear (Thibaut et al., 2005), and episodic events, such as storms (Navarro et al., 2011). Thus, the aims of this study were threefold: (i) to estimate basic life history traits of *C. zosteroides*; (ii) to evaluate the relative importance of the different demographic processes and compare this species with other brown algae and terrestrial plants from the published literature; and (iii) to test its potential response to an increase in the recurrence of large, low-frequency disturbance events (storms) and of local impacts (lost fishing gear).

4.3 Material and Methods

4.3.1 Study species

In the Mediterranean Sea, *Cystoseira* species are the dominant macroalgae of the rocky benthic communities (Gianni et al., 2013). *Cystoseira zosteroides* inhabits rocky substrates from 15 to 50 m depth, with light levels ranging from 1% to 0.3% of surface irradiance (Giaccone and Bruni, 1973). Its distribution spans the western Mediterranean Sea with the exception of the Alboran Sea (Giaccone, 1973); however, recent studies suggest that its distribution is shrinking mainly due to human disturbances (Thibaut et al., 2005, and references therein). This species is characterized by a perennial thallus with reservoir vesicles (tophules) at the top, from which primary branches originate. The deciduous parts of the algae (branches) develop on early spring and they fall at early-autumn, so branches are renewed annually. Ballesteros et al. (2009) found that the length of the main axis (the perennial part) was the best morphological measure for the evaluation of the population structure independently of the season. Its populations are dominated by large individuals (Figure 4.1), with low growth (0.5 cm yr^{-1})

and high survival rates (Ballesteros et al. 2009; Navarro et al. 2011; Chapter 2). *Cystoseira zosteroides* is monoecious with a diplontic and iteroparous life history. Gametes are formed in reproductive structures (receptacles) located at the base of the primary branches, which start to develop at the beginning of spring and early summer to late August (Ballesteros, 1990).

Figure 4.1: Picture of a *Cystoseira zosteroides* canopy (Columbretes Islands, Spain). Photo credit: Diego K. Kersting.

4.3.2 Demographic data

The demographic parameters used in this study are based on the data obtained in a previous study (Chapter 2), in which five *C. zosteroides* populations were monitored at different localities across the NW Mediterranean (two populations of Columbretes Islands, one of the Montgrí coast, one of Medes Islands and one of Cap de Creus), during 3-4 years (2008-2011 in Montgrí and Medes, and 2010-2012 in Columbretes and Cap de Creus).

For the model parametrization, survival and growth rates were obtained from the two undisturbed populations (Columbretes I 39°53′53.2”N 0°41′19.1”E and Columbretes II 39°54′02.2”N 0°41′11.6”E) located at the Columbretes Islands Marine Reserve (Castelló, Spain). Demographic data of survival and growth was obtained from annual monitoring of individuals from three permanent transects installed at two populations of Columbretes Islands, between 20 to 28 m depth in May 2010. Each transect was 1 m wide and 3 m long and was partitioned using 50 x 50 cm^2 quadrats. Sampling was always performed by scuba diving, and transects were visited annually by the same experienced observers from 2010 to 2012 at the beginning of the summer (between July and August), when this species attains its highest seasonal biomass (Ballesteros 1990). A total of 254 *C. zosteroides* individuals were marked (124 in Columbretes I and 130 in Columbretes II). The size of individuals represents the maximum length of the primary perennial axis, which was measured using a caliper with 1 mm accuracy as the distance between the apical part of the axis and the base of the axis insertion of the last tophule (Ballesteros et al., 2009). For each individual, growth (difference in size between two consecutive censuses) and mortality (disappearance of individuals between censuses) was recorded. Recruits were identified as new individuals appearing in the quadrats.

To build the density-dependent recruitment model (see below and Appendix C) we had to pool the data across all study locations (Columbretes but also Montgrí coast, Medes Islands and Cap de Creus; see Chapter 2) to increase the statistical power in the estimation of recruitment at various population densities.

Given the difficulty of measuring fertility and fecundity rates *in situ*, these parameters were obtained by sampling 84 stands (outside the transect) covering a wide size range (1-12.5 cm) during the reproductive season (between early spring and summer). For these individuals, length was measured *in situ* and three secondary branches of each individual were sampled to determine the presence or absence of receptacles in the laboratory. Fertility (the probability of an individual being reproductive) was estimated as the relation between reproductive status and size with a binomial regression (see Table C.1). Fecundity, the number of seedlings produced per adult, was calculated as the product of fertility and the number of recruits per capita observed in the two study locations (the number of recruits at time t+1 divided by the number of reproductive individuals at time t; Caswell 2001).

4.3.3 Model formulation

Using these demographic parameters a size-based matrix model was constructed with five size classes, based on the changes in survival and fertility versus size (Morris and Doak, 2002). The first class represented recruits, individuals between 0.5 and 1 cm height, which are not fertile. The remaining classes were: 1-4 cm, 4-6 cm, 6-10 cm and >10 cm in height (Figure C.1 in Appendix C). All these classes were chosen to have a significant number of individuals at each class. Transition matrices were built from the data obtained from each population and time interval (see Appendix C). Transition probabilities between stages involved the following vital rates: s_i, the survival probability of an individual of class i; g_i, the probability that an individual of class i grows to class $i{+}1$; and f_i, the reproductive output of individuals of class i. This species does not show clonal reproduction nor has a seed bank, so these were not included in the transition matrices.

Previous studies demonstrated that recruitment in *C. zosteroides* populations is subject to negative density-dependent processes (Chapter 2). Consequently, density-dependence was modeled using a generalized linear model (GLM) with Poisson error distribution and a log link function using the data from Chapter 2. Recruits per adult was negatively correlated with adult density (b=-2.06, p<0.001; Table C.2). Density-dependence was incorporated into the matrix $A_{N(t)}$ by setting f_i as a function of the density of adults:

$$recruits/adult = 2.66 - 2.06 \times [adult \quad density] \tag{4.1}$$

In equation 4.1 when adult density was 0, recruitment was considered null, assuming that the arrival of new individuals from other populations was negligible, as *Cystoseira* species present low dispersal abilities (Chapter 3; Mangialajo et al. 2012; Gianni et al. 2013).

We constructed a mean matrix population model for *C. zosteroides* by averaging the survival and growth rates from the two populations studied. Further, for comparative analyses between our studied populations and other brown algal species (see below), we used our density-dependent model after setting it to stationarity ($\lambda = 1$) by iterating densities and changing the reproductive part of the matrix.

4.3.4 Model outputs

For each population and time interval, and for the mean density-dependent model, we calculated several demographic outputs. Yearly population growth rates were approximated as the dominant eigenvalue (λ) of each population and yearly matrix. The damping ratio (ρ), which is a measure of how quickly a population converges to its stable stage distribution, was also estimated (Caswell, 2001). Finally, we estimated life expectancy based on the fundamental matrix approach described in Caswell (2001).

In order to compare the life history traits of *C. zosteroides* with other brown algae and terrestrial plants we compiled demographic data from the public database COMPADRE (Salguero-Gómez et al., 2015) and for brown algae we added three species from the literature (see Appendix C). For terrestrial plants we compiled matrices with the same size range as for algae matrices (see Appendix C), in order to avoid biases in the elasticity values of the different demographic processes due to matrix size (Salguero-Gómez and Casper, 2010). Only matrices coming from non-disturbed populations were used, and for species studied at more than one site or year, mean matrices were used, thus obtaining only one matrix per species. This selection criterion excluded many annual and shrub species, yet we decided to follow it because analysing all groups of terrestrial plants was out of the scope of this study.

Once we obtained the transition matrix from different species we calculated the matrix element elasticity values, which indicate how much a matrix element contributes to λ relative to the contribution of other elements (de Kroon et al. 1986; Caswell 2001). These were estimated for each species and for the density-dependent matrix $A_{N(t)}$ of *C. zosteroides* at demographic equilibrium (λ=1). Each matrix element was identified as a component of growth, survival or fecundity following Silvertown et al. (1992). As the elasticities of all matrix elements sum to unity, we were able to standardize the values obtained from different species and compare them in a triangular ordination plot (Silvertown et al., 1992, 1993). Elasticity matrix elements representing progression to the following size classes were assigned to growth, elements that represented stasis or shrinkage to smaller stages were assigned to survival, and elements representing reproduction were assigned to fecundity. As matrices came from different species, special care was taken to correctly assign elasticity values to the component for each species.

4.3.5 Population projection and disturbance responses

To study the dynamics of a population after a disturbance we started by projecting a population for 50 years, multiplying the density-dependent transition matrix $A_{N(t)}$ by a population vector n_t:

$$n_t + 1_{=} A_{N(t)} \times n_t \tag{4.2}$$

Where the initial n_t vector was taken from the stable stage obtained from the $A_{N(t)}$ at equilibrium, and the matrix $A_{N(t)}$ was updated at each time step to reflect density-dependence in recruitment.

As explained in the introduction 5.2, large and low frequency disturbances such as storms play a major role in the structure of macroalgal populations but these species are usually able to cope with these high mortalities through recruitment pulses. Nevertheless, climate change is expected to increase the frequency and intensity of storms and modeling is an essential tool to predict the future consequences of increasing disturbance frequency at population level. The consequences of the impact of a single large storm have been previously studied for this species and these data have been used to model this disturbance (Navarro et al., 2011). To do this, at year 10 of our simulations, we introduced the effect of a storm that caused 80 % mortality in *C. zosteroides* populations (Navarro et al., 2011).

We evaluated the effect of increasing annual frequency of extreme storms (from 0 to yearly) by simulating different disturbance frequencies (each causing 80% mortality) and projecting the population for up to 100 years with 10,000 iterations. In addition, to explore the consequences of the interaction between local and global stressors on the resilience of *C. zosteroides* populations, we used a similar approximation as Mandle et al. (2015) by simulating different frequencies of mortalities caused by fishing nets (estimated to be about 60% of mortality in a previous study; see Chapter 2) and storms. We did not model other disturbances, such as herbivory or competition, because their effect on this species are negligible (Vergés et al., 2009) or unknown. For each storm recurrence, we calculated the mean matrix components elasticities (which were summed as contributions to survival, growth and fecundity) and the quasi-extinction probability, by using an extinction threshold of 10% of the initial population density. Quasi-extinction probability is the likelihood of a population falling below a minimum number of individuals below which the population is likely to be critically and immediately imperiled (Morris and Doak, 2002). Furthermore, the mean lambda (λ) of the projected population was calculated for each simulation, as well as for the different combinations of disturbances.

All statistical analyses were performed using R software (R Development Core Team, 2014). For the demographic estimates we used the package "popbio" (Stubben and Milligan, 2007).

4.4 Results

4.4.1 *C. zosteroides* life history

Our results show an increase in survival rates with size-classes, ranging from 50 to 92% (Appendix C), with a mean survival rate of 85%. Transitions between stages were quite constant (between 25 to 40%) but lower for the largest size class. We also observed an increase in the probability of being fertile with size (Appendix C).

Deterministic growth rates (λ) for the two *C. zosteroides* populations varied between years and populations, ranging between 0.93 to 1 (Table 4.1). The damping ratio for all years and populations was between 1.12 and 1.33 (Table 4.1), indicating a very slow convergence to the stable structure. In accordance to the variability of lambda values, life span was also very variable. While the population of Columbretes II showed values between 4 and 49 years, Columbretes I showed values between 71 and 76 years (Table 4.1), and for the population at equilibrium, was calculated 64 years (Table 4.1).

Population	Year	λ	ρ	Mean life expectancy
Columbretes I	2010-2011	0.94	1.12	76
	2011-2012	0.94	1.15	71
Columbretes II	2010-2011	1	1.33	4
	2011-2012	0.93	1.18	49
Density-dependent matrix at equilibrium	Mean	1	1.3	64

Table 4.1: Basic demographic outputs for the studied undisturbed *C. zosteroides* populations and for the density-dependent model set at equilibrium. λ: eigenvalue of the matrix. ρ: damping ratio.

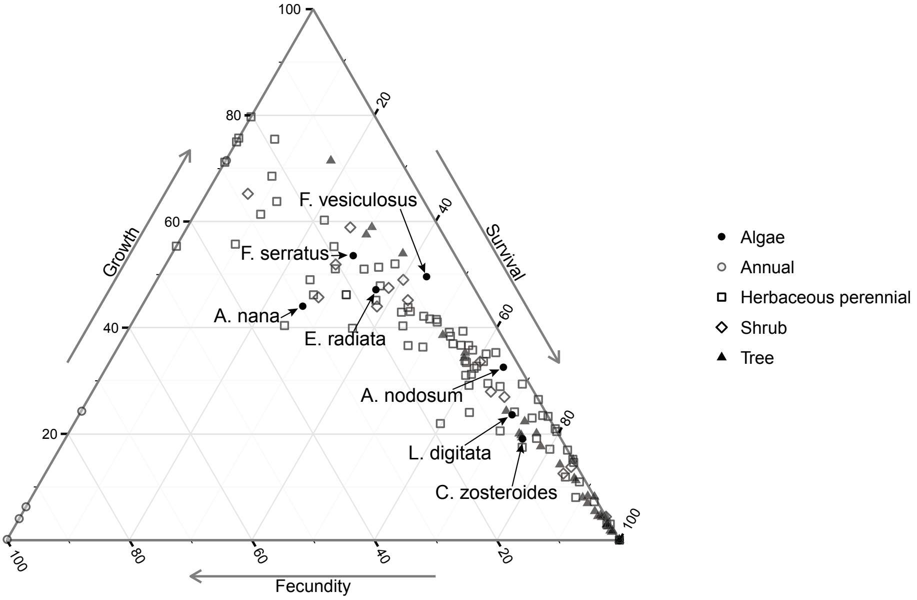

Figure 4.2: Elasticity triangular plot of several brown algae and terrestrial species compiled from the literature.

The triangular plot resulting from the sum of the matrix elasticity components from the different species showed that most brown algae occupied the same region as perennial herbs, shrubs and trees, with high elasticity to survival and relatively little contribution to fecundity and growth (Figure 4.2). Among the studied brown algae, *C. zosteroides* was the species with the largest contribution to survival (with a value of 75 %), and occupied a position in the triangular plot in the vicinity of trees, shrubs and perennials.

The algal species closest to *C. zosteroides* were *Laminaria digitata* and *Ascophyllum nodosum*, with elasticity survival values close to 70%. *Alaria nana*, *Ecklonia radiata*, *Fucus vesiculus* and *Fucus serratus* showed higher elasticities to growth.

4.4.2 Population projection and response to disturbances

When simulating a large perturbation (with 80% mortality) on a natural population striking changes occurred in its size structure in the early phases of recovery (Figure 4.3). After the reduction of large size classes' density, a recruitment pulse occurred. Then, a succession towards an increase in larger size classes until finally, after more than 20 years, the size structure converged to a stage similar to that at equilibrium.

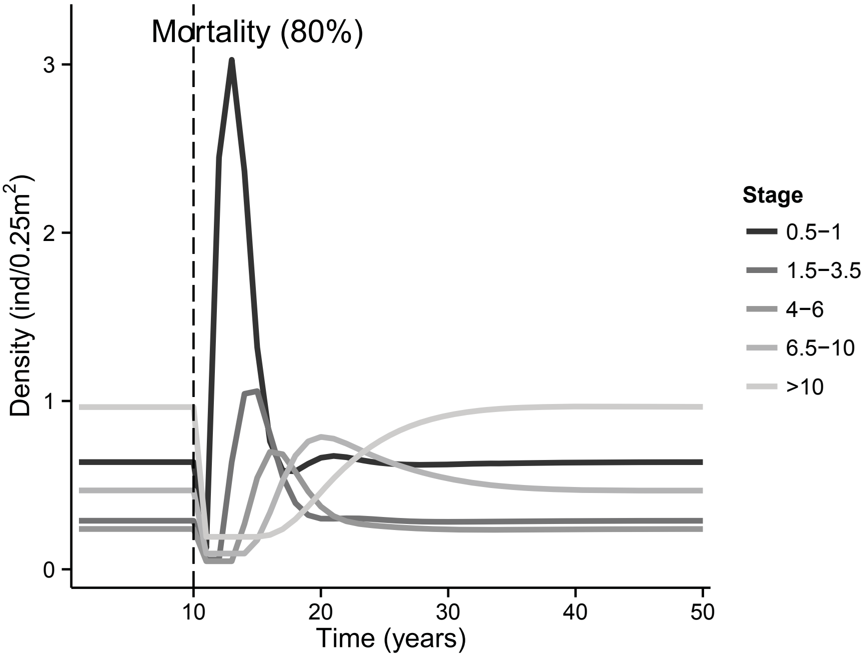

Figure 4.3: Population projection over 50 years and response to a disturbance at year 10, causing an 80% mortality

Cystoseira zosteroides populations are resistant to large disturbances if these occur at low frequencies (Figure 4.4a). The intrinsic population

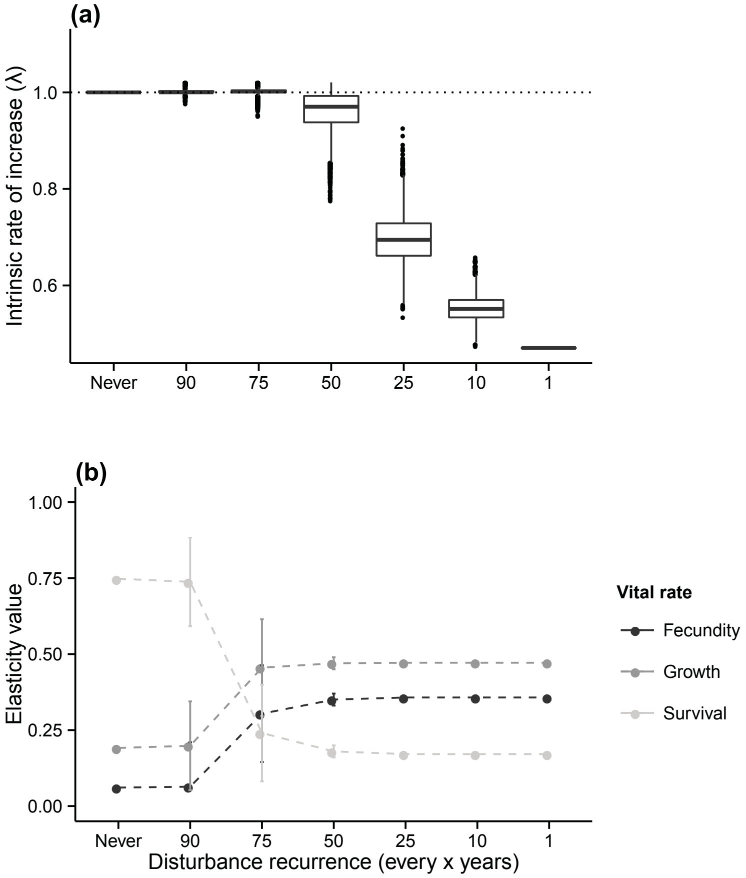

Figure 4.4: Population response to an increase in the frequency of disturbances: (a) Response of lambda to increasing the probability of disturbances; (b) Median and interquartile range of the different demographic components elasticity values (over 10000 iterations and 100 years of simulation) for a range of yearly probabilities of undergoing a disturbance.

growth rate (λ) slightly increased at intermediate frequencies of disturbance (one storm every 90-75 years) due to the positive effect on recruitment as a consequence of adult removal (Figure 4.4a). Nonetheless, at values above one perturbation every 50 years, population growth rates fell below 1. Further, as the frequency of disturbances increased, populations showed a higher dependence on growth and fecundity than on the survival of individuals (Figure 4.4b). Finally, increasing the frequency of disturbances also increased the quasi-extinction risk of this species, with probabilities higher than 90 % in less than 40 years when disturbances occurred every 50 years (Figure 4.5).

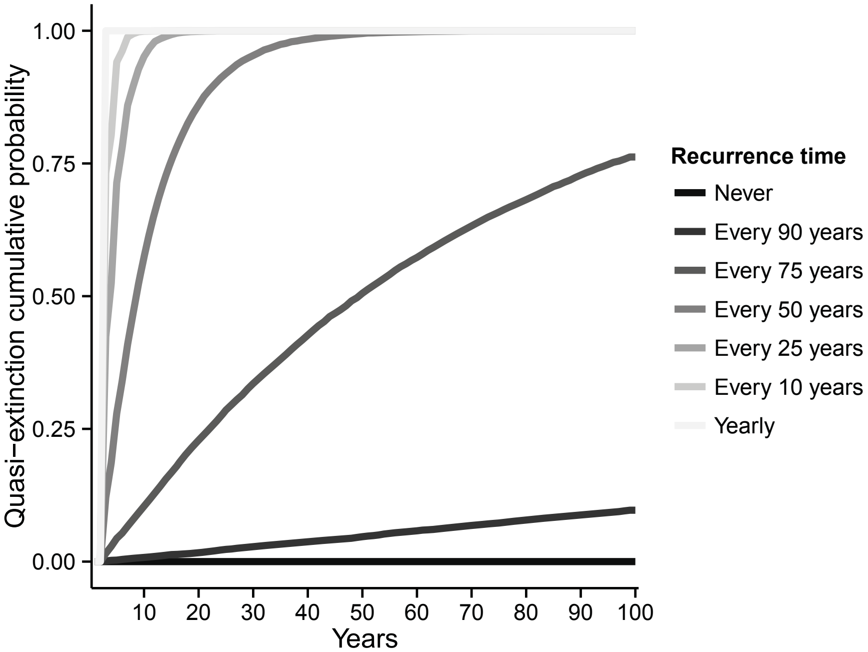

Figure 4.5: Population quasi-extinction probability, with a quasi-extinction threshold of 10% the initial population, for a range of disturbance frequencies (as mean recurrence intervals in years). Grey intensities represent the frequency of storms (i.e. every 90 years).

Simulations showed that *C. zosteroides* was resilient to the impact of fishing nets maintaining growth rate values close to 1. As storm recurrence increased, population growth rates fell rapidly as explained above. The combined action of the two disturbances, lost fishing nets and storms,

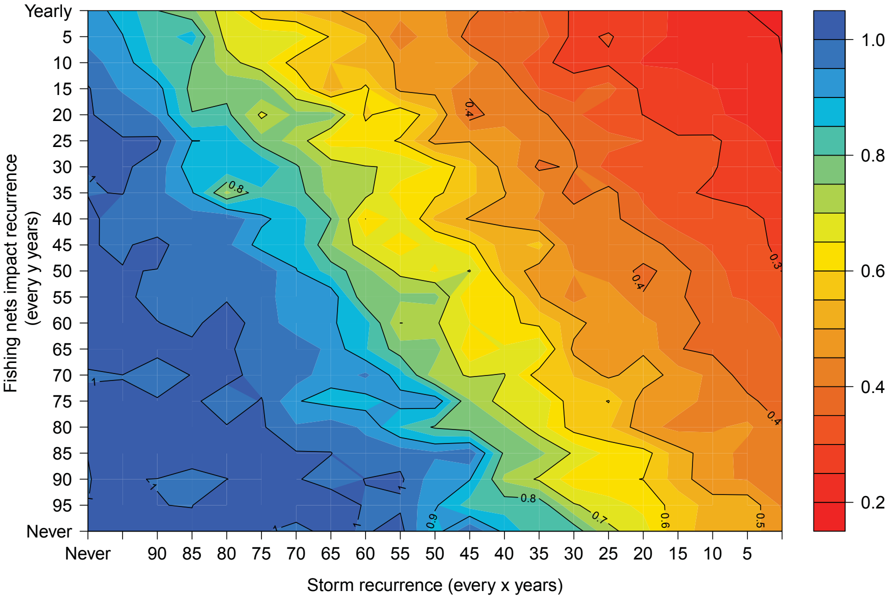

Figure 4.6: Combined effects of increasing the recurrence of mortalities caused by a fishing net (y) and storms (x) on the projected population growth rates (λ) of *C. zosteroides*. The color code indicates simulated population growth rate (λ) values for the projected populations with for a range of disturbance frequencies.

resulted in a higher decrease of population growth rates (reaching values below 0.3 in some cases) than when populations where affected by one single disturbance (Figure 4.6).

4.5 Discussion

4.5.1 Natural dynamics of *Cystoseira zosteroides*

All life history characteristics found in this study place *C. zosteroides* among long-lived algae with slow population dynamics (i.e. slow growth rates and low mortality and recruitment rates; Ballesteros 1990; Ballesteros et al. 2009; Navarro et al. 2011). To our knowledge, this is the first study modeling the demography of a deep-water canopy-forming alga incorporating density-dependence. *Cystoseira zosteroides* survival rates increased with size classes, with large individuals showing values higher than 90%, as reported in other long-term studies (Ballesteros et al., 2009). The lifespan estimates also agree with these previous studies, with values close to 50 years, despite presenting high variability. Population growth rates (λ) were close to 0.9, suggesting that these populations are decreasing, probably because this species is subjected to recruitment pulses (Ballesteros et al., 2009), which were not detected at the time scale of the study. The slow growth and low mortality rates result in low damping ratios, indicating slow convergence to stable size.

The distribution of species across the triangular plot is related to a successional sequence (Silvertown and Franco, 1993). In our analysis, shallow-water algal species occupied the region of the plot mostly dominated by herb-like species (mid-successional stage), whereas the longest-lived species (*Ascophyllum nodosum*, *Laminaria digitata* and *C. zosteroides*; Åberg 1992a; Chapman 1993) occupied the region dominated by shrubs and trees (mid to late successional stage). *C. zosteroides* presented the highest elasticity values to survival, such as *L. digitata* (Chapman, 1993). The high investment of these species in a perennial thallus and, in *C. zosteroides*, reservoir vesicles (tophules; Ballesteros 1990), may ensure their survival through long time periods with low dependency on recruitment at the short-term. In contrast, brown algae thriving on shallow bottoms showed a higher dependence on growth and reproduction, with the exception of the long-lived *A. nodosum*.

Our findings agree with life-history theory, which predicts that species living in stable habitats and with limited resources (i.e. low nutrient concentrations and light availability) should present slow population dynamics and high rates of nutrient retention (Grime, 1977; Silvertown et al., 1992). In deep-water environments, subjected to light and nutrient limitations, increasing survival must be a good strategy to maintain populations. Besides, as depth increases, the risk of breakage diminishes due to the lower frequency of physical disturbances (Garrabou et al., 2002) and decreased herbivory levels (Vergés et al., 2009), thereby liberating resources that can be allocated to structural biomass to maximize survival. These patterns were also observed in a single species, *Sargassum polyceratium*, by Engelen et al. (2005) where shallow populations displayed higher elasticity to fertility, whereas deeper populations depended on the survival and persistence of individuals. Correspondingly, terrestrial habitat-forming species show high investments in structural biomass, increasing long-term survival at the expense of growth and reproduction (Adler et al., 2014). This also agrees with the high survival and structural biomass investment of other long-lived marine sessile and structural species such as gorgonians (Lasker, 1991; Linares et al., 2007) or corals (Hughes and Tanner 2000; Garrabou and Harmelin 2002). Thus, despite the fundamental differences between algae and terrestrial plants, there exist similarities between the life history strategies of these structural organisms independently of their marine or terrestrial origin which support the tree-like population dynamics of our studied alga *C. zosteroides.* Yet, data scarcity on algal demography limits the generalization of our results, so more data and in depth studies are needed to infer general life-history patterns.

4.5.2 Disturbance responses and the importance of density-dependence

Density-dependence is a stabilizing process for *C. zosteroides* populations (Chapter 2). When this species was affected by mortality events, adult removal increased recruitment success, offsetting mortality pulses (Dayton et al., 1992) and maintaining the viability of populations (see Figure 4.4 and Figure 4.5). This is because of the high ability of brown macroalgae to produce large amounts of spores and gametes with relatively little energetic cost (Schiel and Foster 2006; Gianni et al. 2013). Thus, low disturbance frequencies increased *C. zosteroides* populations' growth rates due to these compensatory responses.

High disturbance frequencies diminished the resilience of *C. zosteroides* populations. When disturbances occurred every 75 years, elasticity values for survival started to diminish, attaining their lowest values when disturbances occurred every 50 years. At this frequency of disturbance, when survival was the least important vital rate for the species, the long-term population growth rate started to significantly diminish. Yet, when disturbances became frequent, recruitment was not able to balance adult mortalities, displacing *C. zosteroides* from their dynamic equilibrium, and causing a large decrease in population growth taxes (λ) and higher extinction risks. This was mainly caused by the low survival and relatively late maturation of their recruits.

In contrast to seeds and seed banks of terrestrial plants, early life phases of brown macroalgae are microscopic and free-living stages showing very low survival rates (Dudgeon et al., 2001; Gianni et al., 2013). Moreover, the combined effects of mortalities derived from fishing nets and storms reduced the population growth rates of *C. zosteroides* at lower frequencies than when only affected by extreme disturbances. Hence, local stressors can decrease macroalgae resilience and compromise their viability, exacerbating the effects of other natural stressors (such as storms), to which species are naturally adapted (e.g. Dayton et al., 1992; Navarro et al., 2011). This also supports the view that the compounded effect of increasing local and global stressors (Crain et al., 2008) must be one of the main reasons behind macroalgae declines (Wernberg et al., 2010).

Recurrent extreme disturbances also induced profound changes in *C. zosteroides* population dynamics. As disturbance frequency increased, a higher dependence on reproduction and growth was observed. Post-disturbed subtidal algal populations have been observed to present similar patterns (Engelen et al., 2005; Svensson et al., 2009), but this is in contrast with the natural population dynamics of *C. zosteroides* and with what would be expected for a long-lived organism (e.g. Silvertown et al. 1993; Heppell et al. 2000). This illustrates the importance of recruitment for the long-term persistence of long-lived species populations despite its small contribution at the short-term. Besides the resilience loss of these species, these changes on population dynamics are likely to translate into alterations in community structure and dynamics (Agrawal et al., 2007). The loss of large individuals and the higher dependence on recruitment and growth in disturbed populations have the potential to reduce the structural complexity provided by these algal forests (Graham, 2004; Jenkins et al., 2004; Svensson et al., 2009). Increasing disturbances will also produce the decline or loss of these habitat-forming organisms, leading to the demise of the species associated to them, with major consequences for the ecosystem functioning (Steneck et al. 2002; Graham 2004; Ling et al. 2014). Indeed, recent studies show that different fucoid species have reduced their abundance or even died-off in many regions of the Mediterranean Sea (Thibaut et al. 2005; Gianni et al. 2013) and in temperate seas worldwide (Airoldi and Beck 2007; Strain et al.

2014; Mineur et al. 2015). In addition, we predicted that several decades will be needed to fully recover the structure of natural populations and probably the habitat function of this species (Underwood 1999; Jenkins et al. 2004).

Although our study confirms that the loss of dominant algae canopies has long-term consequences for their communities and can take many years to recover, our model assumptions limit the generalization of these results. Our model considers *C. zosteroides* populations to be closed; however, external sources of recruits, through natural reproduction of nearby populations or drifting adults, could enhance their recovery after disturbances. However, like many other fucoids, *Cystoseira* species have very restricted dispersal abilities (at the scale of meters), mainly due to their reproductive strategy and the size of their zygotes (Schiel and Foster 2006; Mangialajo et al. 2012; Gianni et al. 2013). For this reason, although our simulations suggest that one mass mortality event every 50 years could drive *C. zosteroides* populations to quasi-extinction in 40 years, this seems unlikely to apply to other macroalgal species which can disperse further than 1 km and regenerate quickly after storms (e.g. Dayton et al., 1992; Schiel and Foster, 2006). In addition, due to the difficulties of sampling at the depth where *C. zosteroides* lives, our results come from a restricted sample size and time period (see 4.3), relative to the longevity of the studied species. For example, it cannot be expected that recruitment will be high at all populations and well maintained through time, because numerous local factors may limit recruitment rates (Schiel and Foster, 2006).

Nevertheless, this work reveals the potential of studying the demography of canopy-forming algal forests, not only to understand their population dynamics but also for their conservation implications. Given the widespread collapse of macroalgae populations in many temperate reef ecosystems worldwide (e.g. due to sea urchin proliferation, Ling et al. 2014), future studies should consider including the impact of sea urchins when modeling macroalgae population dynamics to better predict their future trends and how these changes translate to community dynamics. Our findings highlight that underwater forests dominated by brown algae can display slow population dynamics, with life-history strategies similar to late successional terrestrial species (such as shrubs or trees). It is likely that the increase in local stressors and in the frequency of extreme events will erode the resilience of macroalgae. Diminishing local stressors (such as fishing nets), which are more easily managed than global stressors, may improve the resilience of macroalgal forests to other disturbances (Strain et al., 2014, 2015). However, given the difficulty of conducting demographic surveys underwater, there still exist limitations to our understanding of algal demography. In our case, recruitment seems to be an effective method for *C. zosteroides* to replenish populations after disturbances, but very few studies have focused on their early life-history stages (Chapter 2). For long-lived and deep-water algae, we suggest that the most effective management should target adult survival; however, conservation strategies should also consider favouring natural recruitment to ensure the long-term viability of these populations. More studies are needed to promote and develop conservation actions for these habitat-forming organisms but also to improve our understanding of general life history patterns.

4.6 Acknowledgements

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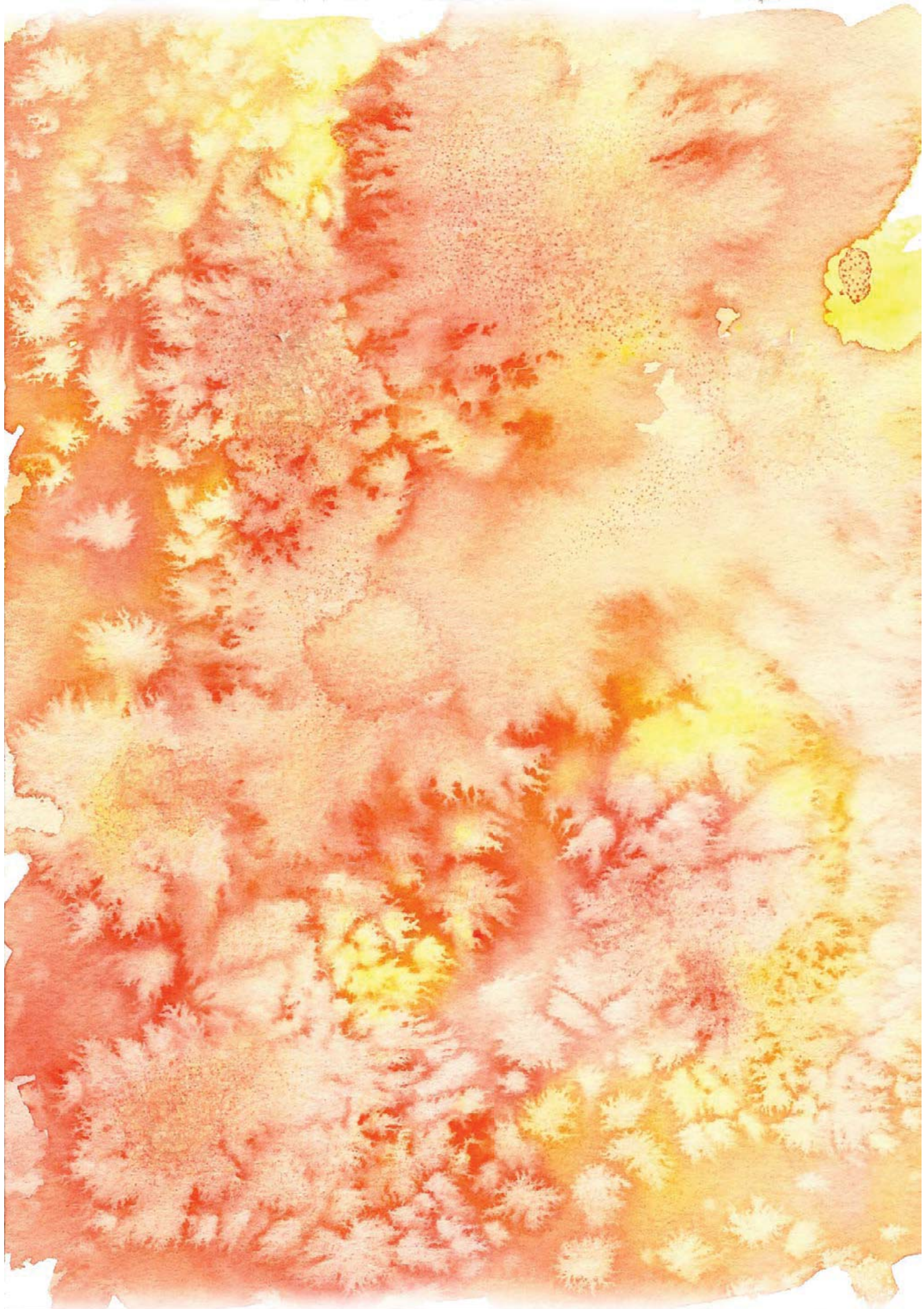

Chapter 5

Warming impacts on early life stages increases the vulnerability and delays the recovery ability of macroalgae populations

5.1 Abstract

Understanding the combined effects of global and local disturbances is crucial for conservation and management, yet challenging due to the different scales at which these take place. Here we studied the effects of one of the most pervasive threats to biodiversity, warming, onto the early stages of the habitat-forming macroalga *Cystoseira zosteroides*, and we explored how this affected their population recovery ability and viability when facing other physical disturbances such as storms and ghost fishing nets. First, we performed a controlled experiment exploring the impacts of warming onto the early life stages of this species. We collected fertile deciduous branches from the field and we cultured them at 16°C (control), 20°C and 24°C. Settlement and the survival of germlings decreased with increasing temperatures. Then, we integrated this information in a stochastic, density-dependent integral projection model (IPM) to predict the long-term consequences of warming at its recovery ability and its combined effect with other physical disturbances. The required time to recover after a minor disturbance significantly increased in warmer scenarios. The stochastic population growth rate (λ_s) of *C. zosteroides* was not strongly affected by warming alone, as high adult survival buffered against temperature-induced recruitment failure. Nevertheless, warming coupled with recurrent physical disturbances had a strong impact on λ_s and population viability. These results highlight how warming may have unnoticed effects that increase the vulnerability of populations to further disturbances, and evidence the need to incorporate abiotic interactions in demographic models.

5.2 Introduction

Global change is predicted to modify the regime and intensity of disturbances in marine ecosystems worldwide (Easterling, 2000; Jentsch et al., 2007). Some chronic stressors, such as global warming (IPCC, 2013) or ocean acidification (Kroeker et al., 2010), are expected to increase in magnitude during the present century. Furthermore, acute, extreme events, such as El Niño (Yeh et al., 2009) or heatwaves (Déqué, 2007; Rose et al., 2012), are expected to become more frequent and intense (Kerr 2011; IPCC 2013). All of these threats are unfolded in a background of human alterations that can exacerbate their consequences (Ling et al. 2009; Hughes et al. 2013). In order to predict the ecological responses of species to global change and design effective conservation actions, we need to understand not only the direct consequences of disturbances but also their combined effects at long-term (Darling and Côté, 2008; Lindenmayer et al., 2017).

The high idiosyncratic nature of ecosystems challenges our comprehension about the combined impacts of global change (Boyd et al., 2014; Krumhansl et al., 2016). Experimental studies have provided crucial insight to understand the underlying (e.g. demographic or physiological) effects of warming or acidification (Wernberg et al. 2010; Kroeker et al. 2013). On the other hand, modelling studies parametrized with field data provide valuable means to project and forecast the fate of populations into various scenarios (Linares and Doak, 2010; Madin et al., 2012). Despite the recent progress in global change research, experimental and modelling approaches have evolved as parallel disciplines, scarcely used together to predict long-term demographic responses of marine species (Russell et al., 2012; Wernberg et al., 2012). Most experimental marine studies focused on a single life stage, yet marine species usually encompass multiple life stages with contrasting responses to threats (Caley et al., 1996; Harley et al., 2012). Because experimental manipulations of complete life histories are not always feasible, exploring the response of key or elusive life stages in controlled conditions coupled with modelling approaches parametrized with field data can provide unique insights (Assis et al., 2017).

In this study, we explore the population-level consequences of warming and its interaction with mortalities caused by physical disturbances, such as storms and ghost fishing nets, on the habitat-forming Mediterranean macroalgae, *Cystoseira zosteroides*. The Mediterranean Sea is a hot spot of biodiversity, but also a focus of human disturbances (Coll et al., 2010). Among these multiple stressors, warming is the most pervasive, impacting regional scales during the last decades (Somot et al. 2008; Lejeusne et al. 2010; Micheli et al. 2013). Heat waves in the Mediterranean can seriously affect marine invertebrates (Garrabou et al., 2009) and encrusting algae (Hereu and Kersting, 2016), with no studies reporting such evidence for brown macroalgae (Ballesteros et al., 2009). In contrast, physical disturbances can heavily impact macroalgae populations, such as lost fishing gears (Thibaut et al., 2005) and low-frequency exceptional storms (Navarro et al., 2011). High temperatures are known to damage algal cells (Harley et al., 2012) and these effects may upscale, lowering growth rates, slowing down development and/or triggering mortality, ultimately impacting population dynamics and species distribution (Wernberg et al. 2010; Harley et al. 2012; Assis et al. 2017). Early stages of macroalgae are usually imperiled by warming (Ladah and Zertuche-González 2007; Andrews et al. 2014), while adult individuals are more prone to physiologically compensate high levels of thermal stress (Jueterbock et al. 2014; Bennett et al. 2015). Thus, it is crucial to determine if the altered mortality of early life stages is important for the overall population persistence.

Here we hypothesize that warming will seriously impact *C. zosteroides* early life stages development, with important consequences for the recovery ability and viability of their populations. We also expect that temperature alone will have little impacts at the population level, given that their populations have little dependence on reproductive processes (Chapter 4). To test these hypotheses, we first experimentally explored the consequences of warming on the survival and development of *C. zosteroides* early life stages, by culturing them into different temperature treatments. We then used these results, coupled with demographic data from five natural populations of *C. zosteroides*, to predict long-term effects of various thermal scenarios and its interactions with recurrent physical disturbances, such as storms and fishing nets.

5.3 Material and Methods

5.3.1 Study species

Cystoseira zosteroides is an endemic alga from the Mediterranean Sea with a critical structural role (Ballesteros et al., 2009). *Cystoseira zosteroides* populations develop important forests in rocky bottoms at 15-50 m depth, mainly in the NW Mediterranean Sea, constituting highly diverse communities in relatively deep water bottoms (Ballesteros et al., 2009). This species typically has slow population dynamics, with low somatic growth (0.5 cm year^{-1}) and long lifespan (∼50 years; Chapter 4). This species presents a diplontic (i.e. only gametes are haploid) and iteroparous life cycle (i.e. multiple reproductive events during their lifetime; Appendix D: Figure D.4). Individuals are monoecious: they can be male and female, although hermaphrodite can occur. Adult individuals can be distinguished by their perennial thallus, except during their first year of life. The top of the thallus contains reservoir vesicles (tophules) from which primary branches emerge from February until October (Ballesteros, 1990). These primary branches contain receptacles, the reproductive structures of mature individuals. Maturity is typically attained at 3-4 years (>1cm) and reproduction starts in late March-early April and ends in June-early July (pers. obs.). Gametes are released and fertilization is external which form a diploid zygote.

5.3.2 Temperature data

To describe the present thermal conditions where this species inhabits, high-resolution hourly temperature recordings were obtained from the T-MedNet platform (`http://www.t-mednet.org/`), which records temperature data over different places at the Mediterranean Sea using *in situ* Stowaway Tidbits autonomous sensors. Here we used data from the Cap de Creus Natural Park (42°20′0.456”N, 3°17′11.6052”E), Montgrí, Medes Islands and Baix Ter Natural Park (42°2′58.92”N, 3°13′31.44”E) and Columbretes Islands Marine Reserve (39°53′30.1122”N, 0°40′15.9312”E), three locations where *C. zosteroides* populations are monitored (Appendix D: Table D.1 and Figure D.1). Temperature recordings were only analyzed at a depth range of 20-35 m and since 2008 to 2015, the depth range and time period that we have studied this species (see Demographic modelling, Appendix D: Table D.1 and Figure D.1). Note that in Columbretes Islands data from 25 to 35 m depth is shown because in that location *C. zosteroides* does not develop populations at shallower depths than 25 m.

5.3.3 Experimental design

Early life stages of *C. zosteroides*, typical of any macroalgae, are very distinct from adult stages in terms of size and demography (Chapter 2). Thus, to accurately measure the settlement rate and survival of early life stages of *C. zosteroides*, 27 branches from nine fertile individuals were collected by scuba diving from a well-developed *C. zosteroides* population between 20 and 25 m depth in Montgrí, Medes Islands and Baix Ter Natural Park (NW Mediterranean Sea, 42°2′34.026" N, 3°13′36.3576"E) in April 2016. Fertile branches were transported in seawater containers (∼3 h) to the Experimental Field Services of Barcelona University. Branches were then placed in small plastic bags with seawater inside fridges kept at 12°C to promote the liberation of gametes (Susini et al. 2007). After 24 hours, three branches were placed in each of nine 12 L aquaria, where three Petri dishes were set at the bottom as a substrate for zygote settlement. Four 1 cm^2 quadrats were haphazardly marked on each Petri dish as a sampling surface (Appendix D: Figure D.2). See Appendix D for further details about the experimental design.

To examine the effects of temperature on settlement and survival rates of early stages three temperature treatments were implemented. Each treatment was replicated within three separate aquaria (Appendix D: Figure D.2). The chosen temperature levels were 16°C, 20°C and 24°C. During the reproductive season of *C. zosteroides* seawater temperature increases from ∼14°C to over 17°C, with a mean value of ∼16°C, and so here we treat the 16°C treatment as our control (Appendix D: Figure D.3). The 20°C treatment mimic the values attained during previous warming years (see section 5.4.1). The 24°C simulates the increase of 3.5°C scenario for the 21st century in the NW Mediterranean (Somot et al. 2008; IPCC 2013). Indeed, during warm years, natural populations at present experience this temperature by the end of the reproductive season and mainly between July and August, during the recruits' development (see Results Temperature data in section 5.4.1).

A week after the branches were placed in the aquaria, once enough time had elapsed for the zygotes to settle and be distinct from non-fertilized eggs (Irving et al., 2009), branches were removed from the aquaria. Then, we estimated the number of zygotes observed per cm^2 observed inside the four quadrats marked on the Petri dishes. Survival of zygotes (σ_s) was quantified weekly during a period of six weeks as the proportion of zygotes remaining from the previous week.

5.3.4 Settlement and survival statistical analysis

To quantify the effect of temperature on the settlement of *C. zosteroides* we used generalized linear mixed models (GLMM), with a Poisson error distribution and a logit link function. The independent variable was the number of zygotes, temperature was treated as a fixed variable and we used the ID of each quadrat of the Petri dishes as a random variable. Similarly, to test the effect of temperature and time (fixed factors) on germling survival, we used a GLMM with a binomial error distribution and a logit link function. Again, we used the ID of each quadrat of each Petri dish as a random variable to deal with the lack of independence between observations repeated at different times and a binomial error distribution was assumed to deal with the binary response variable (survive *vs.* die). For the two fitted models, we applied a Type II Wald χ^2 test to determine the effect of fixed variables. All analyses were performed using the statistical software R (R Development Core Team, 2014), models were fitted using the function "glmer" from the lme4 package (Bates et al., 2014), and the Wald χ^2 test was performed using the "Anova" function from the car package (Fox and Weisberg, 2011). For multiple comparisons, we applied the Tukey test using the "glht" function from the multcomp package (Hothorn et al., 2008).

5.3.5 Demographic censuses

We estimated the survival (σ), growth (γ) and recruitment rates (Appendix D: Table D.2) by monitoring individuals along permanent transects at five

C. zosteroides populations along the NW Mediterranean (one at Cap de Creus Natural Park, two at Montgrí, Medes and Baix Ter Natural Park and, two populations at Columbretes Islands Marine Reserve; Appendix D: Figure D.1), during 3–4 years (see Appendix D: Table D.1). Sampling was performed by scuba diving, and transects were visited annually by experienced observers at the beginning of the summer (between July and August) when *C. zosteroides* attains its highest seasonal biomass (Ballesteros, 1990). Vital rates were estimated according to the size of individuals, measured as the maximum length of the perennial axis, which typically spans from 0.5 cm to 16 cm (Ballesteros et al., 2009). Each transect was 1 m wide and 3-10 m long, depending on the morphology of each sampling zone (see Appendix D: Table D.1 for details). Transects were installed in the summer of 2008 at Montgrí, Medes and Baix Ter Natural Park Islands at ∼20 m depth, where 209 and 181 individuals were mapped respectively, while at Cap de Creus Natural Park and Columbretes Islands Marine Reserve transects were installed in May 2010 at 23, 28 and 24 m depth, mapping 175, 124, and 130 individuals, respectively.

5.3.6 Model parametrization

We used Integral Projection Models (IPMs; Easterling 2000) to examine the overall effects of projected increasing temperature and its combined impact with other physical disturbances (see below section 5.3.7). Because IPMs are based on regression models, they can easily estimate the variation of vital rates with continuous stages (Ellner and Rees, 2006), such as size in *C. zosteroides*, and they are robust when parametrizations are based on populations with few individuals (Ramula et al., 2009). The overall structure of the IPMs used here is described in detail in Appendix D.

To parameterize the vital rate functions that conform the IPM, we used data for each year and population. Medes and Montgrí coast populations were both impacted by an extraordinary storm in 2008 and Montgrí population also suffered a mortality event caused by a ghost fishing net in 2009 (Chapter 2), so these two populations were not considered for the survival and growth parametrization to avoid misleading estimations. Instead, they were used to guide our simulations about fishing and storm mortalities, as well as their interactions (see section 5.3.7). Thus, the IPM was built from the data obtained from each non-disturbed population and time interval (Columbretes I: two from 2010-2012; Columbretes 2: two from 2010-2012; Cap de Creus: two from 2010-2012).

5.3.7 Demographic projections

We used continuous size-based vital rates functions to build our set of IPMs. The IPM's state variable for its continuous component was the size of the perennial thallus (in cm). To account for the variation between populations and years, we generated random transition kernels for each time step by sampling from the estimated distribution of populations and year effects in survival and growth.

To estimate the effect of temperature on the ability of *C. zosteroides* populations to recover after disturbances, we simulated a small impact (10% mortality) on a population and then we projected it 100 years, 1000 times for each thermal scenario. To do so, we multiplied the density-dependent IPM by a population vector n_t

$$n_{t+1} = IPM \times n_t \tag{5.1}$$

where the initial n_t density function was taken from the stable size distribution obtained from the IPM at its stationary equilibrium (λ=1). Given that choosing a density function from the multiple years and populations that we had would be a non-objective process, we decided to use a simulated well-preserved density function instead of a “natural” one, in order to make fair comparisons between treatments (below). At each time step, the IPM was updated to reflect density-dependence and the impacts of temperature in recruitment, as well as to account for the variation in survival and growth rates.

To estimate population resilience, we quantified an index that measures the minimum time necessary for a density of individuals larger than 10 cm to be achieved in a newly established populations. This threshold was 0.2 large individuals/0.25 m^2, which was established according to the mean density of such mature individuals in both Columbretes populations, the best-preserved ones studied here. We accounted for the number of large individuals instead of total density to consider the structural complexity of the population (Ballesteros et al., 2009). We recalculated this index, for each thermal scenario and projection, and tested for potential differences between treatments using an ANOVA.

Finally, we evaluate the consequences of interactive disturbances under the different thermal scenarios. To do so, we projected the simulated populations increasing the annual frequency of two relevant physical disturbances: extreme storms and fishing nets, each causing a mortality of 80% and 60% individuals respectively. We used these mortality levels for each disturbance based on empirical values obtained in a previous study (Chapter 2). The frequencies ranged from Never to every 5 years, at intervals of 25 years. For each of the aforementioned combinations, populations were projected for up to 100 years with 1000 iterations.

For each of the projected populations and for each disturbance combination, we calculated the stochastic population growth rate (λ_s) as:

$$\log(\lambda_s) = \frac{log(N_t) - log(N_0)}{T} \tag{5.2}$$

where N_0 is the mean population size at time $t = 0$ and N_t the mean projected population size at time T. When $\log(\lambda_s) < 0$ the population decreases, $\log(\lambda_s) = 0$ population is stable and $\log(\lambda_s) > 0$ population growths. To quantify the repercussion of these combined disturbances to the viability of *C. zosteroides* populations, we also obtained the probability of quasi-extinction at t=50 years (Morris and Doak, 2002). For each simulation, we calculated the number of simulated populations that fell below a conservative extinction threshold, of 1% of the initial population size.

5.4 Results

5.4.1 Temperature data

The seawater temperature had a marked seasonality, with a summer maxima of 23, 24 to 27°C and a winter minima of 10, 12 to 13°C at the shallowest depth in Cap de Creus, Montgrí and Medes Islands, and Columbretes Islands respectively (Figure 5.1 and Appendix D: Figure D.3). Thus, Cap de Creus and, Mongrí and Medes Islands have a cooler thermal regime than Columbretes Islands, located further south (Appendix D: Figure D.1).

Considering the reproductive period of *C. zosteroides*, from April to July, there were similar thermal conditions at all studied sites (Figure 5.1b,c). Mean temperatures were between 15-17°C with colder temperatures at 35 m depth, with some years attaining values close to 20°C at all sites (Figure 5.1b). Maximum annual temperatures during the reproductive season over the studied period ranged from 17°C in Montgrí and Medes Islands at 35 m to 25°C in Columbretes Islands at 25m (Figure 5.1c).

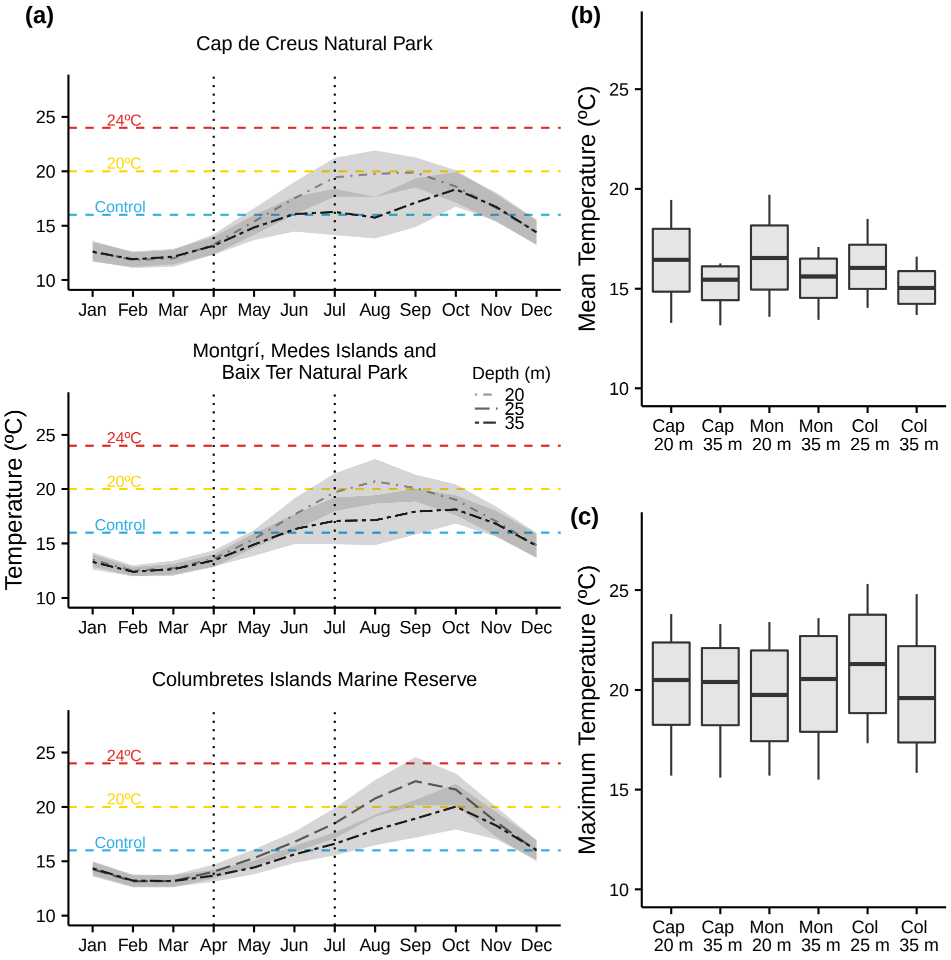

Figure 5.1: Thermal regimes at the three locations where *Cystoseira zosteroides* populations were monitored at the depth range and years that were studied. Monthly mean temperature cycle (±SD) at 20 and 35 m depth for Cap de Creus Natural Park and Montgrí, Medes Islands and Baix Ter Natural Park, and at 25 and 35 m depth in Columbretes Islands Marine Reserve (see map at Figure D.1). Vertical dotted lines indicate the reproductive period of *Cystoseira zosteroides*. Horizontal lines indicate the treatments used in our experiment. Boxplots of mean hourly temperature records (of all studied years) considering the April to July *Cystoseira zosteroides* reproductive period (b) and boxplots considering only the maximum annual temperature records (c). Cap 20 m and Cap 35 m: Cap de Creus Natural Park data at 20 and 35 m depth respectively. Mon 20 m and Mon 35 m: Montgrí, Medes Islands and Baix Ter Natural Park data at 20 and 35 m depth respectively. Col 25 m and Col 35 m: Columbretes Islands Marine Reserve at 25 and 35 m depth.

5.4.2 Effects of temperature on settlement and germling survival

Increasing temperatures provoked a decline in zygotes settlement (χ^2_2=171.35, p-value<0.001). Although settlement did not show significant differences between the 16°C (control) and 20°C treatment (Tukey test, z=0.30, p=0.951), we found a significant drop in zygote settlement when comparing the 24° treatment to the control (Tukey test, z=-12.22, p<0.001; Figure 5.2).

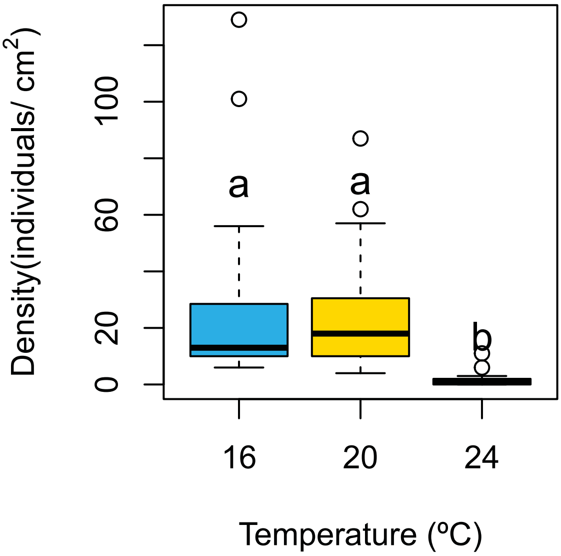

Figure 5.2: Density of recruits (individuals/cm^2) after one week of culturing fertile branches in the aquaria at the treatments of 16°C, 20°C, and 24°C. Different letters indicate statistically significant different groups between treatments according to the Tukey test. Boxes represent the interquartile range, the horizontal line represents the median, vertical line represents the upper and lower extreme values, and dots are the outlier values.

Germlings survivorship decreased gradually during the first six weeks of aquarium monitoring in all treatments (χ^2_4=17614336, p<0.001; Figure 5.3) but varied significantly between temperature treatments (χ^2_2=23254947, p<0.001). The survivorship of germlings remained almost constant during the six weeks of observation at 16°C, attaining values close to 90% at the end of the experiment. However, survival was lower at 20°C (z=-2635, p<0.001), with final values of ~50%, and at 24°C, with the lowest survivorship being

~30% at week six (16-24: z=-4039, p<0.001; 20-24: z=-993, p<0.001; Figure 5.3). According to the fitted model, there was a reduction in the survivorship of about the 42% and 67% at the 20°C and 24°C treatments, respectively to the control treatment.

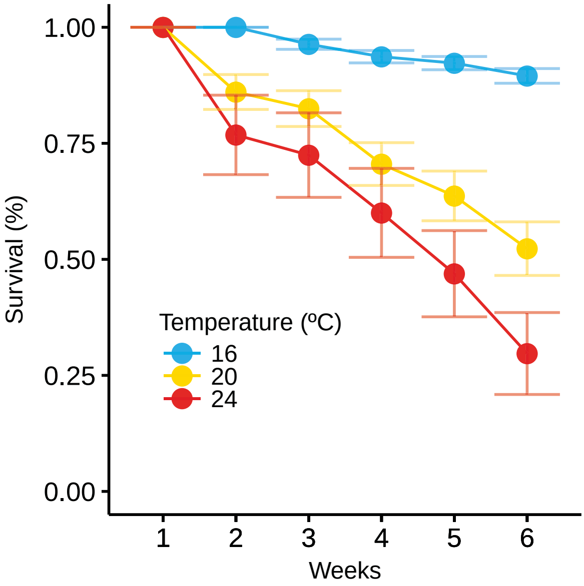

Figure 5.3: Proportion of surviving germlings at the different culturing temperatures during the 6 weeks of the experiment. Dots represent the mean survival, and error bars its standard error.

5.4.3 Effects of temperature on populations' recovery ability

Warming lowers the resilience of *C. zosteroides* populations to small disturbances (Figure 5.4). Using the threshold of 0.2 large individuals/0.25 cm^2, warming significantly increased the recovery time (one-way ANOVA; F_1,1592= 98.08, p<0.001), with a mean value of 44.80 years (±20.18) at 16°C, 55.26 years (±21.69) at 20°C and no recovery at 24°C (Figure 5.4). 91.90%, 67.50% and 0 of the projections surpassed the threshold at the 16°C, 20°C and 24°C treatments respectively (Appendix D: Figure D.6).

5.4.4 Combined effects of temperature and recurrent impacts of two physical disturbances

When we implemented the different perturbations under different temperature regimes, we observed a general pattern: increasing temperatures decrease $\log(\lambda_s)$ (Figure 5.5a,c) and raise their quasi-extinction probability (Figure 5.5b,d). In the absence of further disturbances, *C. zosteroides* populations showed little or no effect of temperature on their long-term projections (Figure 5.5a,c), nor on their quasi-extinction probability (Figure 5.5b,d). Under present conditions (16°C), they had some ability to buffer the mortalities caused by a major storm. Recurrences higher or equal to one exceptional storm every 50 years, provoked the depiction of $\log(\lambda_s)$ from 0 (i.e. population stability) and quasi-extinction probabilities surpassed the 50% (Figure 5.5a,b). Also in this control scenario, mortality caused by

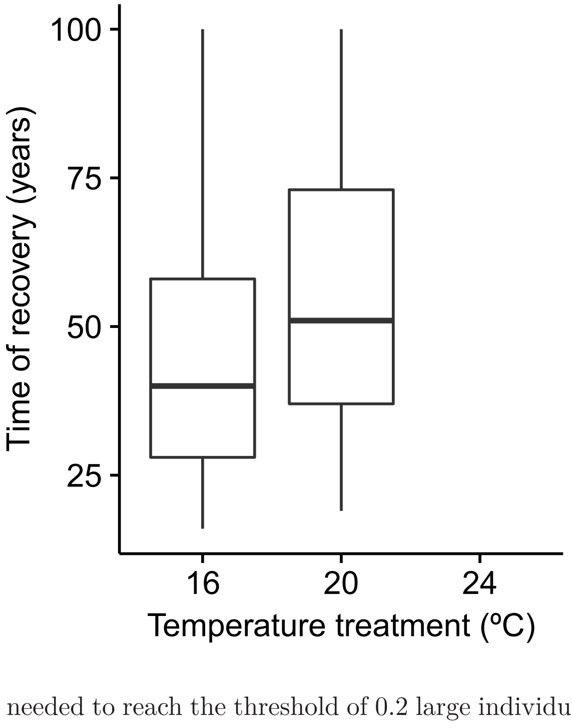

Figure 5.4: Years needed to reach the threshold of 0.2 large individuals/0.25 cm^2 for 1000 projected populations at the different temperature scenarios. Boxes represent the interquartile range, the horizontal line represents the median, vertical line represents the upper and lower extreme values, and black dots represent outliers, defined as points out of the 95% of the interquartile range.

fishing nets had little effect on the projected population (Figure 5.5c), with 0 probability of quasi-extinction at any recurrence (Figure 5.5d). Under the 20°C scenario, populations maintained some degree of buffering to recurrent storms (Figure 5.5a,b), being greater in the case of fishing-induced mortalities (Figure 5.5c,d), but to a lesser degree than under the control scenario. Finally, the 24°C scenario had the highest impact on the stochastic population growth rate under increasing storm and fishing recurrence (Figure 5.5a,c), rapidly driving a 100% of quasi-extinction probability (Figure 5.5b,d).

5.5 Discussion

We provide evidence that warming impacts on early life stages has profound consequences for the population dynamics and structure of macroalgae populations. We have shown the negative effects of projected warming on the settlement and survivorship of *Cystoseira zosteroides* early life stages through laboratory experiments. Coupling these results with full life-cycle demographic models enabled us to anticipate that warming does not severely imperil the populations of this long-lived macroalga, confirming our initial hypothesis that adult survival would buffer the mortality of early stages. Yet, considering the likely scenario of multiple disturbances such as the impact of physical disturbances (e.g. exceptional storms or fishing nets), warming will delay *C. zosteroides* populations recovery and will lead them more vulnerable to further disturbances, by preventing their buffering through the arrival of recruits. Identifying and quantifying the impacts of temperature into these key demographic processes take us one step closer towards dampening the impacts of climate change on macroalgae forests.

We found that increasing temperatures negatively affects key processes of macroalgae early life stages. *C. zosteroides* zygotes settlement decreased and early mortality significantly increased in the temperature treatments of 20°C and 24°C. These are likely temperature scenarios in the Mediterranean Sea during the forthcoming decades (Somot et al., 2008). In fact, during exceptionally hot years temperatures can exceed 25°C in summer and 20°C at the end of *C. zosteroides* reproductive season at 20 m depth (Figure 5.1).

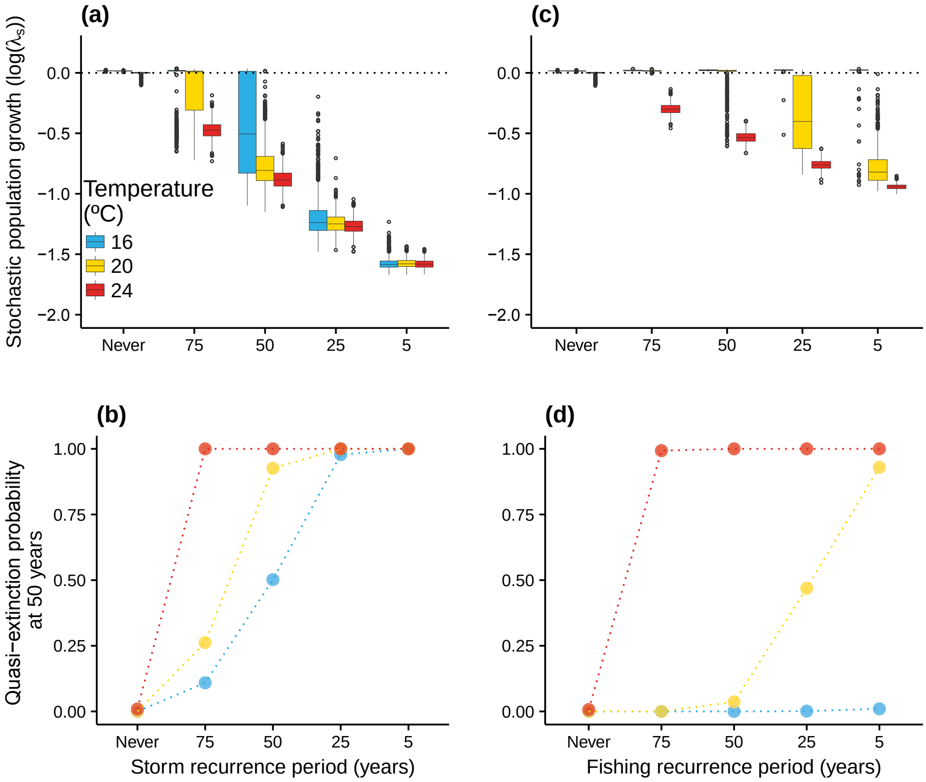

Figure 5.5: Stochastic population rate of increase (λ_s; a, c) and quasi-extinction probability at 50 years (b, d) of 1000 simulated populations projected over 100 years at different yearly temperature scenarios and increasing physical disturbances, such as storm mortality recurrence (a, b) and fishing mortality recurrence (c,d). Boxes represent the interquartile range, the horizontal line represents the median, vertical line represents the upper and lower extreme values, and black dots represent outliers, defined as points out of the 95% of the interquartile range. The quasi-extinction probability was estimated over 1000 simulated populations. The extinction threshold was assumed to be 1% of the initial population.

This indicates that in the absence of thermal adaptation these processes will be seriously imperilled under a warming scenario. Thermal limits can be highly variable among macroalgae species (Harley et al., 2012), and some species display a wider range of thermal resistance than *C. zosteroides* early stages (e.g. *Ecklonia radiata*, Mohring et al. 2014). This is likely because intertidal or shallow water species experience a wider range of daily thermal fluctuations than deeper water species, such as *C. zosteroides* (Harley et al., 2012; Wernberg et al., 2016b).

Despite the reduced recruitment on increasing temperature scenarios, *C. zosteroides* populations are able to compensate warming effects in the absence of other impacts. Such resistance was primarily conferred via the high survival of large individuals. These findings agree with life history theory which predicts that long-lived species are buffered against climatic changes (Morris et al. 2008; Koons et al. 2009; Doak and Morris 2010). These species often invest more resources to maximize the survival of late stages, which are presumably more resistant to physiological stress (e.g. such as in trees; Kelly and Bowler 2002). Hence, increasing the variation on reproductive patterns have little to no effects on the population growth of long-lived species (Morris et al. 2008; Koons et al. 2009). Undisturbed *C. zosteroides* populations hinge on adult stands (Chapters 2 and 4; Ballesteros et al., 2009), and so temperature-altered survival of the early life stages has a low impact on the population maintenance. That is, the detrimental effects caused by temperature on recruitment can be buffered by the high survival of adults. Therefore, our findings suggest that temperature *per se* is not an imminent threat for this macroalgae, or at least within the range of values that we explored here (20-24 °C), assuming that adult survival is not affected by temperature.

Given the lack of direct field-based evidence of warming-related adult mortalities, we did not consider it into the modelling process, and thus our results are likely conservative. Many studies have provided evidence that brown macroalgae adult individuals have physiological mechanisms to compensate temperature fluctuations (Pearson et al. 2009; Jueterbock et al. 2014; Graiff et al. 2015). However, these mechanisms are only effective for a given range of temperature conditions until reaching a threshold, above which macroalgae cannot physiologically adjust (Graiff et al., 2015; Wernberg et al., 2016b), what may cause extensive canopy loss (Wernberg et al., 2016a). The lack of field evidence of warming-related mortality in adult *C. zosteroides* populations suggests that this temperature threshold has not been surpassed yet, probably because of their deep-water distribution. This highlights that there is still a window of opportunity for this species to escape from the consequences of global change. Identifying those species with such characteristics, coupled with proper management, brings a chance of reversing or dampening the effects of climate change on macroalgae-dominated communities.

Nevertheless, warming lowered *C. zosteroides* recovery ability and rendered their populations more vulnerable to further stressors. Some macroalgae populations are able to withstand mortality events by recruitment pulses as a consequence of relaxing negative density-dependence (Dayton and Tegner 1984; Schiel and Foster 2006; Navarro et al. 2011), a widespread mechanism among sessile organisms (e.g. trees, Volkov et al. 2005; corals, Vermeij and Sandin 2008). Yet, the negative effects of temperature on reproduction and early life stages development exacerbate the cumulative effects of other disturbances. Similarly, many macroalgae species experience a reduction on their reproductive outputs in populations located at warmer latitudes (Wernberg et al. 2010; Viejo et al. 2011). Some studies have shown that these edge populations sometimes are able to persist through remaining adults, but this always comes through a reduction of their resilience (Pearson et al., 2009; Wernberg et al., 2010). Given the likely scenario of multiple disturbances, our work illustrates that temperature will render macroalgae populations more vulnerable to further disturbances.

Increasing the vulnerability of habitat-forming species in warmer waters can drive major shifts in ecological systems. For example, extreme heat waves have been reported to cause extensive loss of *Macrocystis pyrifera* in California, resulting in a reduction of the canopy cover from 600 to 40 ha with the subsequent depletion of the associated community (Dayton and Tegner, 1984). However, following that disturbance, the community experienced a rapid recovery primarily due to the long-range dispersal of propagules and adults of the species mediated by upstream currents (Dayton and Tegner, 1984). Our work illustrates that if temperature maintains its current rise, the recovery of macroalgae forests after major disturbances is very unlikely. Indeed, a recent study showed that an extreme heat wave on the west coast of Australia catapulted the collapse of kelp forest (Wernberg et al., 2016a). The recruitment limitation, driven by several stressors, such as competition with corals and the herbivory of tropical fishes, prevented the recovery of kelp beds, what resulted in a completely changed community at the northern latitudes (Wernberg et al., 2016a). This illustrates that the impacts of temperature on key demographic processes may have consequences for macroalgae populations functioning, with effects scaling up to the communities that they structure.

Numerous reports agree on the projected losses of macroalgae worldwide (Thibaut et al. 2005; Airoldi and Beck 2007; Krumhansl et al. 2016; Assis et al. 2017). Forecasting the consequences of increasing temperatures is challenging, as global change can have knock-down effects that may add additional layers of complication to such predictions (Vergés et al., 2014; Wernberg et al., 2016a). Here we show that high temperatures have the potential to impact the demographic structure of macroalgae populations; this, coupled with the predicted increase of disturbances frequency, may drive local extinctions (Thibaut et al. 2005; Airoldi and Beck 2007) or even cause distributional range contractions (Smale et al. 2013; Assis et al. 2017). In any case, anticipating the direction of change is crucial for the preservation of these habitat-forming organisms, but doing so often requires integrative approaches only achieved by combining field, experimental and modelling approaches, to identify key processes driving populations' decline. Given our predictions, and those of others, about the increasing vulnerability of macroalgae (Wernberg et al., 2016a, 2010, ; Mineur et al. 2015), reinforcing their protection against additional human disturbances might make the difference between local extinctions or demographic viability.

5.6 Acknowledgements

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Chapter 6

General Discussion

Quantifying algae population dynamics still remains a big challenge for ecologists. Despite the ecological relevance of macroalgae in temperate marine ecosystems worldwide, few studies have explored the demography and life history traits of such habitat-forming species. Probably because of the difficulty to monitor their different life stages and the myriad of processes that determine their population dynamics. This dissertation is an attempt to disclose the main processes determining the life history, natural dynamics and disturbance responses of the model species *Cystoseira zosteroides*. Overall, in our opinion, with this thesis we provided important insights into the current ecological knowledge about macroalgae populations, rendering essential information that may help to assess their conservation status, and design effective management tools.

In the following lines, we will discuss most of the elements covered throughout the thesis in order to provide a broader view of its contribution, as well as to bring up some remaining questions and hypothesis derived from our work, that may worth to be explored in the future.

6.1 *Cystoseira zosteroides* is a long-lived species with slow population dynamics

In Chapters 4 and 5 we provided important insights into the use of demographic modelling tools to describe and predict the population dynamics of macroalge. We present quantitative evidence that natural and undisturbed *C. zosteroides* populations are dominated by large individuals, with little dependence on reproductive processes and very limited dispersal abilities (Chapters 2, 3 and 4), what previous authors already suggested (Ballesteros 1990; Hereu et al. 2008a; Ballesteros et al. 2009). This species also showed very slow growth rates, and adult individuals have high survival, with predicted life spans over 50 years (Chapter 4). These results rank *C. zosteroides* among the most long-lived macroalgae studied to date.

Considering the deep-water environments at which *C. zosteroides* inhabits, it is not surprising that this species displays a very slow population dynamics. Environmental conditions have a strong influence on the life history of species (see General Introduction 1). In general, deep-water marine environments are more stable than shallower ones, in terms of annual variability of key environmental factors, with light becoming a limiting factor (Garrabou et al., 2002). Under these conditions, this species must maximize their photosynthetic efficiency. Hence, compared to other *Cystoseira* species, *C. zosteroides* has the lowest compensation points (I_c) and the fastest saturation points (I_k) (Sant, 2003). Besides, *C. zosteroides* must maximize the absorption of nutrients during the periods of high productivity, by developing their deciduous branches, with which it photosynthesises and store the products in the tophules and perennial parts as reservoirs, to overcome nutrient limitation during the rest of the year (Box 2; Ballesteros, 1990). This investment on a perennial thallus and the formation of tophules to retain resources maximizes the survival and lifespan of individuals, but lowers their vegetative growth and reproductive rates (Chapter 4). This results in stable populations maintained by persistent adults, with population growth rates close to stationary (λ=1).

6.2 Trees, shrubs or algae? On the life history strategies of macroalgae

Macroalgae populations have been perceived as the trees of the sea for so long (Darwin, 1972; Steneck et al., 2002). Despite this interesting analogy between large brown algae and seed plants, we still do not know if the differences between their life histories and environments may require different conceptual approaches. Life history principles should transgress marine and terrestrial environments, but still few studies have tested for the existence of differences between ecological theories in these realms (Steele, 1991; Webb, 2012). For this reason, in Chapter 4 we dug deeper into the natural dynamics of brown algae under a backdrop of a theoretical terrestrial life history framework.

In contrast to the general perception that macroalgae are “fast” or “r-strategist” species, reflected even in some textbooks (e.g. Miller and Spoolman 2011), in Chapter 4 we illustrated that macroalgae can display contrasting life history strategies, with similar patterns of terrestrial species. Most kelp and intertidal fucoid populations depend on reproduction and growth; in contrast to long-lived species, such as *Ascophyllum nodosum*, *Laminaria digitata* and *C. zosteroides*, which almost depend on survival. Many kelp forests are highly dynamic, with frequent local extinction and colonization events driven by high recruitment and fast individual growth rates (Edwards 2004; Castorani et al. 2017). However, this temporal variation contrasts with the dynamics of other marine foundation species such as seagrasses (Shelton et al., 2017) and corals (Hughes et al., 1999), which tend to present “slower” population dynamics and lower recovery rates. With some of the results of this thesis, we provided strong evidence that this is not the case for all macroalgae species, and they can present very different life history strategies, similar to those found in terrestrial plants.

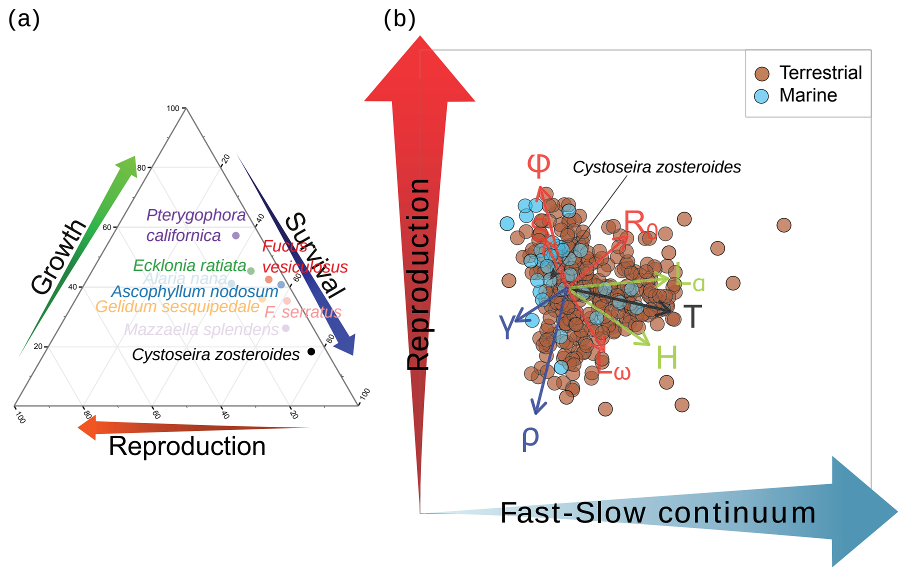
In Chapter 4 we also illustrated the need to study the life history and population dynamics of macroalgae species, especially in a conservation context. Despite the emerging literature and data availability, most ecological models about macroalgae are still developed at the community-level (Littler and Littler 1980; Steneck and Dethier 1994; Jänes et al. 2016). The basis of these models is to group similar species accordingly to their morphological and/or functional traits. Then, functional groups are linked to abiotic factors, in order to predict community composition in a given environment, according to the levels of disturbances or/and productivity (Steneck and Dethier, 1994). This method should enable to compare between very different systems; however, functional traits are often subjective to define and are difficult to adapt to the particularities of different macroalgal assemblages worldwide (e.g. Phillips et al. 1997). In this thesis, we evidence that the ternary plot may provide a useful framework to classify and predict macroalgae dynamics. Still, how these patterns translate into communities and ecosystem functioning remains an open question. The reduced number of population studies about macroalgae limits the generalities of our results, but provides interesting insights with potential contributions into general ecological principles (Box 3).

Box 3: Exploring macroalgae life history strategies.

The framework used in Chapter 4 has limitations that worth to mention. The triangular ordination is limited by mathematical constraints (Shea et al. 1994; Enright et al. 1995) and it does not take into account the indirect effects that demographic parameters have on each other (Tienderen 1995; Franco and Silvertown 2004). Thus, to overcome these drawbacks and to see the consistency of our results, here we applied more sophisticated analyses and also we put our results in a broader context.

First, in (a) we used vital rate elasticities instead of matrix elements' (Franco and Silvertown, 2004), and we added new data with more species, including red algae. We had to exclude some species such as *L. digitata*, because of the lack of vital rates data.

The patterns in (a) remained more or less consistent with those observed in Chapter 4. Kelp and intertidal fucoid populations depended mostly on reproduction and growth. *C. zosteroides* remained as the species with the highest dependence on survival processes, while *A. nodosum* showed lower values than in Chapter 4. Interestingly, *Mazzaella splendens* and *Gelidium sesquipedale*, showed a high dependency on survival. In Chapter 4 we excluded these species because of the complexities of their matrices (Enright et al., 1995). These red algae display isomorphic biphasic life cycles, alternating haploid and diploid phases, with tetraspores and carpospores as resistant stages. In intertidal environments with high hydrodynamic stress, this life cycle and the high dependency of their populations on survival processes, has been also argued to be a “storage effect”. Under the stochastic environments where these red algae inhabit, recruitment is not constant, so to maintain the population during unfavourable periods, some holdfasts do not produce reproductive organs every year and remain latent, increasing survival (Engel et al., 2001). Overall, (a) evidence that the patterns observed in Chapter 4 are consistent and ecologically informative.



In (b) we exposed the results of Chapter 4 to a broader context, by placing *C. zosteroides* in a more recently developed life history framework (Salguero-Gómez, 2017; Salguero-Gómez et al., 2016b). To do so, we incorporated animal studies from COMADRE Animal Matrix Database (Salguero-Gómez et al., 2016a) and plant studies from the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015). Overall, we compiled demographic data on 69 populations of 40 marine species (blue dots) and 1374 populations of 535 terrestrial species (brown dots) of sessile or of limited mobility. We derived a set of key life history traits for each species that measured investments in population turnover, longevity, growth or reproduction (listed in Salguero-Gómez et al., 2016b). To account for the lack of independence between related species (Blomberg et al., 2003), we also constructed a species-level phylogenetic tree using the "rotl" package in R (R Development Core Team, 2014). We acquired the algae, plant and animal trees from the Open Tree of Life (Hinchliff et al., 2015, ; `https://tree.opentreeoflife.org`). Then, we used a phylogenetically corrected principal component analyses (PCA; B) to ordinate species according to an axis (X) related to the fast-slow continuum, and an axis (Y) related to their reproductive strategy.

Surprisingly, *C. zosteriodes* was not located at any extreme of the range of life history strategies. Considering the results of Chapter 4, we expected that *C. zosteroides* would be a very "slow" species, located at the right corner of the X axis. Moreover, we awaited *C. zosteroides* to be placed at the bottom of Y axis, with low frequencies of reproduction. Overall, this suggests that considered in a broader context, *C. zosteroides* life history is not as extreme as we initially assumed. However, here, we just scratched the surface of what trans-realm comparative demography may offer to general life history theory, but it provides a baseline of future work with potential contributions into general ecological principles, life history evolution and conservation science[a].

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[a] The results presented here are part of an ongoing collaboration with Roberto Salguero-Gómez from the University of Oxford and Maria Beger from the University of Leeds.

6.3 Density-dependence is an important macroalgal population process

Intraspecific interactions are one of the key elements that determine population dynamics of macroalgae, what has a strong influence on their ability to resist to disturbances, through positive/negative feedbacks on recovery processes. The drivers of density-dependence can be very different in macroalgae (Scrosati 2005; Schiel and Foster 2006), with both positive (Creed et al. 1996; Bennett and Wernberg 2014) and negative (Reed 1990b; Ang and de Wreede 1992) interactions being possible.

In Chapters 2 and 3 we evidence that the recruitment of *C. zosteroides* populations is subject to negative density-dependence. Indeed, previously to our works, a long-term monitoring study showed that *C. zosteroides* recruitment was almost absent over 10 years in natural and well-preserved populations in Scandola Natural Park (Corsica, France; Ballesteros et al. 2009). These authors hypothesized that recruitment limitation could be a consequence of the negative influence of adult stands on the early survival of recruits (i.e. negative density-dependence) or due to the presence of invasive species, such as *Womersleyella setacea* (Ballesteros et al., 2009).

In December 2008 an extreme storm wiped out a substantial number of adult *C. zosteroides* stands along the Catalan coast, what triggered recruitment rates in some of our monitored populations (Navarro et al., 2011). We took advantage of this serendipitous event, and in Chapter 2 we correlated the number of adult individuals with the number of recruits. The correlation was significantly negative, suggesting that in some way the presence of adult stands exerted a negative effect on the recruitment. Still, this did not disentangle if density-dependence was caused due to a reduction in recruitment rates and/or a decrease in recruit survival. To shed some light on this hypothesis, in Chapter 3 we measured the difference between recruit survival inside and outside adult canopy. We observed that, although recruitment rates were high inside *C. zosteroides* populations, underneath the canopy recruit survival was significantly lower.

Quantifying the effect of adult density on recruitment enabled us to more accurately predict the disturbance responses of *C. zosteroides*, by incorporating this process into demographic models (Chapters 4 and 5). We demonstrated that density-dependence plays a key role in the recovery processes of this macroalgae species. However, despite being a widespread mechanism in many natural systems, to our knowledge, this thesis is the first attempt to incorporate density-dependence into a macroalgal population model.

The underlying mechanisms behind this negative density-dependence remain to be discovered, and multiple hypotheses arose from our results. From one hand, given the deep distribution of *C. zosteroides*, light inhibition by conspecifics could be a major restricting factor. Indeed, light limitation can diminish growth and survival rates of early macroalgal stages, negatively affecting their development (Cervin et al., 2005; Irving et al., 2009). Another possible explanation would be that the associated community thriving underneath the canopy reduced recruit survival by competition with the underlying community (Vadas et al. 1992; Bulleri et al. 2002). Indeed, in Chapter 3 we observed that plates located inside the adult canopy were colonized by different species of sponges, turf-forming algae and invertebrates. Finally, propagules arriving in high densities at natural gaps can experience higher mortality than those distributed sparsely over larger areas (Kendrick, 1994; Steen and Scrosati, 2004). This suggests that early competition could be another possible explanation for the observed negative density-dependence.

The hypothesis presented here could explain our results by themselves, but they are not mutually excluding. Given the importance of density-dependence processes for population persistence, it is clear that more studies are needed to disentangle the underlying mechanisms driving density-dependence in macroalgal forests and elucidate which factors determine their variation among species.

6.4 Ecological and management implications of limited dispersal

Dispersal is a key life history trait, which encapsulates multiple processes linking population dynamics with the spatial distribution of species (Clobert et al., 2012). In Chapter 3 we demonstrated the importance of understanding the effective dispersal patterns of macroalgae. Cumulative disturbances worldwide have resulted in a widespread habitat loss, rendering populations smaller, isolated and more vulnerable to environmental and demographic stochasticity. Therefore, elucidating the dispersal scales of species is critical for the conservation and the restoration of ecosystems (Baguette et al. 2013; Aben et al. 2016).

Historically, marine systems have been assumed to be connected over larger spatial scales than terrestrial systems (Caley et al. 1996; Gaylord and Gaines 2000; Carr et al. 2003). The fluid dynamics of water and its density, coupled with the relatively small size of marine spores, eggs, zygotes and larvae, were thought to enable marine propagules to last longer on the water column, increasing their dispersal potential (Bradbury and Snelgrove, 2001; Carr et al., 2003). Yet, as the number of studies about the dispersal of marine taxa increases, the picture becomes more complex, questioning the paradigm that marine populations are demographically “open” (Swearer et al. 2002; Palumbi 2004; Levin 2006; Cowen and Sponaugle 2009).

Our findings in Chapter 3 challenge the “open” hypothesis and support that macroalgae disperse at very small spatial scales (Kinlan and Gaines, 2003; Kinlan et al., 2005). By reviewing direct estimates of settlement and recruitment from different studies about fucoid and kelp species, we observed that maximum dispersal estimates did not exceed 500 m for any species. Moreover, although macroalgal propagules may have behaviors that can facilitate settlement (Santelices, 1990), they are only effective at the scale of millimeters (Gaylord et al., 2002; Graham, 2003). Our findings support that macroalgae dispersal is a very passive process, given that propagules only remain suspended in the water column for a few hours to weeks, what limits their dispersal from few meters to few kilometers, in contrast to most of invertebrate or fish larvae (Kinlan and Gaines, 2003; Kinlan et al., 2005).

Although this was previously demonstrated by a bunch of studies (Kinlan and Gaines 2003; Kinlan et al. 2005; Durrant et al. 2014), these often pool all macroalgae species in the same basket, again without accounting for potential differences driven by their particular life histories. In Chapter 3 we highlighted the differences between fucoids and kelps, with the former having lower dispersal estimates than the later. Indeed, *C. zosteroides* has a mean dispersal distance of few meters, with maximum estimates that do not exceed 20 m. This is further supported by the high genetic differentiation found in *Cystoseira* populations (Buonomo et al., 2017), as well as other fucoid species, such as *Fucus vesiculosus* (Assis et al., 2014), *Pelvetia canaliculata* (Neiva et al., 2014) or *Bifurcaria bifurcata* (Neiva et al., 2015).

Understanding dispersal patterns is relevant to comprehend the population dynamics and management of species, highlighting the importance of dispersal patterns in ecology but also in conservation biology. Recruitment from propagules is the only means of colonization for sessile marine organisms, and the constraints on propagule supply are particularly important in systems subjected to frequent disturbances. Higher dispersal distances may result in more homogenous recovery following large disturbances, what may explain the rapid recovery of some kelp species (Reed et al., 2000). The higher density (i.e. bigger size and heavier) of fucoid propagules may be the main cause of their lower dispersal potential (Schiel and Foster, 2006), limiting their recovery abilities. In the case of *C. zosteroides*, with slow growth rates and late reproductive age, its poor dispersal abilities may worsen the impact of disturbances and highlight their vulnerability. In addition, it suggests that the loss of this species from large, fragmented areas would be hardly reversible even by restoration actions, as limited dispersal would prevent recolonization at short time scales.

6.5 Disturbances strongly influence macroalgae population dynamics

Disturbances play a crucial role structuring natural systems (Levin and Paine, 1974), but human-derived activities have altered their frequency and intensity (Jentsch et al., 2007). Hence, under the current global change scenario, it is fundamental not only to understand the natural dynamics of species but also to predict their responses to altered disturbance regimes. For this reason, a substantial part of this thesis is oriented towards disclosing the responses of *C. zosteroides* populations to disturbances.

Given that marine ecosystems worldwide are facing multiple disturbances (Halpern et al., 2008; Poloczanska et al., 2013); in Chapters 4 and 5 we explored the combined effect of local and global stressors. Ecosystems are sometimes exposed to acute events of high intensity, that take place suddenly but with low frequency (Jentsch et al., 2007), such as storms (Navarro et al., 2011) or heatwaves (Wernberg et al., 2012). Some species can compensate these punctual mortality events, for example, through the arrival of new recruits (Dayton et al., 1999). However, these punctual disturbances are currently occurring within a background of chronic stressors, which act with low intensity but over longer time periods, such as global warming (Stuart-Smith et al., 2015) or ocean acidification (Kroeker et al., 2013). In addition, there are punctual human-derived disturbances that may add additional mortalities (Strain et al., 2014).

In Chapter 4 we simulated the consequences of the combined effect of two major physical (local and global) disturbances impacting macroalgal communities, such as ghost fishing nets and storms (Strain et al., 2014). By simulating different frequencies of those disturbances, taking place at the same time, we demonstrated that even low levels of local perturbations result in a high decrease of *C. zosteroides* ability to compensate further mortality events (such as major storms). Complementary, in Chapter 5 we explored the impact of warming on vulnerable stages (recruits) and how this could affect the population-level responses to further physical disturbances. Our findings highlighted that ocean warming is unlikely to be a direct threat to *C. zosteroides* populations. However, reduced resilience of *Cystoseira* forests, as a consequence of decreased recruitment, will exacerbate effects of concurrent stressors and disturbances, including major storms (Navarro et al., 2011), ghost fishing nets (Thibaut et al., 2005), or even water quality (Sales et al., 2011).

The temporal scales that these species need to recover from disturbances are also fundamental to understand and predict their viability in a changing world. We showed that *C. zosteroides* would probably need decades to recuperate their initial population structure (Chapter 4), and this could be worsened by rising temperatures or further stressors (Chapters 4 and 5). These results contrast with those observed in some kelp forests, which usually need only a few years to recover after major disturbances (Dayton and Tegner, 1984; Tegner et al., 1997). Consequently, if disturbances increase in number and intensity, according to current predictions (Harley et al., 2012; IPCC, 2013), the paucity of *C. zosteroides* (Chapters 2 and 4), together with its low dispersal ability (Chapter 3) and narrow distribution (mainly found in the NW Mediterranean), suggest that they may have nowhere to go but deeper waters, where light conditions and nutrient availability may preclude its viability (Ballesteros et al., 2009).

Nevertheless, an encouraging finding is the observed natural resilience of *C. zosteroides*, suggesting that this species is still able to resist major disturbances. In contrast to many other co-occurring and habitat-forming species in the NW Mediterranean (e.g. *Paramuricea clavata*, Linares et al. 2007), we showed that, to some extent, *C. zosteroides* is able to buffer high mortality pulses. Although it is likely that this response will not be the same for all populations and disturbances, it suggests that by reducing the impact of local stressors, we could enhance the natural resilience of *C. zosteroides* populations and increase their viability in the current global change scenario. In addition, these results highlight the importance of understanding the factors influencing *C. zosteroides* early dynamics, which in turn determines the “windows” of recruitment that maintains their populations.

6.6 Insights for *C. zosteroides* conservation and management

The knowledge provided in this dissertation establishes a basis to develop conservation actions and restoration tools for *C. zosteroides*. The paucity of their populations suggest that adult transplantation could cause a high impact in natural/donor populations; thus, restoration actions are being developed to take advantage of the high fertility of their branches without damaging adult individuals (a technique already applied in other macroalgae species; Hernández-Carmona et al. 2000; Falace et al. 2006). However, high recruitment success under cleared canopies, points that *C. zosteroides* is able to recover after major disturbances, if there is recruitment substrate available, without the need of any previous adult facilitation (Bulleri 2009; Bennett et al. 2015).

Furthermore, cultured individuals in Chapter 5 provided us fundamental information about the viability of maintaining this species in aquaria. This is now being used to design *ex situ* transplantation actions. Moreover, the high recruitment rates observed in the collectors displayed during Chapter 3, suggests that this can be used as a source of individuals for transplantation actions. Indeed, the individuals that we first observed in the collectors at the beginning of this thesis are now 3 years old and have been transplanted to degraded populations, to be evaluated as a transplantation method. In this regard, we also have precisely measured the fertility period of this species, what may be fundamental to further develop these "seedling techniques". Finally, considering that the mean dispersal of this species is very limited, we know now that transplants should be placed at distances closer than 5 m, to promote the effective dispersal and ensure the viability of restoration actions.

To integrate the information provided by this thesis in a management context, here we built a workflow, which may also apply to other *Cystoseira* or macroalgae species (Figure 6.1). The sampling design (i.e. number of sites, temporal scale, etc.) should be adapted to the life history of the species. By monitoring populations through space and time, we would be able to detect changes in the number of individuals and, their structure and dynamics. In addition, field or laboratory experiments would be needed to understand particular population processes. With this information in hand, it would be possible to determine if populations suffered mortality/ies pulse/s or other threats by direct estimation, or indirectly by observing populations dominated by reproductive processes and/or small-sized individuals (Chapters 2 and 4). Given that during this period their populations are very vulnerable, further protection to local disturbances should be promoted. In addition, the demographic information collected annually should be incorporated into the models to forecast their extinction probabilities. When extinction is imminent or when population recovery is very unlikely, restoration actions should be taken. By monitoring these altered or restored populations we could decide if further management actions are needed.

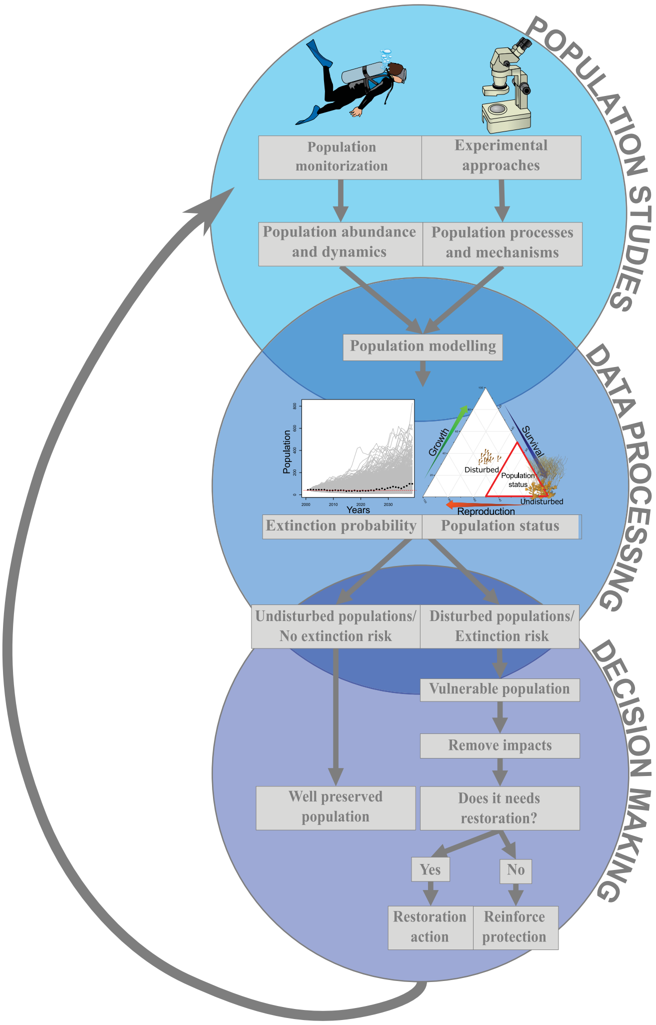

Figure 6.1: Workflow for appropriate conservation and management of *Cystoseira* populations in the Mediterranean Sea. This flow-chart encompasses different stages, which *per se* are complicate processes that will require appropriate knowledge of the studied system: (1) Population studies, which represent *in situ* monitoring, to see changes in their abundance and/or dynamics, this is fundamentally coupled with field or laboratory experiments, to unveil population-related processes; (2) Analysis, this part is fundamental to objectively interpret the patterns observed in the field, and determine the conservation status of the population; (3) Decision making, with the analytical part in hand we will be able to decide whether the population needs a conservation or restoration action.

6.7 Limitations

Still the results of this thesis have their own limitations that be must taken into account. Here we have listed those that we considered more relevant within the context of this dissertation.

On the first place, our data come from a limited number of years and a relatively small number of populations. The main reason behind this is because of the difficulty of *in situ* studies for this species and limited funding for macroalgae monitoring studies. Another potential bias of our studied populations is that we studied them at the shallowest part of their vertical distribution. Because of time restrictions diving at the depths at which *C. zosteroides* is located, we tend to study these populations at their shallowest vertical distribution. Indeed, some populations in Medes Islands and Montgrí Coast are found as shallow as 15 m. Yet we still do not know if they display contrasting population dynamics at different depths. That would require a high level of adaptation to local conditions, which is likely for this species, given their restricted dispersal abilities (Chapter 3). Thus, this brings up an interesting question, which also may be worth to explore.

In addition, most of the populations studied here come from marine protected areas, suggesting potential differences with unprotected populations. This could slightly bias our perception about the natural dynamics of this species. However, some of our unpublished data suggest that their population dynamics is not related to their protection status. We also must take into account that we are probably studying already altered populations. In fact, long-lived and slow species do not always respond rapidly to disturbances; instead, they remain in a borrowed time of altered condition before their disappearance (Hughes et al., 2013). Evidence of this is that our studied populations show slightly lower survival than those found in Scandola Marine Reserve (Ballesteros et al., 2009), probably the most pristine population studied to date. Nevertheless, this suggests that there is still an important window of opportunity to recover such systems (Hughes et al., 2013).

Finally, here we have provided a simplified view of how this species may respond to disturbances. However, larger spatial and temporal scales are needed to make robust predictions. Furthermore, here we did not take into account the physiological consequences or the sub-lethal effects of stressors. Even, the number of disturbances explored here are still limited, and the effects of other threats, such as ocean acidification or pollution, remain to be tested. Aside from these drawbacks, we evidence that altered perturbation regimes, are increasing the susceptibility of *Cystoseira* forests. Thus, further protection, coupled with restoration actions may be needed to ameliorate *Cystoseira* conservation status.

6.8 Future perspectives

6.8.1 Depth as a life history gradient

In general, our findings about the *C. zosteroides* dynamics raise some hypotheses to elucidate the role of depth as a potential driver of life history strategies. Here we have observed that this species presents a very "slow" population dynamics, ranking among the longest-lived macroalgae species. On the light of these results, it would be worth to explore the dynamics of other *Cystoseira* and/or macroalgae species living in shallower environments. The main environmental factors relevant to the organization of benthic communities vary predictably with depth (Zabala and Ballesteros 1989; Ballesteros 1991; Garrabou et al. 2002). Light intensity, temperature and wave impact decrease with depth, both in magnitude and in temporal variability. This environmental gradient is coupled with changes in communities, with an increase of diversity and species richness (i.e. community structure), and a decrease of turnover rates and species growth rates (i.e. community dynamics) with depth (Garrabou et al., 2002). Considering these early studies in the Mediterranean we venture to guess that shallower species may present faster population dynamics than deeper-water species. This may be especially true for macroalgae, given that light attenuation is intensified with depth. Under light limitation conditions, species must lower metabolic rates and must store the few available resources into long-lived stages, which ensure the viability of their populations. Indeed, some of the results of Chapter 4, pointed towards that direction.

With the results of this thesis, these conclusions are rather speculative. However, we strongly believe that the vertical distribution of *Cystoseria* species would provide the ideal means of testing such hypothesis. With intertidal *Cystoseira* species presumably being “faster” than those living in deeper waters, with *C. zosteroides* probably representing the “slowest” end of such continuum. By using *Cystoseira* genus we would be able to isolate or minimize the evolutionary history effect in such tightly related taxa and test the environmental filtering effect caused by increasing depth. The relevance of such results stretches beyond ecological theory, as they would help us to predict which species present higher abilities to respond to disturbances and to find optimal management strategies according to depth ranges.

6.8.2 Intraspecific interactions across depth gradients

The previous hypothesis also raises the question of how intraspecific interactions may change with increasing water depth. Competition has been argued to be a prevailing interaction in subtidal environments (Schiel and Foster, 2006), but positive interactions are more widespread than previously thought in intertidal marine systems (Bulleri, 2009). Indeed, Bennett et al. (2015) suggested that under a depth gradient, intraspecific interactions of macroalgae may change from positive to neutral.

In shallow environments, macroalgal canopy can provide protection against physical stress, for example by retaining moisture (Johnson and Brawley, 1998), dampening water motion (Schiel and Foster, 1986) or protecting from excessive sunlight (Bennett and Wernberg, 2014). As depth increases, there is no need for protection from desiccation or high radiation, so interactions should become neutral (Bennett et al., 2015). Our findings of negative interactions among *C. zosteroides* conspecifics challenge this hypothesis. However, it may also extend it, given that Bennett et al. (2015) only considered a depth gradient of almost 10 m, while we extended it to 30 m. As depth increases light becomes a limiting factor and if canopy reduces light availability to the understory, it may inhibit the development of recruits (Reed, 1990b).

Again, we consider that *Cystoseira* species provide a great opportunity to test changes in intraspecific interactions with depths. By experimentally exploring the changes on the intraspecific interactions of different *Cystoseira* species along a depth gradient, would enable us to confirm, refute or extend the hypothesis proposed by Bennett et al. (2015).

6.8.3 Long-distance dispersal and population genetics

The patterns found in Chapter 3 also raise new questions to be answered about the dispersal of *Cystoseira* and macroalagae species. In addition to the effective dispersal at small scales, long-distance dispersal events (LDD) are still poorly understood, which are more relevant for the colonization of new or fragmented habitats (Clark et al., 2003). Most of these LDD events in macroalgae may come from drifting fragments that can travel long distances (Hernández-Carmona et al., 2006), what is difficult to quantify (Castorani et al., 2017). Thus, the patterns of connectivity at larger scales can only be unraveled using genetic tools, with which we may obtain crucial insights for the management of macroalgae (Coleman et al., 2011b; Durrant et al., 2014). Genetic markers for *Cystoseira* species still remain poorly resolved (Buonomo et al., 2017), so further development of genetic tools should be promoted for these species.

The differences in the ability of propagule dispersal between the two major brown algae groups also suggest a linkage between the life history of species and their dispersal ability. Do "faster" species have higher ability to disperse and colonization ability? Which is the influence of short- *vs* large-distance dispersal into the population dynamics of macroalgae? These and many other questions relating the role of dispersal as a key life history may be also worth to explore.

6.8.4 Impacts of global warming into the whole life cycle

One of the main drawbacks of Chapter 5 was our lack of data about warming effects on adults stages. Despite the lack of field evidences of adult mortalities in *C. zosteroides* during extreme temperatures, it is likely that changing temperature regimes will impact their demographic performance (Harley et al., 2012). For this reason, it would be worth to explore the physiological and demographic responses of this species exposed to a set of temperatures in controlled conditions, in order to identify the critical thresholds of their thermal resistance. This information would improve our predictions about the long-term and short-term impacts of global warming.

6.8.5 Life history strategies across terrestrial and marine realms

A key idea that emerged from our comparative analyses in Chapter 4, was the existence of different life history principles ruling marine and terrestrial realms. The development of life history theory suffers from systematic taxonomic and ecosystem biases, with most life history “generalities” derived from terrestrial and emblematic taxa such as birds, reptiles, mammals or flowering plants, and it has been especially neglectful of marine species. All organisms are governed by the same demographic processes of maintenance, development, and reproduction, and by combining these demographic processes species have evolved a myriad of life history strategies. However, marine and terrestrial environments strongly differ in the spatial and temporal variability of biological, physical and chemical processes. For this reason, further testing of classical life history principles on marine species would enlighten the generalities of such ecological theories.

6.8.6 The need for integrative approaches in ecology

In this thesis we evidence that the quantification of life-history strategies is fundamental to advance ecology towards a predictive science enabling reliable forecasting, with its direct application to conservation. Still, our predictions do not fully characterize the range of likely biological changes in the future for *C. zosteroides*. Here we focused on the demography and dispersal of a particular model species, but that is only a part of the history. To accurately predict the fate of species in a global change scenario integrative approaches are needed, not only including demography and dispersal (such in our case), but should also incorporate distribution patterns, physiology, species interactions, and evolution (Urban et al., 2016).

6.9 Concluding remarks

Understanding the complex patterns of nature comes through the development of appropriate theoretical frameworks. However, ignoring the idiosyncratic character of the systems that we want to comprehend has the risk into falling in over-simplifications of reality. This thesis is an attempt to improve the current view about the population ecology of macroalgae. We consider that we have contributed beyond the mere description of the population dynamics of *C. zosteroides*, with important insights into general ecological theory. We challenged early perceptions about the population dynamics of macroalgae, by providing quantitative evidence that they can be long-lived and present relatively “slow” life histories. Furthermore, although general life history models seem to apply to macroalgae, further testing and development is still needed.

We also evidence the need for long-term monitoring programs about macroalgae populations, what also applies to other ecologically relevant species. Despite the few years that we have studied the dynamics of *C. zosteroides*, throughout this thesis we have provided important insights about their population dynamics. Nevertheless, ecological and evolutionary processes affecting populations often occur over multiple years or decades (Clutton-Brock and Sheldon, 2010). In addition, there is a current underrepresentation about macroalgae demographic studies, and even in plants, their average duration is close to 4 years (e.g. Salguero-Gómez et al., 2015), corresponding to the length of an average Ph.D. project or that of most funding agencies. Thus, the study of *C. zosteroides* populations needs continuity during the forthcoming years. In addition, natural populations’ studies still require broader spatial and temporal scales to adequately quantify the demographic rates controlling their abundances, to integrate environmental stochasticity, to understand the evolutionary processes that may promote adaptation and to define how population changes echoes into community processes.

In this PhD, we have just scratched the surface of macroalgae life histories, and future studies should explore the gaps pointed here, coupling new analytical tools and available data, to better comprehend their dynamics, as well as to enlighten their future in our changing world.

6.10 General Conclusions

Chapter 2

- The investment of *C. zosteroides* in perennial thallus and reservoir vesicles (tophules) confers a high survival to adult individuals, while recruits, which do not have perennial thallus and tophules, present substantially lower survival rates.

- Large disturbances play a key role structuring *C. zosteroides* populations. While undisturbed populations are dominated by large individuals, occasional disturbances clear up space promoting recruitment. Thus, similarly to many other long-lived species, their populations are conformed by intense pulses of recruitment, which produce cohorts that survive over long time periods.

- The contrasting size structure and recruitment dynamics suggested that this species is strongly influenced by density-driven responses, with adult canopy having a negative effect on the recruitment success. Adult densities are negatively correlated with recruit density, suggesting a negative density-dependence influence on recruitment success.

Chapter 3

- Yearly survival of early *C. zosteroides* stages is lowered inside the canopy of developed populations.

- For this species, effective dispersal is limited to few meters from populations' sources.

- Dispersal patterns show a high level of heterogeneity at small-scale, what suggest that underling factors driving these differences among populations must be studied.

- Our comparative analysis supports that brown macroalgae have a very restricted effective dispersal. However, kelp species seem to have a higher dispersal potential, given the small size and density of their spores.

Chapter 4

- All the life-history traits and population dynamics placed *C. zosteroides* among the most long-lived macroalgae species. They maximize survival by investing in a perennial thallus and reservoir vesicles, at the expense of growth and reproduction. This pattern is shared by other late successional terrestrial plants such shrubs and trees.

- Using the ternary elasticity plot we could identify different life history strategies among macroalgae. The comparative analyses suggested interesting parallelisms between the life histories of macroalgae and terrestrial plants.

- Density-dependence is a key process for *C. zosteroides* population dynamics. This species is able to buffer mortality pulses by increasing the number of recruits due to the new space liberated and, therefore, lower intraspecific competition. However, this modifies the population dynamics of the species, from depending on the survival of individuals to depend on reproductive processes.

- Despite the observed high resilience of this species, recurrent major disturbances (e.g. major storm), can drive the collapse of their populations. Indeed, local disturbances (e.g. ghost fishing nets) with lower impact, demise their ability to recover from further disturbances. This highlights that increases in local and global stressors may erode the resilience of macroalgae, resulting in a loss of structural complexity in the benthic communities of temperate seas.

Chapter 5

- Temperature highly impacts the development of *C. zosteroides* early life stages, by significantly decreasing their settlement and survival rates.

- Despite its impact on early stages, temperature *per se* did not significantly affect to the long-term viability of *C. zosteroides* populations given that the high adult survival buffered against temperature-induced recruitment failure.

- Temperature had a negative effect on the recovery abilities of *C. zosteroides*. High temperatures rendered their populations more vulnerable to other sources of disturbances, such as storms or ghost fishing nets.

- These results highlight how warming may have unnoticed effects that increase the vulnerability of populations to further disturbances, and evidence the need to incorporate abiotic interactions in demographic models.

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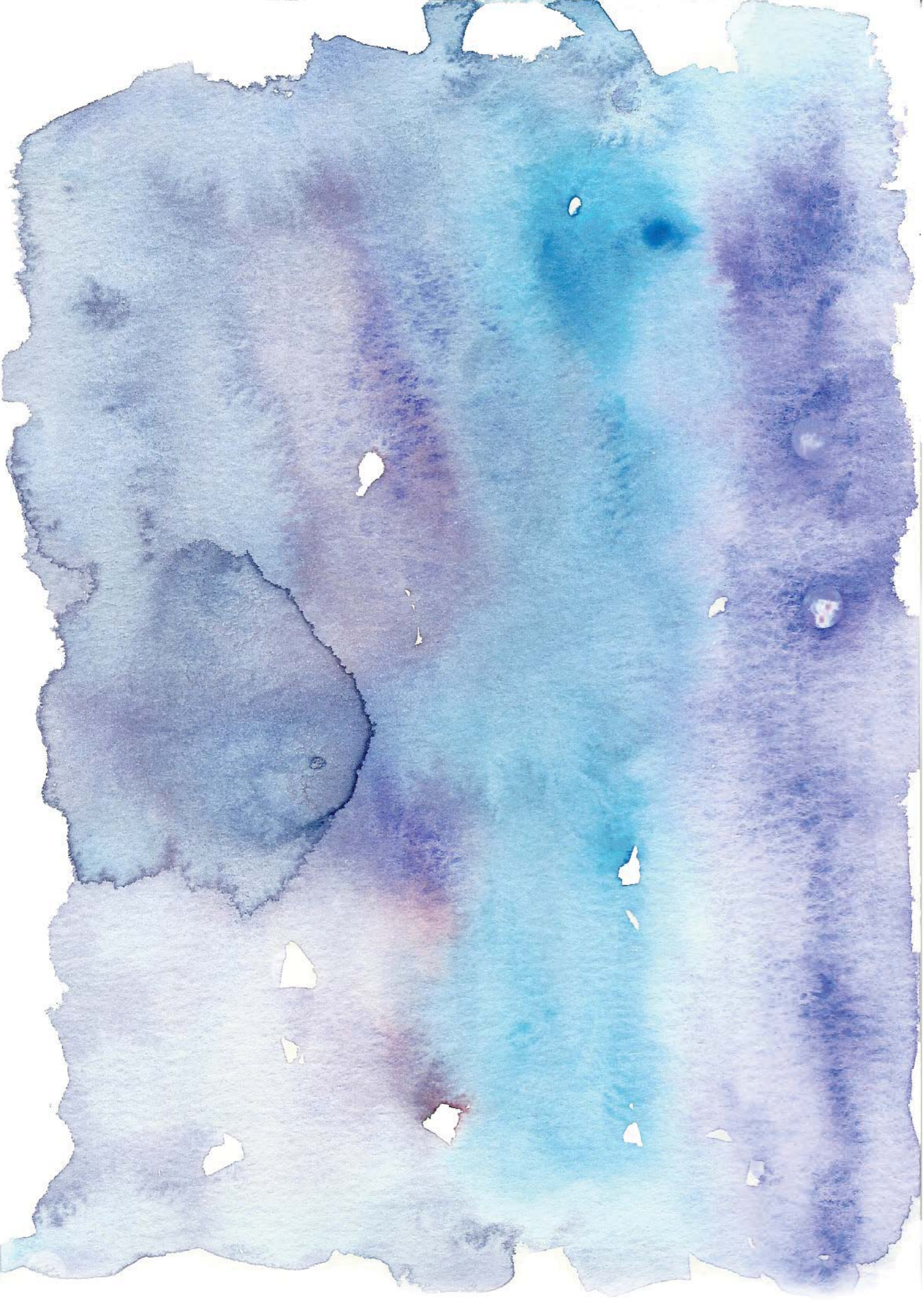

Appendix A

Chapter 2 Supporting Information

Table A.1: Characteristics of sample sites.

Sampling site	Mean depth (m)	Substrate type	Number of transects	Sampled area (m^2)
Medes Islands	20	Small rocks and stones	2	10
Montgrí Coast	20	Big rocky boulders	3	14
Columbretes I	28	Rocky bottom	3	9
Columbretes II	24	Rocky bottom	3	9
Cap de Creus	23	Big rocky boulders surrounded by sand	2	19

Table A.2: Results from the two-sample Kolmogrov-Smirnov test of the comparison between size-structure distributions of populations.

Population 1	Population 2	D	P-value
2010 Columbretes I	2010 Columbretes I	0.00	1.00
2010 Columbretes I	2011 Columbretes I	0.14	0.18
2010 Columbretes I	2012 Columbretes I	0.23	<0.001
2010 Columbretes I	2010 Columbretes II	0.17	0.04
2010 Columbretes I	2011 Columbretes II	0.38	<0.001
2010 Columbretes I	2012 Columbretes II	0.48	<0.001
2010 Columbretes I	2008 Medes	0.83	<0.001
2010 Columbretes I	2009 Medes	0.91	<0.001
2010 Columbretes I	2010 Medes	0.90	<0.001
2010 Columbretes I	2011 Medes	0.91	<0.001
2010 Columbretes I	2010 Cap de Creus	0.72	<0.001
2010 Columbretes I	2011 Cap de Creus	0.71	<0.001
2010 Columbretes I	2012 Cap de Creus	0.70	<0.001
2010 Columbretes I	2008 Montgrí	0.32	<0.001
2010 Columbretes I	2009 Montgrí	0.32	<0.001
2010 Columbretes I	2010 Montgrí	0.42	<0.001
2010 Columbretes I	2011 Montgrí	0.35	<0.001
2011 Columbretes I	2010 Columbretes I	0.14	0.18
2011 Columbretes I	2011 Columbretes I	0.00	1.00
2011 Columbretes I	2012 Columbretes I	0.11	0.40
2011 Columbretes I	2010 Columbretes II	0.10	0.60
2011 Columbretes I	2011 Columbretes II	0.26	<0.001
2011 Columbretes I	2012 Columbretes II	0.39	<0.001
2011 Columbretes I	2008 Medes	0.84	<0.001
2011 Columbretes I	2009 Medes	0.91	<0.001
2011 Columbretes I	2010 Medes	0.90	<0.001
2011 Columbretes I	2011 Medes	0.91	<0.001
2011 Columbretes I	2010 Cap de Creus	0.72	<0.001
2011 Columbretes I	2011 Cap de Creus	0.73	<0.001
2011 Columbretes I	2012 Cap de Creus	0.70	<0.001

2011 Columbretes I	2008 Montgrí	0.45	<0.001
2011 Columbretes I	2009 Montgrí	0.45	<0.001
2011 Columbretes I	2010 Montgrí	0.51	<0.001
2011 Columbretes I	2011 Montgrí	0.48	<0.001
2012 Columbretes I	2010 Columbretes I	0.23	0.00
2012 Columbretes I	2011 Columbretes I	0.11	0.40
2012 Columbretes I	2012 Columbretes I	0.00	1.00
2012 Columbretes I	2010 Columbretes II	0.12	0.33
2012 Columbretes I	2011 Columbretes II	0.18	0.02
2012 Columbretes I	2012 Columbretes II	0.28	<0.001
2012 Columbretes I	2008 Medes	0.88	<0.001
2012 Columbretes I	2009 Medes	0.93	<0.001
2012 Columbretes I	2010 Medes	0.92	<0.001
2012 Columbretes I	2011 Medes	0.93	<0.001
2012 Columbretes I	2010 Cap de Creus	0.79	<0.001
2012 Columbretes I	2011 Cap de Creus	0.80	<0.001
2012 Columbretes I	2012 Cap de Creus	0.77	<0.001
2012 Columbretes I	2008 Montgrí	0.50	<0.001
2012 Columbretes I	2009 Montgrí	0.51	<0.001
2012 Columbretes I	2010 Montgrí	0.56	<0.001
2012 Columbretes I	2011 Montgrí	0.53	<0.001
2010 Columbretes II	2010 Columbretes I	0.17	0.04
2010 Columbretes II	2011 Columbretes I	0.10	0.60
2010 Columbretes II	2012 Columbretes I	0.12	0.33
2010 Columbretes II	2010 Columbretes II	0.00	1.00
2010 Columbretes II	2011 Columbretes II	0.27	<0.001
2010 Columbretes II	2012 Columbretes II	0.36	<0.001
2010 Columbretes II	2008 Medes	0.90	<0.001
2010 Columbretes II	2009 Medes	0.94	<0.001
2010 Columbretes II	2010 Medes	0.92	<0.001
2010 Columbretes II	2011 Medes	0.94	<0.001
2010 Columbretes II	2010 Cap de Creus	0.81	<0.001

2010 Columbretes II	2011 Cap de Creus	0.82	<0.001
2010 Columbretes II	2012 Cap de Creus	0.79	<0.001
2010 Columbretes II	2008 Montgrí	0.48	<0.001
2010 Columbretes II	2009 Montgrí	0.49	<0.001
2010 Columbretes II	2010 Montgrí	0.56	<0.001
2010 Columbretes II	2011 Montgrí	0.51	<0.001
2011 Columbretes II	2010 Columbretes I	0.38	<0.001
2011 Columbretes II	2011 Columbretes I	0.26	<0.001
2011 Columbretes II	2012 Columbretes I	0.18	0.02
2011 Columbretes II	2010 Columbretes II	0.27	<0.001
2011 Columbretes II	2011 Columbretes II	0.00	1.00
2011 Columbretes II	2012 Columbretes II	0.15	0.03
2011 Columbretes II	2008 Medes	0.95	<0.001
2011 Columbretes II	2009 Medes	0.97	<0.001
2011 Columbretes II	2010 Medes	0.97	<0.001
2011 Columbretes II	2011 Medes	0.97	<0.001
2011 Columbretes II	2010 Cap de Creus	0.86	<0.001
2011 Columbretes II	2011 Cap de Creus	0.87	<0.001
2011 Columbretes II	2012 Cap de Creus	0.84	<0.001
2011 Columbretes II	2008 Montgrí	0.63	<0.001
2011 Columbretes II	2009 Montgrí	0.64	<0.001
2011 Columbretes II	2010 Montgrí	0.70	<0.001
2011 Columbretes II	2011 Montgrí	0.66	<0.001
2012 Columbretes II	2010 Columbretes I	0.48	<0.001
2012 Columbretes II	2011 Columbretes I	0.39	<0.001
2012 Columbretes II	2012 Columbretes I	0.28	<0.001
2012 Columbretes II	2010 Columbretes II	0.36	<0.001
2012 Columbretes II	2011 Columbretes II	0.15	0.03
2012 Columbretes II	2012 Columbretes II	0.00	1.00
2012 Columbretes II	2008 Medes	0.95	<0.001
2012 Columbretes II	2009 Medes	0.97	<0.001
2012 Columbretes II	2010 Medes	0.97	<0.001

2012 Columbretes II	2011 Medes	0.97	<0.001
2012 Columbretes II	2010 Cap de Creus	0.89	<0.001
2012 Columbretes II	2011 Cap de Creus	0.89	<0.001
2012 Columbretes II	2012 Cap de Creus	0.87	<0.001
2012 Columbretes II	2008 Montgrí	0.72	<0.001
2012 Columbretes II	2009 Montgrí	0.71	<0.001
2012 Columbretes II	2010 Montgrí	0.76	<0.001
2012 Columbretes II	2011 Montgrí	0.73	<0.001
2008 Medes	2010 Columbretes I	0.83	<0.001
2008 Medes	2011 Columbretes I	0.84	<0.001
2008 Medes	2012 Columbretes I	0.88	<0.001
2008 Medes	2010 Columbretes II	0.90	<0.001
2008 Medes	2011 Columbretes II	0.95	<0.001
2008 Medes	2012 Columbretes II	0.95	<0.001
2008 Medes	2008 Medes	0.00	1.00
2008 Medes	2009 Medes	0.75	<0.001
2008 Medes	2010 Medes	0.56	<0.001
2008 Medes	2011 Medes	0.46	<0.001
2008 Medes	2010 Cap de Creus	0.22	<0.001
2008 Medes	2011 Cap de Creus	0.17	0.01
2008 Medes	2012 Cap de Creus	0.19	0.00
2008 Medes	2008 Montgrí	0.80	<0.001
2008 Medes	2009 Montgrí	0.79	<0.001
2008 Medes	2010 Montgrí	0.54	<0.001
2008 Medes	2011 Montgrí	0.68	<0.001
2009 Medes	2010 Columbretes I	0.91	<0.001
2009 Medes	2011 Columbretes I	0.91	<0.001
2009 Medes	2012 Columbretes I	0.93	<0.001
2009 Medes	2010 Columbretes II	0.94	<0.001
2009 Medes	2011 Columbretes II	0.97	<0.001
2009 Medes	2012 Columbretes II	0.97	<0.001
2009 Medes	2008 Medes	0.75	<0.001

2009 Medes	2009 Medes	0.00	1.00
2009 Medes	2010 Medes	0.45	<0.001
2009 Medes	2011 Medes	0.41	<0.001
2009 Medes	2010 Cap de Creus	0.69	<0.001
2009 Medes	2011 Cap de Creus	0.63	<0.001
2009 Medes	2012 Cap de Creus	0.74	<0.001
2009 Medes	2008 Montgrí	0.91	<0.001
2009 Medes	2009 Montgrí	0.89	<0.001
2009 Medes	2010 Montgrí	0.63	<0.001
2009 Medes	2011 Montgrí	0.79	<0.001
2010 Medes	2010 Columbretes I	0.90	<0.001
2010 Medes	2011 Columbretes I	0.90	<0.001
2010 Medes	2012 Columbretes I	0.92	<0.001
2010 Medes	2010 Columbretes II	0.92	<0.001
2010 Medes	2011 Columbretes II	0.97	<0.001
2010 Medes	2012 Columbretes II	0.97	<0.001
2010 Medes	2008 Medes	0.56	<0.001
2010 Medes	2009 Medes	0.45	<0.001
2010 Medes	2010 Medes	0.00	1.00
2010 Medes	2011 Medes	0.10	0.38
2010 Medes	2010 Cap de Creus	0.55	<0.001
2010 Medes	2011 Cap de Creus	0.50	<0.001
2010 Medes	2012 Cap de Creus	0.50	<0.001
2010 Medes	2008 Montgrí	0.90	<0.001
2010 Medes	2009 Montgrí	0.89	<0.001
2010 Medes	2010 Montgrí	0.62	<0.001
2010 Medes	2011 Montgrí	0.79	<0.001
2011 Medes	2010 Columbretes I	0.91	<0.001
2011 Medes	2011 Columbretes I	0.91	<0.001
2011 Medes	2012 Columbretes I	0.93	<0.001
2011 Medes	2010 Columbretes II	0.94	<0.001
2011 Medes	2011 Columbretes II	0.97	<0.001

2011 Medes	2012 Columbretes II	0.97	<0.001
2011 Medes	2008 Medes	0.46	<0.001
2011 Medes	2009 Medes	0.41	<0.001
2011 Medes	2010 Medes	0.10	0.38
2011 Medes	2011 Medes	0.00	1.00
2011 Medes	2010 Cap de Creus	0.47	<0.001
2011 Medes	2011 Cap de Creus	0.43	<0.001
2011 Medes	2012 Cap de Creus	0.42	<0.001
2011 Medes	2008 Montgrí	0.91	<0.001
2011 Medes	2009 Montgrí	0.90	<0.001
2011 Medes	2010 Montgrí	0.63	<0.001
2011 Medes	2011 Montgrí	0.80	<0.001
2010 Cap de Creus	2010 Columbretes I	0.72	<0.001
2010 Cap de Creus	2011 Columbretes I	0.72	<0.001
2010 Cap de Creus	2012 Columbretes I	0.79	<0.001
2010 Cap de Creus	2010 Columbretes II	0.81	<0.001
2010 Cap de Creus	2011 Columbretes II	0.86	<0.001
2010 Cap de Creus	2012 Columbretes II	0.89	<0.001
2010 Cap de Creus	2008 Medes	0.22	<0.001
2010 Cap de Creus	2009 Medes	0.69	<0.001
2010 Cap de Creus	2010 Medes	0.55	<0.001
2010 Cap de Creus	2011 Medes	0.47	<0.001
2010 Cap de Creus	2010 Cap de Creus	0.00	1.00
2010 Cap de Creus	2011 Cap de Creus	0.09	0.45
2010 Cap de Creus	2012 Cap de Creus	0.06	0.94
2010 Cap de Creus	2008 Montgrí	0.64	<0.001
2010 Cap de Creus	2009 Montgrí	0.67	<0.001
2010 Cap de Creus	2010 Montgrí	0.41	<0.001
2010 Cap de Creus	2011 Montgrí	0.54	<0.001
2011 Cap de Creus	2010 Columbretes I	0.71	<0.001
2011 Cap de Creus	2011 Columbretes I	0.73	<0.001
2011 Cap de Creus	2012 Columbretes I	0.80	<0.001

2011 Cap de Creus	2010 Columbretes II	0.82	<0.001
2011 Cap de Creus	2011 Columbretes II	0.87	<0.001
2011 Cap de Creus	2012 Columbretes II	0.89	<0.001
2011 Cap de Creus	2008 Medes	0.17	0.01
2011 Cap de Creus	2009 Medes	0.63	<0.001
2011 Cap de Creus	2010 Medes	0.50	<0.001
2011 Cap de Creus	2011 Medes	0.43	<0.001
2011 Cap de Creus	2010 Cap de Creus	0.09	0.45
2011 Cap de Creus	2011 Cap de Creus	0.00	1.00
2011 Cap de Creus	2012 Cap de Creus	0.11	0.16
2011 Cap de Creus	2008 Montgrí	0.64	<0.001
2011 Cap de Creus	2009 Montgrí	0.67	<0.001
2011 Cap de Creus	2010 Montgrí	0.41	<0.001
2011 Cap de Creus	2011 Montgrí	0.54	<0.001
2012 Cap de Creus	2010 Columbretes I	0.70	<0.001
2012 Cap de Creus	2011 Columbretes I	0.70	<0.001
2012 Cap de Creus	2012 Columbretes I	0.77	<0.001
2012 Cap de Creus	2010 Columbretes II	0.79	<0.001
2012 Cap de Creus	2011 Columbretes II	0.84	<0.001
2012 Cap de Creus	2012 Columbretes II	0.87	<0.001
2012 Cap de Creus	2008 Medes	0.19	0.00
2012 Cap de Creus	2009 Medes	0.74	<0.001
2012 Cap de Creus	2010 Medes	0.50	<0.001
2012 Cap de Creus	2011 Medes	0.42	<0.001
2012 Cap de Creus	2010 Cap de Creus	0.06	0.94
2012 Cap de Creus	2011 Cap de Creus	0.11	0.16
2012 Cap de Creus	2012 Cap de Creus	0.00	1.00
2012 Cap de Creus	2008 Montgrí	0.64	<0.001
2012 Cap de Creus	2009 Montgrí	0.65	<0.001
2012 Cap de Creus	2010 Montgrí	0.40	<0.001
2012 Cap de Creus	2011 Montgrí	0.53	<0.001
2008 Montgrí	2010 Columbretes I	0.32	<0.001

2008 Montgrí	2011 Columbretes I	0.45	<0.001
2008 Montgrí	2012 Columbretes I	0.50	<0.001
2008 Montgrí	2010 Columbretes II	0.48	<0.001
2008 Montgrí	2011 Columbretes II	0.63	<0.001
2008 Montgrí	2012 Columbretes II	0.72	<0.001
2008 Montgrí	2008 Medes	0.80	<0.001
2008 Montgrí	2009 Medes	0.91	<0.001
2008 Montgrí	2010 Medes	0.90	<0.001
2008 Montgrí	2011 Medes	0.91	<0.001
2008 Montgrí	2010 Cap de Creus	0.64	<0.001
2008 Montgrí	2011 Cap de Creus	0.64	<0.001
2008 Montgrí	2012 Cap de Creus	0.64	<0.001
2008 Montgrí	2008 Montgrí	0.00	1.00
2008 Montgrí	2009 Montgrí	0.04	1.00
2008 Montgrí	2010 Montgrí	0.29	<0.001
2008 Montgrí	2011 Montgrí	0.14	0.25
2009 Montgrí	2010 Columbretes I	0.32	<0.001
2009 Montgrí	2011 Columbretes I	0.45	<0.001
2009 Montgrí	2012 Columbretes I	0.51	<0.001
2009 Montgrí	2010 Columbretes II	0.49	<0.001
2009 Montgrí	2011 Columbretes II	0.64	<0.001
2009 Montgrí	2012 Columbretes II	0.71	<0.001
2009 Montgrí	2008 Medes	0.79	<0.001
2009 Montgrí	2009 Medes	0.89	<0.001
2009 Montgrí	2010 Medes	0.89	<0.001
2009 Montgrí	2011 Medes	0.90	<0.001
2009 Montgrí	2010 Cap de Creus	0.67	<0.001
2009 Montgrí	2011 Cap de Creus	0.67	<0.001
2009 Montgrí	2012 Cap de Creus	0.65	<0.001
2009 Montgrí	2008 Montgrí	0.04	1.00
2009 Montgrí	2009 Montgrí	0.00	1.00
2009 Montgrí	2010 Montgrí	0.28	<0.001

2009 Montgrí	2011 Montgrí	0.13	0.41
2010 Montgrí	2010 Columbretes I	0.42	<0.001
2010 Montgrí	2011 Columbretes I	0.51	<0.001
2010 Montgrí	2012 Columbretes I	0.56	<0.001
2010 Montgrí	2010 Columbretes II	0.56	<0.001
2010 Montgrí	2011 Columbretes II	0.70	<0.001
2010 Montgrí	2012 Columbretes II	0.76	<0.001
2010 Montgrí	2008 Medes	0.54	<0.001
2010 Montgrí	2009 Medes	0.63	<0.001
2010 Montgrí	2010 Medes	0.62	<0.001
2010 Montgrí	2011 Medes	0.63	<0.001
2010 Montgrí	2010 Cap de Creus	0.41	<0.001
2010 Montgrí	2011 Cap de Creus	0.41	<0.001
2010 Montgrí	2012 Cap de Creus	0.40	<0.001
2010 Montgrí	2008 Montgrí	0.29	<0.001
2010 Montgrí	2009 Montgrí	0.28	<0.001
2010 Montgrí	2010 Montgrí	0.00	1.00
2010 Montgrí	2011 Montgrí	0.18	0.13
2011 Montgrí	2010 Columbretes I	0.35	<0.001
2011 Montgrí	2011 Columbretes I	0.48	<0.001
2011 Montgrí	2012 Columbretes I	0.53	<0.001
2011 Montgrí	2010 Columbretes II	0.51	<0.001
2011 Montgrí	2011 Columbretes II	0.66	<0.001
2011 Montgrí	2012 Columbretes II	0.73	<0.001
2011 Montgrí	2008 Medes	0.68	<0.001
2011 Montgrí	2009 Medes	0.79	<0.001
2011 Montgrí	2010 Medes	0.79	<0.001
2011 Montgrí	2011 Medes	0.80	<0.001
2011 Montgrí	2010 Cap de Creus	0.54	<0.001
2011 Montgrí	2011 Cap de Creus	0.54	<0.001
2011 Montgrí	2012 Cap de Creus	0.53	<0.001
2011 Montgrí	2008 Montgrí	0.14	0.25

2011 Montgrí	2009 Montgrí	0.13	0.41
2011 Montgrí	2010 Montgrí	0.18	0.13
2011 Montgrí	2011 Montgrí	0.00	1.00

Appendix B

Chapter 3 Supporting Information

B.1 Recruit survival over census times

To test for differences in recruit survival between sites and time (fixed factor), we applied generalized linear mixed models (GLMM), with a binomial error distribution and a logit link function, using the ID of each tile as a random factor. We applied a Type II Wald χ^2 test over the fitted model to determine the effect of site and time on recruit survival. GLMMs were used to deal with the non-independence between observations (i.e. repeated measures) and a binomial distribution was assumed to deal with the dichotomous response variable (survive or not survive).

Survival since the first census decreased substantially with time, reaching values lower than 50% after a year (Figure B.1). Significant differences were found in recruit survival among the three populations studied ($\chi^2 = 17.73$, df = 2, P < 0.01) and between the consecutive years ($\chi^2 = 753.52$, df = 2, P < 0.01), with a significant interaction between the aforementioned factors ($\chi^2 = 7.82$, df = 4, P = 0.02).

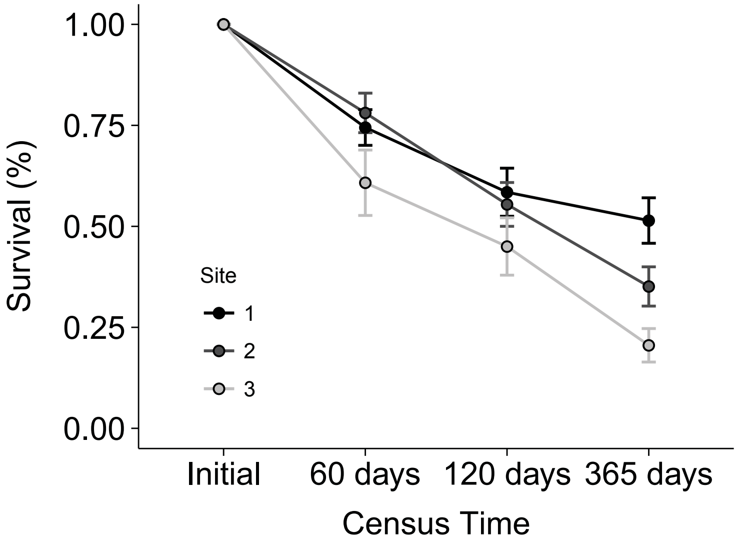

Figure B.1: Recruit survival (mean ± SE) vs census time. Grey scale indicates the different populations studied.

B.2 Diagnostics of glmm and glm models.

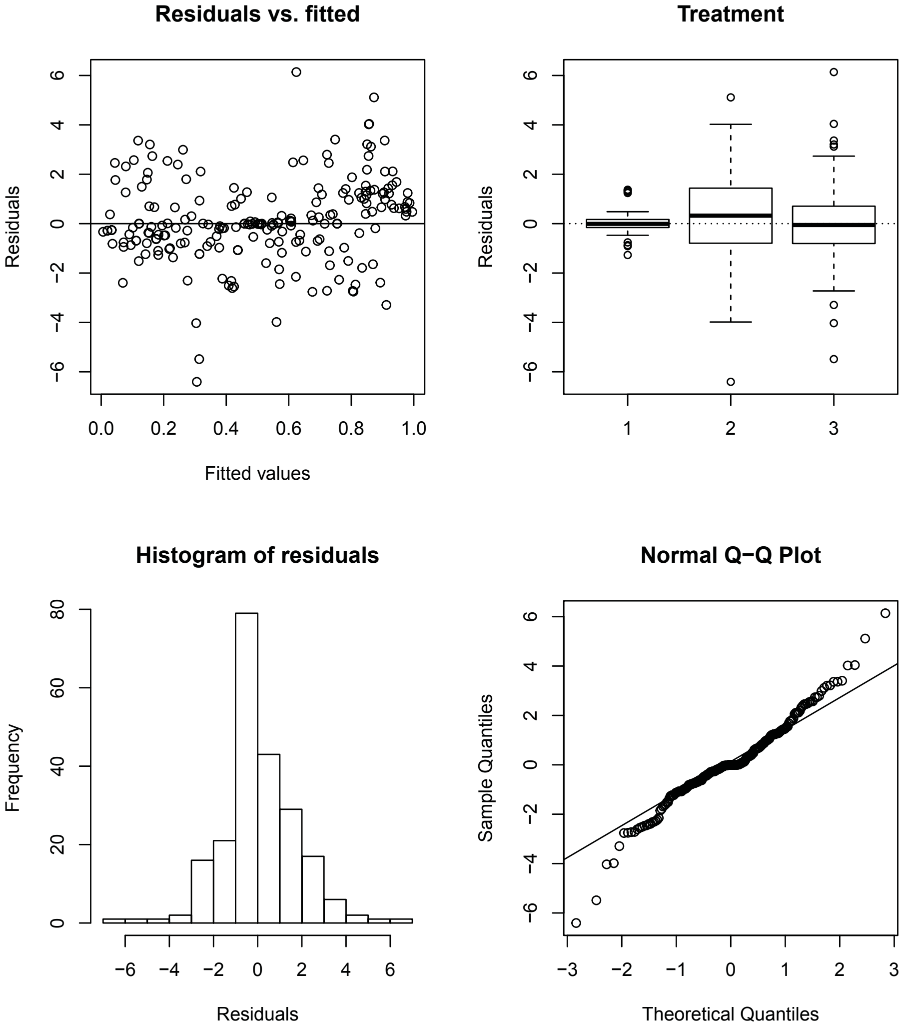

Figure B.2: Diagnostics of the generalized linear mixed model, with a binomial distribution and a logit link function, for recruit survival between sites and time (fixed factors) using plate as a random factor.

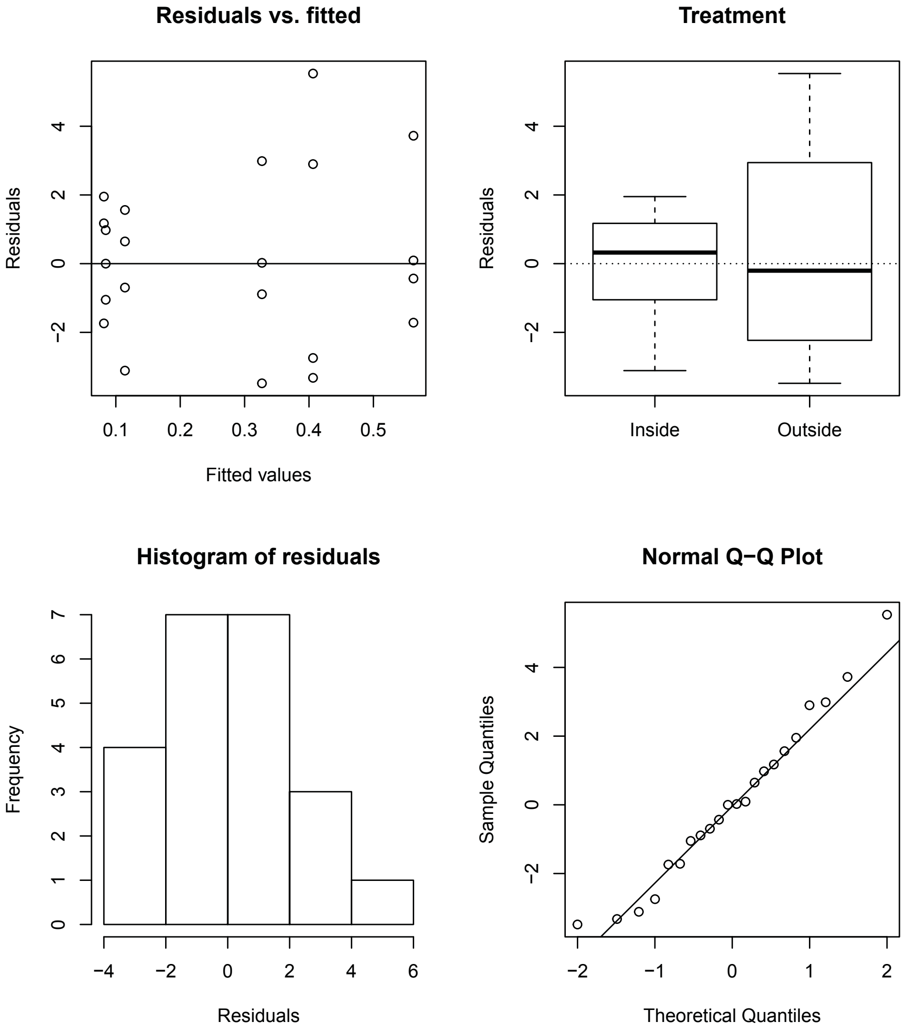

Figure B.3: Diagnostics of the generalized linear model, with a binomial distribution and a logit link function, for yearly recruit survival between inside and outside the adult canopy.

B.3 Dispersal model outputs and selection criteria

Table B.1: Maximum-likelihood estimates of all the models fitted to the data, for each site and orientation. The a and b values are the scale and shape parameters respectively, for each of the functions. *Log(Q)* is also a fitted parameter, which represents the logarithm of the number of propagules liberated for each direction.

Site	**Orien -tation**	**Function**	**Parameters**	**z-value**	**p-value**
1	E	2Dt	**a = 4,364**	**$3{,}639 \cdot 10^{8}$**	**<0,001**
			$b = 0{,}87 \cdot 10^{3}$	**11,486**	**<0,001**
			log(Q)= 15,992	**$2{,}147 \cdot 10^{8}$**	**<0,001**
1	E	Negative Exponential	**a = 3,025**	**6,631**	**<0,001**
			log(Q)= 10,372	**40,089**	**<0,001**
1	E	Power Exponential	*a = 1,596*	*2,258*	*0,024*
			b = 0,472	*2,8*	*0,005*
			log(Q)= 10,422	**6,906**	**<0,001**
1	E	Gaussian	**a = 4,947**	**9,557**	**<0,001**
			log(Q)= 15,992	**56,388**	**<0,001**
1	E	Inverse Gausian	**a = 247,250**	**$3{,}639 \cdot 10^{8}$**	**<0,001**
			b = 0,237	**65,347**	**<0,001**
			log(Q)= 10,269	**74,531**	**<0,001**
1	E	Log-normal	**$a = 5{,}756 \cdot 10^{4}$**	**$1{,}548 \cdot 10^{10}$**	**<0,001**
			b = 2,690	**$1{,}090 \cdot 10^{2}$**	**<0,001**
			log(Q)= 17,773	**71,622**	**<0,001**
1	E	Weibull	*a = 8,563*	*3,0876*	*0,002*
			b = 1,802	**44,056**	**<0,001**
			log(Q)= 10,654	**23,357**	**<0,001**
1	N	2Dt	**a = 1957,446**	**$12{,}888 \cdot 10^{3}$**	**<0,001**
			b = 44,124	**6,583**	**<0,001**
			log(Q)= 11,859	**88,58**	**<0,001**
1	N	Negative Exponential	**a = 7,212**	**6,542**	**<0,001**
			log(Q)= 12,772	**47,742**	**<0,001**
1	N	Power Exponential	**a = 224,606**	**9628,707**	**<0,001**
			b = 0,411	**5,262**	**<0,001**
			log(Q)= 23,289	**14,606**	**<0,001**
1	N	Gaussian	**a = 6,645**	**13,41**	**<0,001**

			log(Q)= 11,853	**90,214**	**<0,001**
1	N	Inverse Gausian	**a = 867,700**	**$4,143 \cdot 10^{10}$**	**<0,001**
			b = 0,268	**105,61**	**<0,001**
			log(Q)= 11,742	**199,34**	**<0,001**
1	N	Log-normal	a = 63,538	1,823	0,068
			b = 1,701	**21,462**	**<0,001**
			log(Q)= 13,775	**27,544**	**<0,001**
1	N	Weibull	**a = 5,520**	**16,343**	**<0,001**
			b = 2,121	**89,856**	**<0,001**
			log(Q) = 11,816	**118,595**	**<0,001**
1	W	2Dt	**a = 2,002**	**$3,130 \cdot 10^{8}$**	**<0,001**
			b = $4,437 \cdot 10^{-4}$	**11,83**	**<0,001**
			log(Q)= 15,940	**$9,579 \cdot 10^{8}$**	**<0,001**
1	W	Negative Exponential	**a = 2,437**	**7,64**	**<0,001**
			log(Q)= 9,915	**44,931**	**<0,001**
1	W	Power Exponential	*a = 1,198*	*2,971*	*0,003*
			b = 0,529	**4,62**	**<0,001**
			log(Q)= 10,818	**14,051**	**<0,001**
1	W	Gaussian	**a = 4,825**	**10,026**	**<0,001**
			log(Q)= 10,239	**58,892**	**<0,001**
1	W	Inverse Gausian	**a = 263,220**	**$6,270 \cdot 10^{8}$**	**<0,001**
			b = 0,229	**65,943**	**<0,001**
			log(Q)= 9,866	**77,263**	**<0,001**
1	W	Log-normal	**a = 22,597**	**$1,809 \cdot 10^{5}$**	**<0,001**
			b = 2,052	**107,19**	**<0,001**
			log(Q)= 12,645	**75,78**	**<0,001**
1	W	Weibull	**a = 8,560**	**3,416**	**<0,001**
			b = 1,756	**46,219**	**<0,001**
			log(Q)= 10,398	**25,329**	**<0,001**
1	S	2Dt	**a = 540,102**	**$7,151 \cdot 10^{4}$**	**<0,001**
			b = 3,486	**3,35**	**<0,001**
			log(Q)= 12,790	**47,214**	**<0,001**
1	S	Negative Exponential	**a = 16,628**	**3,595**	**<0,001**
			log(Q)= 14,098	**27,735**	**<0,001**
1	S	Power Exponential	**a = 31,835**	**$8,599 \cdot 10^{3}$**	**<0,001**
			b = $0,10^{5}$	**497,16**	**<0,001**
			log(Q)= 54,744	**478,24**	**<0,001**
1	S	Gaussian	**a = 11,361**	**8,315**	**<0,001**

			log(Q)= 12,609	**58,985**	**<0,001**
1	S	Inverse Gausian	**a = 843,340**	**3,836 · 10^{10}**	**<0,001**
			b = 0,263	**103,33**	**<0,001**
			log(Q)= 11,510	**193,61**	**<0,001**
1	S	Log-normal	**a =5,590**	**1,823**	**<0,001**
			b = 2,932	**21,462**	**<0,001**
			log(Q)= 24,662	**151,9**	**<0,001**
1	S	Weibull	**a= 9,936**	**9,097**	**<0,001**
			b= 2,046	**82,523**	**<0,001**
			log(Q) = 12,480	**72,72**	**<0,001**
2	E	2Dt	**a = 7,710**	**4,130 · 10^{8}**	**<0,001**
			b = 0,182·10-3	**16,779**	**<0,001**
			log(Q)= 16,559	**8,317 · 10^{7}**	**<0,001**
2	E	Negative Exponential	**a = 3,670**	**9,703**	**<0,001**
			log(Q)= 11,541	**69,808**	**<0,001**
2	E	Power Exponential	*a = 1,807*	*3,047*	*0,002*
			b = 0,438	**3,824**	**<0,001**
			log(Q)= 13,693	**9,249**	**<0,001**
2	E	Gaussian	**a = 5,717**	**14,209**	**<0,001**
			log(Q)= 11,442	**96,438**	**<0,001**
2	E	Inverse Gausian	**a = 376,100**	**2,769 · 10^{9}**	**<0,001**
			b = 0,242	**100,82**	**<0,001**
			log(Q)= 11,368	**142,85**	**<0,001**
2	E	Log-normal	**a = 2,782 · 10^{6}**	**4,906 · 10^{13}**	**<0,001**
			b = 3,058	**1,704 · 10^{2}**	**<0,001**
			log(Q)= 22,181	**1,233·10^{2}**	**<0,001**
2	E	Weibull	**a = 8,954**	**5,511**	**<0,001**
			b = 1,817	**70,477**	**<0,001**
			log(Q)= 11,680	**45,893**	**<0,001**
2	N	2Dt	**a = 10,700**	**7,413·10^{8}**	**<0,001**
			b = 0,002	**17,337**	**<0,001**
			log(Q)= 17,705	**8,469·10^{7}**	**<0,001**
2	N	Negative Exponential	**a = 4,460**	**8,775**	**<0,001**
			log(Q)= 12,111	**63,786**	**<0,001**
2	N	Power Exponential	**a = 4,035**	**6,307**	**<0,001**
			b = 0,788	**5,153**	**<0,001**
			log(Q)= 12,507	**25,719**	**<0,001**
2	N	Gaussian	**a = 6,215**	**13,284**	**<0,001**

			log(Q)= 11,867	**92,536**	**<0,001**
2	N	Inverse Gausian	**a = 508,890**	**$7{,}015 \cdot 10^{10}$**	**<0,001**
			b = 0,251	**107,33**	**<0,001**
			log(Q)= 11,784	**157,01**	**<0,001**
2	N	Log-normal	**a = 107,920**	**$1{,}257 \cdot 10^{7}$**	**<0,001**
			b = 2,170	**0,018**	**<0,001**
			log(Q)= 15,891	**0,015**	**<0,001**
2	N	Weibull	**a= 8,162**	**6,871**	**<0,001**
			b= 1,897	**77,255**	**<0,001**
			log(Q) = 12,016	**57,628**	**<0,001**
2	W	2Dt	**a = $4{,}751 \cdot 10^{3}$**	**$1{,}144 \cdot 10^{4}$**	**<0,001**
			b = 112,183	**6,327**	**<0,001**
			log(Q)= 11,885	**86,087**	**<0,001**
2	W	Negative Exponential	**a = 5,508**	**7,301**	**<0,001**
			log(Q)= 12,399	**53,378**	**<0,001**
2	W	Power Exponential	**a = 4,049**	**11,027**	**<0,001**
			b = 0,152	**23,924**	**<0,001**
			log(Q)= 34,338	**27,036**	**<0,001**
2	W	Gaussian	**a = 6,469**	**12,808**	**<0,001**
			log(Q)= 11,875	**87,102**	**<0,001**
2	W	Inverse Gausian	**a = 254,420**	**$9{,}297 \cdot 10^{8}$**	**<0,001**
			b = 0,229	**106,76**	**<0,001**
			log(Q)= 11,542	**159,48**	**<0,001**
2	W	Log-normal	**a = $1{,}471 \cdot 10^{9}$**	**$1{,}054 \cdot 10^{19}$**	**<0,001**
			b = 3,515	**$1{,}882 \cdot 10^{2}$**	**<0,001**
			log(Q)= 28,849	**$1{,}299 \cdot 10^{19}$**	**<0,001**
2	W	Weibull	**a = 8,208**	**6,969**	**<0,001**
			b = 1,904	**77,881**	**<0,001**
			log(Q)= 12,020	**56,758**	**<0,001**
2	S	2Dt	a = 27,666	1,683	0,092
			b = 0,967	1,267	0,205
			log(Q)= 11,736	**44,245**	**<0,001**
2	S	Negative Exponential	**a = 3,760**	**10,533**	**<0,001**
			log(Q)= 11,817	**75,241**	**<0,001**
2	S	Power Exponential	**a = 4,389**	**9,758**	**<0,001**
			b = 1,390	**6,633**	**<0,001**
			log(Q)= 11,598	**87,606**	**<0,001**
2	S	Gaussian	**a = 5,213**	**16,527**	**<0,001**

			log(Q)= 11,586	**110,201**	**<0,001**
2	S	Inverse Gausian	**a = 232,790**	**$6,754 \cdot 10^{8}$**	**<0,001**
			b = 0,250	**106,6**	**<0,001**
			log(Q)= 11,720	**155,76**	**<0,001**
2	S	Log-normal	**a =381,410**	**$1,749 \cdot 10^{6}$**	**<0,001**
			b = 2,042	**178,84**	**<0,001**
			log(Q)= 14,905	**151,41**	**<0,001**
2	S	Weibull	**a= 5,751**	**12,419**	**<0,001**
			b= 1,940	**81,325**	**<0,001**
			log(Q) = 11,576	**98,197**	**<0,001**
3	E	2Dt	**a = 0,150**	**3,505**	**<0,001**
			b = 0,017	0,853	0,393
			log(Q)= 10,698	**9,383**	**<0,001**
3	E	Negative Exponential	**a = 1,355**	**1,037**	**<0,001**
			log(Q)= 9,533	**54,458**	**<0,001**
3	E	Power Exponential	a = 0,004	1,247	0,213
			b = 0,198	**15,077**	**<0,001**
			log(Q)= 13,151	**$6,334 \cdot 10^{4}$**	**<0,001**
3	E	Gaussian	**a = 4,102**	**11,726**	**<0,001**
			log(Q)= 10,547	**70,751**	**<0,001**
3	E	Inverse Gausian	**a = 315,910**	**$7,291 \cdot 10^{8}$**	**<0,001**
			b = 0,193	**38,738**	**<0,001**
			log(Q)= 9,084	**40,405**	**<0,001**
3	E	Log-normal	**a = $2,519 \cdot 10^{11}$**	**$1,404 \cdot 10^{23}$**	**<0,001**
			b = 4,440	**71,4**	**<0,001**
			log(Q)= 26,543	**41,27**	**<0,001**
3	E	Weibull	**a = $1,302 \cdot 10^{3}$**	**$2,624 \cdot 10^{6}$**	**<0,001**
			b = 1,423	**33,328**	**<0,001**
			log(Q)= 16,398	**36,082**	**<0,001**
3	N	2Dt	a = 0,062	1,825	0,068
			b = 0,037	0,501	0,616
			log(Q)= 9,032	**5,114**	**<0,001**
3	N	Negative Exponential	**a = 4,460**	**8,775**	**<0,001**
			log(Q)= 12,111	**63,786**	**<0,001**
3	N	Power Exponential	**a = 0,001**	**0,558**	**0,577**
			b = 0,196	**6,763**	**<0,001**
			log(Q)= 9,916	**$1,476 \cdot 10^{4}$**	**<0,001**
3	N	Gaussian	**a = 1,466**	**14,364**	**<0,001**

			log(Q)= 9,097	**66,333**	**<0,001**
3	N	Inverse Gausian	**a = 49,765**	**$1,681 \cdot 10^{6}$**	**<0,001**
			b = 0,177	**19,464**	**<0,001**
			log(Q)= 8,352	**19,708**	**<0,001**
3	N	Log-normal	**a = 466,810**	**$5,932 \cdot 10^{7}$**	**<0,001**
			b = 2,941	**28,977**	**<0,001**
			log(Q)= 11,855	**18,606**	**<0,001**
3	N	Weibull	**a= 30,823**	**$1,593 \cdot 10^{3}$**	**<0,001**
			b= 1,198	**15,421**	**<0,001**
			log(Q) = 9,448	**17,15**	**<0,001**
3	W	2Dt	a = 117,342	NA	NA
			b = 3,706	NA	NA
			log(Q)= 11,890	**103,06**	**<0,001**
3	W	Negative Exponential	**a = 4,321**	**10,289**	**<0,001**
			log(Q)= 12,180	**73,827**	**<0,001**
3	W	Power Exponential	**a = 4,846**	**10,071**	**<0,001**
			b = 1,367	**6,081**	**<0,001**
			log(Q)= 11,916	**79,868**	**<0,001**
3	W	Gaussian	**a = 5,652**	**16,777**	**<0,001**
			log(Q)= 11,867	**112,965**	**<0,001**
3	W	Inverse Gausian	**a = 312,810**	**$1,698 \cdot 10^{9}$**	**<0,001**
			b = 0,255	**120,99**	**<0,001**
			log(Q)= 12,071	**170,18**	**<0,001**
3	W	Log-normal	**a = 350,410**	**$1,576 \cdot 10^{6}$**	**<0,001**
			b = 2,015	**202,24**	**<0,001**
			log(Q)= 15,094	**165,04**	**<0,001**
3	W	Weibull	**a = 6,229**	**12,274**	**<0,001**
			b = 1,948	**90,152**	**<0,001**
			log(Q)= 11,870	**99,73**	**<0,001**
3	S	2Dt	**a = 2,148**	**$4,400 \cdot 10^{9}$**	**<0,001**
			b = $1,540 \cdot 10^{4}$	**16,881**	**<0,001**
			log(Q)= 17,912	**$1,276 \cdot 10^{10}$**	**<0,001**
3	S	Negative Exponential	**a = 2,490**	**10,208**	**<0,001**
			log(Q)= 10,789	**66,725**	**<0,001**
3	S	Power Exponential	a = 0,279	1,029	0,303
			b = 0,2310	*2,65*	*0,008*
			log(Q)= 18,009	**3,313**	**<0,001**
3	S	Gaussian	**a = 5,157**	**11,724**	**<0,001**

			log(Q)= 11,151	**76,234**	**<0,001**
3	S	Inverse Gausian	**a = 280,050**	**$1{,}038 \cdot 10^{9}$**	**<0,001**
			b = 0,227	**92,058**	**<0,001**
			log(Q)= 10,729	**114,78**	**<0,001**
3	S	Log-normal	**a =$7{,}091 \cdot 10^{6}$**	**$3{,}048 \cdot 10^{12}$**	**<0,001**
			b = 2,998	**152,84**	**<0,001**
			log(Q)= 20,197	**103,76**	**<0,001**
3	S	Weibull	**a= 7,050**	**8,277**	**<0,001**
			b= 5,491	**10,923**	**<0,001**
			log(Q) = 5,469	**9,764**	**<0,001**

Table B.2: Results of AIC analysis for the seven competing dispersal models fitted by site and direction. Here are presented: the log-likelihood score (L); the *AIC* estimates; the ΔAIC_i, which is the difference between AIC_i and the minimum value [AIC_i − min(AIC)]; and the rounded Akaike weights $wAIC_i$. Models are ranked according to their goodness-of-fit, from best to worst fitted. Best-fitted models are highlighted in grey background.

Site	Orientation	Function	L	AIC	ΔAIC_i	$wAIC_i$
1	E	Power Exponential	-55,40	116,90	0,00	0,34
1	E	Weibull	-55,50	117,10	0,20	0,31
1	E	Log-normal	-55,50	117,10	0,20	0,31
1	E	Negative Exponential	-58,80	121,70	4,80	0,03
1	E	2Dt	-60,00	126,00	9,10	0,00
1	E	Gaussian	-68,90	141,80	25,00	<0,001
1	E	Inverse Gausian	-90,40	186,80	69,90	<0,001
1	N	Log-normal	-77,80	161,70	0,00	1,00
1	N	Weibull	-90,80	187,70	26,00	<0,001
1	N	Gaussian	-104,60	213,20	51,50	<0,001
1	N	2Dt	-104,60	215,20	53,50	<0,001

1	N	Negative Exponential	-114,80	233,50	71,80	<0,001
1	N	Power Exponential	-135,10	276,20	114,50	<0,001
1	N	Inverse Gausian	-217,30	440,60	278,90	<0,001
1	W	Log-normal	-57,10	120,20	0,00	0,74
1	W	Power Exponential	-58,30	122,60	2,30	0,23
1	W	2Dt	-61,00	127,90	7,70	0,02
1	W	Weibull	-61,40	128,70	8,50	0,01
1	W	Negative Exponential	-64,20	132,40	12,20	0,00
1	W	Inverse Gausian	-80,30	166,60	46,30	<0,001
1	W	Gaussian	-84,40	172,90	52,60	<0,001
1	S	Weibull	-76,00	157,90	0,00	0,59
1	S	Gaussian	-77,70	159,40	1,50	0,28
1	S	2Dt	-77,90	161,70	3,80	0,09
1	S	Log-normal	-78,80	163,60	5,70	0,04
1	S	Negative Exponential	-80,80	165,60	7,70	0,01
1	S	Power Exponential	-105,80	217,60	59,60	<0,001
1	S	Inverse Gausian	-402,00	810,00	652,10	<0,001
2	E	Weibull	-71,90	149,80	0,00	0,82
2	E	Power Exponential	-73,80	153,70	3,80	0,12
2	E	Log-normal	-74,60	155,20	5,40	0,06
2	E	Negative Exponential	-81,30	166,60	16,80	<0,001
2	E	2Dt	-86,70	179,30	29,50	<0,001

2	E	Gaussian	-98,20	200,50	50,60	<0,001
2	E	Inverse Gausian	-202,50	411,00	261,20	<0,001
2	N	Log-normal	-70,00	146,00	0,00	0,60
2	N	Negative Exponential	-72,10	148,30	2,30	0,19
2	N	Power Exponential	-71,30	148,60	2,60	0,16
2	N	2Dt	-72,70	151,30	5,30	0,04
2	N	Weibull	-75,00	155,90	9,90	0,00
2	N	Gaussian	-84,70	173,40	27,40	<0,001
2	N	Inverse Gausian	-181,20	368,30	222,30	<0,001
2	W	Weibull	-90,30	186,60	0,00	0,99
2	W	Negative Exponential	-97,10	198,10	11,50	0,00
2	W	Gaussian	-98,10	200,30	13,60	0,00
2	W	Power Exponential	-97,90	201,80	15,20	<0,001
2	W	2Dt	-98,10	202,30	15,60	<0,001
2	W	Log-normal	-98,40	202,70	16,10	<0,001
2	W	Inverse Gausian	-302,40	610,80	424,20	<0,001
2	S	2Dt	-102,80	211,60	0,00	0,55
2	S	Weibull	-103,80	213,60	1,90	0,21
2	S	Power Exponential	-104,00	214,00	2,40	0,17
2	S	Negative Exponential	-106,10	216,20	4,50	0,06
2	S	Gaussian	-107,20	218,40	6,80	0,02
2	S	Log-normal	-115,90	237,80	26,20	<0,001
2	S	Inverse Gausian	-242,40	490,70	279,10	<0,001

3	E	Weibull	-38,70	83,40	0,00	0,82
3	E	Log-normal	-40,90	87,70	4,30	0,10
3	E	Power Exponential	-41,00	87,90	4,50	0,09
3	E	2Dt	-64,70	135,50	52,10	<0,001
3	E	Inverse Gausian	-76,20	158,40	75,00	<0,001
3	E	Negative Exponential	-107,60	219,20	135,80	<0,001
3	E	Gaussian	-175,50	354,90	271,50	<0,001
3	N	Weibull	-18,90	43,80	0,00	0,38
3	N	Log-normal	-19,20	44,30	0,50	0,29
3	N	Power Exponential	-19,20	44,40	0,60	0,29
3	N	2Dt	-21,30	48,50	4,70	0,04
3	N	Inverse Gausian	-22,70	51,40	7,60	0,01
3	N	Negative Exponential	-31,80	67,50	23,70	<0,001
3	N	Gaussian	-61,90	127,90	84,10	<0,001
3	W	Weibull	-37,20	80,50	0,00	0,41
3	W	Power Exponential	-37,50	81,10	0,60	0,30
3	W	Negative Exponential	-39,20	82,40	1,90	0,15
3	W	2Dt	-38,80	83,70	3,20	0,08
3	W	Gaussian	-40,20	84,50	4,00	0,05
3	W	Log-normal	-44,90	95,70	15,20	<0,001
3	W	Inverse Gausian	-171,10	348,30	267,80	<0,001
3	S	Power Exponential	-36,20	78,40	0,00	0,74
3	S	Log-normal	-37,20	80,50	2,10	0,26

3	S	2Dt	-61,00	128,00	49,60	<0,001
3	S	Negative Exponential	-63,30	130,50	52,20	<0,001
3	S	Gaussian	-106,60	217,10	138,80	<0,001
3	S	Inverse Gausian	-120,90	247,70	169,40	<0,001
3	S	Weibull	-373,90	753,80	675,50	<0,001

Table B.3: Number of times each of the models was the best-fitted to the data, for each site and direction. The selection criteria was AIC, see methods and Table B.2.

Model	**Times best-fitted**
2Dt	1/12
Negative Exponential	0/12
Power Exponential	2/12
Gaussian	0/12
Inverse Gausian	0/12
Log-normal	3/12
Weibull	6/12

B.4 Literature survey outputs.

Table B.4: Results of the literature survey on the dispersal distances of macroalgae species. The mean dispersal distance is reported (in m) as well as the order of the species, the source reference and the quantification method of the dispersal distance (propagule settlement or recruitment).

Species name	**Order**	**Method**	**Mean dispersal (m)**	**Reference**
Alaria esculenta	Laminariales	settlement	10	Kinlan and Gaines 2003
Fucus distichus	Fucales	settlement	1	Pearson and Brawley, 1996
Laminaria hyperborea	Laminariales	settlement	200	Fredriksen et al., 1995
Macrocystis pyrifera	Laminariales	settlement	25	Reed et al., 1988
Pterygophora californica	Laminariales	settlement	500	Reed et al., 1988
Postelsia palmaeformis	Laminariales	settlement	3	Dayton, 1973
Sargassum muticum	Fucales	recruitment	3	Deysher and Norton, 1982
Sargassum polyceratium	Fucales	recruitment	1	in Engelen et al., 2001
Cystoseira compressa	Fucales	recruitment	0.02	Mangialajo et al., 2012
Cystoseira amentacea	Fucales	recruitment	0.02	Mangialajo et al., 2012
Cystoseira zosteroides	Fucales	recruitment	6.42	this study
Sargassum spinuligerum	Fucales	settlement	0.25	Kendrick and Walker, 1991
Sargassum spp.	Fucales	settlement	0.25	Kendrick and Walker, 1995
Ascophyllum nodosum	Fucales	recruitment	1	Dudgeon et al., 2001
Undaria pinnatifida	Laminariales	settlement	0.02	Schiel and Thompson, 2012
Lessonia spicata	Laminariales	settlement	0.5	Parada et al., 2016
Sargassum horneri	Fucales	settlement	6.3	Kang et al., 2016

Appendix C

Chapter 4 Supporting Information

C.1 Density-dependent recruitment model

Table C.1: Table showing parameters for the recruitment model. SE=Standard Error

	Coefficient	**SE**	***P-value***
Intercept	2.66	0.07	<0.001
Adult/quadrat	-2.06	0.06	<0.001
Null deviance = 3079.6 **Residual deviance= 811.5**			

Table C.2: Fertility model parameters. SE=Standard Error.

	Coefficient	**SE**	***P-value***
Intercept	-0.31	1.23	0.80
Size	0.62	0.27	0.02
Null deviance = 32.163 **Residual deviance= 25.01**			

C.2 Transition matrices

Transition matrices for (C.3) the density-dependent model at equilibrium and each of the undisturbed populations (C.4, C.5, C.6 and C.7). Shown below each matrix are S_x, the mean survival of size class x; and F_x, the mean fertility value of size class x.

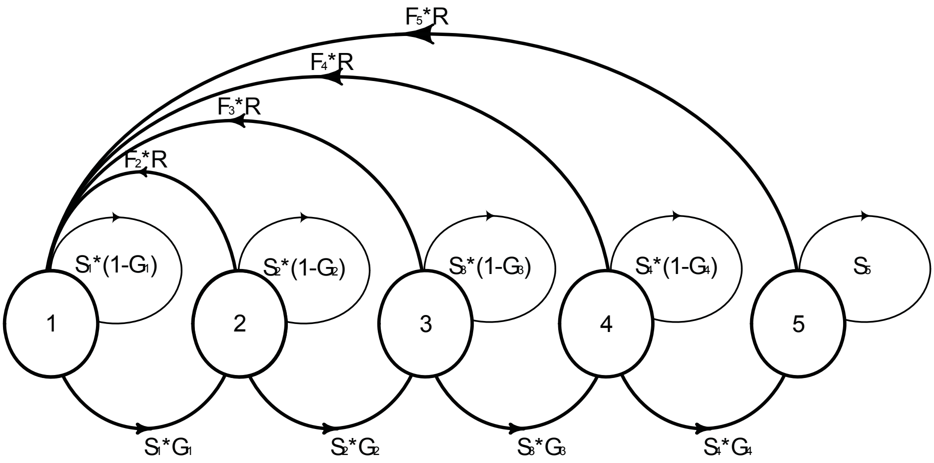

Figure C.1: Diagram representing different size classes and transitions considered in *C. zosteroides* life-cycle. S_x=survival of class *x*; G_x=growth of class *x*; F_x=Fertility of class *x*; R= recruits/adult. Recruits are size class 1, whereas size classes 2 through 5 comprise individuals between 1-4 cm, 4-6 cm, 6-10 cm and >10 cm, respectively.

Table C.3: Density-dependent matrix at equilibrium (λ=1)

	1	2	3	4	5
1	0.25	0.2	0.25	0.25	0.25
2	0.25	0.45	0	0	0
3	0	0.38	0.54	0	0
4	0	0	0.36	0.81	0
5	0	0	0	0.14	0.93
Sx	0.5	0.83	0.9	0.95	0.93
Fx	0	0.78	0.99	0.99	1

Table C.4: Columbretes I 2010-2011

	1	2	3	4	5
1	0.25	0	0	0	0
2	0.25	0.5	0	0	0
3	0	0.5	0.57	0	0
4	0	0	0.40	0.89	0
5	0	0	0	0.10	0.92
Sx	0.50	1	0.97	0.99	0.92
Fx	0	0.78	0.99	0.99	1

Table C.5: Columbretes I 2011-2012

	1	2	3	4	5
1	0.25	0	0	0	0
2	0.25	0.67	0	0	0
3	0	0.33	0.54	0	0
4	0	0	0.38	0.82	0
5	0	0	0	0.10	0.94
Sx	0.50	1	0.92	0.92	0.94
Fx	0	0.78	0.99	0.99	1

Table C.6: Columbretes II 2010-2011

	1	2	3	4	5
1	0.25	0	0	0	0
2	0.25	0.34	0	0	0
3	0	0.34	0.50	0	0
4	0	0	0.44	0.75	0
5	0	0	0	0.23	1
Sx	0.50	0.68	0.94	0.98	1
Fx	0	0.78	0.99	0.99	1

Table C.7: Columbretes II 2011-2012

	1	2	3	4	5
1	0.25	0	0	0	0
2	0.25	0.34	0	0	0
3	0	0.34	0.54	0	0
4	0	0	0.23	0.79	0
5	0	0	0	0.15	0.86
Sx	0.50	0.68	0.77	0.94	0.86
Fx	0	0.78	0.99	0.99	1

C.3 Comparative analyses

Table C.8 brown algal species selected for the analyses, and Table C.9 algal species excluded from the analyses. Table C.9, shows terrestrial plant species selected.

Table C.8: Brown algal species selected for the comparative analyses.

Species	Matrix dimension	Mean depth study zone	Populations	Justification	Reference
Alaria nana	6	0 m (Intertidal)	1	The only data available	Pfister and Wang 2005
Ascophyllum nodosum	6	9 m	1 (France)	One population selected because it is the one that accordingly to authors best represents its natural dynamics.	Araújo et al. 2014
Ecklonia radiata	8	3 m	2	Mean matrix of the two populations	Lees 2001
Fucus distichus	9	0 m (Intertidal)	1	The only data available	Ang and de Wreede 1993
Fucus serratus	6	9 m	1 (France)	One population selected because it is the one that accordingly to authors best represents its natural. dynamics	Araújo et al. 2014
Laminaria digitata	5	11 m	1	The only data available	Chapman 1990

Table C.9: Algal species found in the literature but excluded from the comparative analyses, and justification for exclusion.

Species	Matrix dimension	Justification	Reference
Sargassum siliquosum	7	Unrealistic matrix calculations that do not fit with those presented in the literature.	Ang and de Wreede 1990
Laminaria longicruris	6	Unrealistic matrix calculations that do not fit with those presented in the literature.	Ang and de Wreede 1990
Gelidium sesquipedale	12	Red alga with matrix size too big to compare with other matrices.	Vieira and Santos 2010
Iridaea splendents	8	Red alga	Ang et al. 1990
Macrocystis pyrifera	8	Unrealistic matrix outputs. Elasticity 100 % to the size class 6.	Chapman 1990

C.3.1 References

Araújo, R.M., Serraõ, E.A., Sousa-Pinto, I. and Åberg P. (2014) Spatial and temporal dynamics of fucoid populations (Ascophyllum nodosum and Fucus serratus): a comparison between central and range edge populations. PLoS ONE, 9, e92177.

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Pfister, C.A. and Wang, M. (2005) Beyond size: matrix projection models for populations where size is an incomplete descriptor. Ecology, 86, 2673-2683.

Vieira, V. and Santos, R. (2010) Demographic mechanisms determining the dynamics of the relative abundance of phases in biphasic life cycles. Journal of Phycology, 46, 1128–1137.

Table C.10: COMPADRE table showing terrestrial plant species selected in this study for the comparative analyses

Species	**DOI/ISBN**	**Matrix dimension**
Aeschynomene virginica	10.1890/02-5219	5
Schizachyrium brevifolium	None	6
Brassica napus	None	5
Bromus tectorum	10.1890/08-1446.1	5
Collinsia verna	10.2307/1940182	7
Lactuca serriola	10.1890/09-0750	5
Melampyrum pratense	10.1016/j.actao.2007.11.005	6
Persicaria perfoliata	10.1007/s10530-004-5572-9	5
Salsola kali	10.1111/j.1365-3180.2009.00703.x	7
Aconitum noveboracense	10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2	5
Actaea elata	10.1007/s00442-010-1809-8	6
Actaea spicata	10.1139/B03-099	6
Agropyron cristatum	10.1111/j.1365-2664.2006.01145.x	8
Anthyllis vulneraria	10.2307/2261628	6
Anthyllis vulneraria	10.1093/aob/mcp047	5
Arisaema triphyllum	10.2307/2937350	7

Asclepias meadii	978-3-642-07869-9	6
Astragalus cremnophylax	10.1046/j.1523-1739.1997.96159.x	5
Astragalus peckii	10.1007/s10144-012-0318-5	5
Astragalus scaphoides	10.1890/03-0256	5
Astragalus tyghensis	10.1890/0012-9658(2003) 084[1464:TEOSTO]2.0.CO;2	5
Balsamorhiza sagittata	10.1111/j.1365-2664.2009.01635.x	5
Dioscorea chouardii	10.1016/S0006-3207(01)00113-6	6
Bouteloua rigidiseta	10.1890/05-1197	5
Calathea micans	10.1016/j.ecolmodel.2005.05.009	5
Calathea ovandensis	10.2307/2937136	8
Centaurea horrida	10.1007/s11258-012-0110-9	5
Chamaecrista lineata keyensis	10.1890/03-5382	8
Cleistesiopsis divaricata	10.2307/2261246	5
Cochlearia bavarica	10.1007/BF02803075	5
Cryptantha flava	10.1111/j.1365-2745.2007.01350.x	7
Cypripedium calceolus	10.1111/j.1523-1739.2010.01466.x	5
Danthonia sericea	10.3354/meps045001	6
Dicerandra frutescens	10.1016/j.biocon.2005.08.002	6

Digitalis purpurea	10.1111/j.1365-2745.2007.01287.x	6
Dipsacus fullonum	10.2307/1936930	7
Epilobium latifolium	10.2307/1941457	5
Erigeron kachinensis	10.2307/2426659	5
Eriogonum longifolium	10.1890/1051-0761(2002) 012[1672:ASBPVI]2.0.CO;2	5
Eryngium cuneifolium	10.1890/03-4029	6
Fritillaria meleagris	10.1111/j.1600-0587.1985.tb01174.x	8
Gaura neomexicana coloradensis	10.1086/297607	5
Gentiana pneumonanthe	10.2307/2261351	5
Gentianella campestris	10.1046/j.1365-2745.2001.00566.x	6
Geranium sylvaticum	10.1086/512040	8
Heliconia acuminata	10.1890/0012-9658(2003) 084[0932:APPIFH]2.0.CO;2	6
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Hudsonia ericoides montana	10.1111/j.1523-1739.1998.97285.x	5
Hydrastis canadensis	10.1007/s11258-010-9749-2	5
Hypericum cumulicola	10.1046/j.1523-1739.2003.01431.x	6
Ipomopsis aggregata	10.1111/j.2007.0030-1299.15705.x	7

Isatis tinctoria	10.3719/weed.33.Suppl_103	5
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Leptocoryphium lanatum	10.1016/j.ecolmodel.2003.12.044	5
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Panax quinquefolius	10.1046/j.1523-1739.1996.10020608.x	6
Panax quinquefolius	10.2307/2260724	6

Pedicularis furbishiae	10.1111/j.1523-1739.1990.tb00267.x	6
Periandra mediterranea	10.1016/S0378-1127(02)00566-2	8
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Plantago media	10.2307/3236803	5
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Primula veris	10.1111/j.1365-2664.2005.01015.x	6
Primula veris	10.1111/j.1523-1739.2006.00368.x	6
Primula veris	10.1007/s11258-004-0026-0	6
Ramonda myconi	10.1023/A:1020310609348	5
Sanicula elata	10.1034/j.1600-0706.2003.11493.x	5
Saussurea medusa	10.1007/s11258-010-9761-6	5
Scorzonera humilis	10.1111/j.1365-2745.2006.01147.x	5
Silene regia	10.1046/j.1365-2745.1998.00234.x	6
Syngonanthus nitens	10.1016/j.biocon.2012.03.018	5
Themeda triandra	10.2307/2404276	5

Tragopogon dubius	10.1890/09-0750.1	6
Trillium grandiflorum	10.3732/ajb.90.8.1207	6
Trollius laxus	10.1016/j.biocon.2012.01.061	5
Viola montana	10.1078/0367-2530-00151	5
Viola pumila	10.2478/s11756-009-0002-1	5
Acacia bilimekii	10.1016/j.jaridenv.2005.07.002	6
Acacia victoriae	10.1111/j.1442-9993.1994.tb01537.x	7
Ambrosia deltoidea	10.2307/1937693	6
Ardisia elliptica	10.1890/04-1483	8
Dubautia sandwicensis	10.1007/s00442-003-1295-3	7
Atriplex acanthocarpa	10.1007/s00442-008-0980-7	5
Banksia ericifolia	10.1111/j.1442-9993.1988.tb00999.x	9
Clidemia hirta	10.1007/s10530-005-5277-8	5
Cytisus scoparius	10.1111/j.0272-4332.2004.00481.x	7
Fumana procumbens	10.2307/2261672	6
Gardenia actinocarpa	10.1016/S0006-3207(02)00417-2	9
Lantana camara	10.1007/s10144-013-0364-7	6
Lupinus arboreus	10.1086/507877	9

Purshia subintegra	10.1111/j.1523-1739.2006.00272.x	5
Hymenanthes maxima	10.2307/2444780	9
Verticosa staminosa staminosa	10.1071/BT06032	9
Abies concolor	0.1111/j.1365-2745.2005.01007.x	5
Abies homolepis	10.1658/1100-9233(2007)18[379:VIJSAR]2.0.CO;2	6
Abies sachalinensis	10.1007/BF02523604	8
Abies sachalinensis	10.2307/3237309	5
Acer palmatum	10.3170/2007-8-18342	8
Aesculus turbinata	10.1046/j.1442-1984.1999.00007.x	7
Alnus incana rugosa	10.2307/1939207	5
Aquilaria crassna	10.1016/j.biocon.2008.04.015	8
Aquilaria malaccensis	10.1016/S0006-3207(00)00089-6	9
Araucaria hunsteinii	10.1111/j.1442-9993.1982.tb01304.x	8
Avicennia germinans	10.1111/j.1365-2745.2007.01298.x	7
Bursera glabrifolia	10.1016/j.foreco.2005.10.072	5
Callitris columellaris	10.2307/2846032	6
Calocedrus decurrens	10.1111/j.1365-2745.2005.01007.x	5
Camellia japonica	10.1111/j.1442-1984.2007.00190.x	5

Cecropia obtusifolia	10.1086/285599	8
Choerospodnias axillaris	10.1890/08-0111.1	6
Dicorynia guianensis	10.1016/j.ecolmodel.2010.06.010	9
Entandrophragma cylindricum	10.1016/j.foreco.2008.02.041	7
Eperua falcata	10.1111/j.1467-9876.2008.00657.x	6
Fagus grandifolia	10.2307/176863	9
Fagus sylvatica	10.1051/forest:2007037	5
Guettarda viburnoides	10.1890/09-0480.1	5
Khaya senegalensis	10.1111/j.1523-1739.2009.01345.x	5
Manilkara zapota	10.1017/S0266467408005713	9
Melaleuca viridiflora	10.1111/j.1442-9993.2008.01921.x	5
Microberlinia bisulcata	10.1890/10-2268.1	6
Parkinsonia aculeata	10.1111/j.1440-6055.2006.00556.x	6
Phyllanthus emblica	10.1111/j.1365-2664.2012.02156.x	7
Pinus lambertiana	10.1016/j.foreco.2011.05.011	6
Pinus nigra	10.1111/j.1365-2664.2005.01100.x	8
Pinus palustris	10.1086/284803	8
Pinus strobus	10.1371/journal.pone.0056953	9

Pinus sylvestris	10.2307/2401258	6
Prioria copaifera	10.1016/0378-1127(93)90045-O	8
Prosopis glandulosa	10.1046/j.1365-2745.1999.00420.x	9
Scaphium macropodum	10.1111/j.1365-2745.2006.01209.x	9
Sequoia sempervirens	10.1086/282913	5
Styrax obassia	10.2307/3237044	5
Taxus floridana	10.1111/j.1523-1739.2004.00567.x	9
Torreya taxifolia	10.1046/j.1523-1739.2000.98393.x	5
Tsuga canadensis	10.1016/j.foreco.2005.02.056	6
Vochysia ferruginea	10.1016/S0378-1127(96)03890-X	5

Appendix D

Chapter 5 Supporting Information

D.1 Details of the study sites

Here we present some complementary information to the main text about the studied *Cystoseira zosteroides* populations. The demographic censuses were conducted in three populations in the NW Mediterranean.

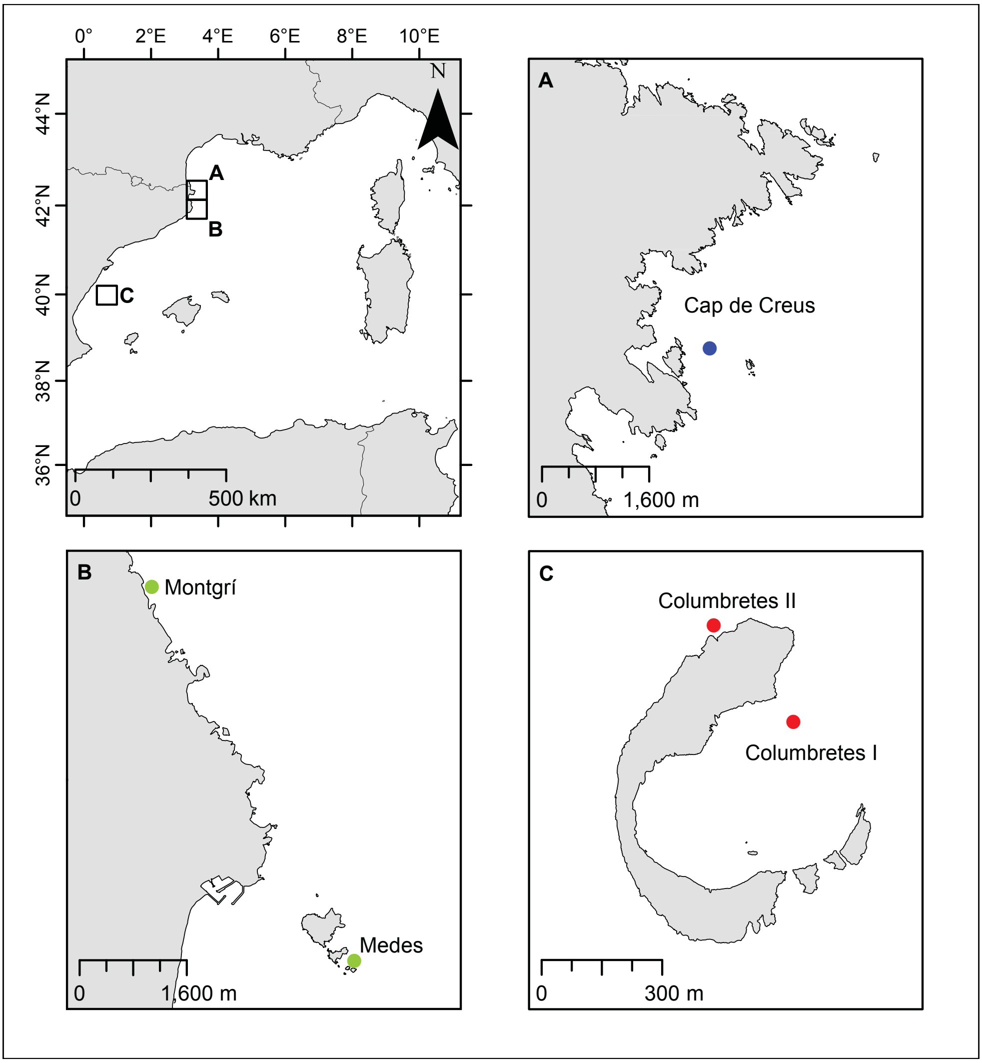

Figure D.1: Locations in NW Spain (study area), where the monitoring of *C. zosteroides* populations was conducted: A. Cap de Creus Natural Park population (2010-2012); B. Montgrí and Medes populations at Montgrí, Medes and Baix Ter Natural Park (2008-2010); C. Columbretes I and II populations at Columbretes Islands Marine Reserve (2010-2012).

Table D.1: Methodological details of the demographic studied sites. A total of 12 permanent transects were installed at five *Cystoseira zosteroides* populations, covering different areas, according to the morphology of the bottom and the extension of the population. Here we show some of the characteristics; mean depth (m), the number of permanent transects installed, the number of tagged individuals (at the first census), sampled area and the years when this species was monitored.

Population	Mean depth (m)	Number of transects	Number of individuals	Sampled Area	Years
Medes Islands	20	2	209	10 m^2	2008-2011
Montgrí Coast	20	3	181	14 m^2	2008-2011
Columbretes I	28	3	124	9 m^2	2010-2012
Columbretes II	24	3	130	9 m^2	2010-2012
Cap de Creus	23	2	175	19 m^2	2010-2012

D.2 Details about the experimental design

Here we show a schematic view of the experimental deployment to test the effect of temperature on the settlement and germling survival (Figure D.2), as well as the thermal cycle at which *Cystoseira zosteroides* monitored populations are exposed (Figure D.3).

27 fertile branches were placed at 3 aquaria (12 L) per treatment (16, 20 and 24°C). 3 Petri dishes were placed at the bottom of each aquarium, with 4 permanent quadrats of 1cm^2, where the zygotes from fertile branches settled. The temperature was maintained by placing aquaria inside two thermo-regulated incubation chambers and at 130 μmol photons m^{-2}s^{-1} of light intensity (similar to natural conditions exposure; pers. obs.) with a 12:12h light:dark cycle. The first chamber was kept at 16°C and contained three aquaria, and the second was kept at 20°C with six aquaria, containing the 20°C and 24°C treatments (Figure D.4). The temperature of the 24°C treatment was maintained by immersing aquaria in containers filled with water kept at 24°C by an aquarium heater (250 W ThermoControl, EHEIM JAGER GmbH and Co., KG). To ensure homogeneous water temperature conditions, a water pump was used to circulate the water inside aquaria and inside the containers (Figure D.4). The temperature was daily measured at each aquarium using a digital thermometer with a ±0.1°C resolution (TP3001, Labbox) and was continuously recorded using temperature logger with ±0.02°C resolution (HOBO Water Temperature Pro v2 Data Logger, ONSET computer corp., USA). Every week, seawater was replaced in all aquaria with filtered seawater previously acclimatized to each temperature treatment.

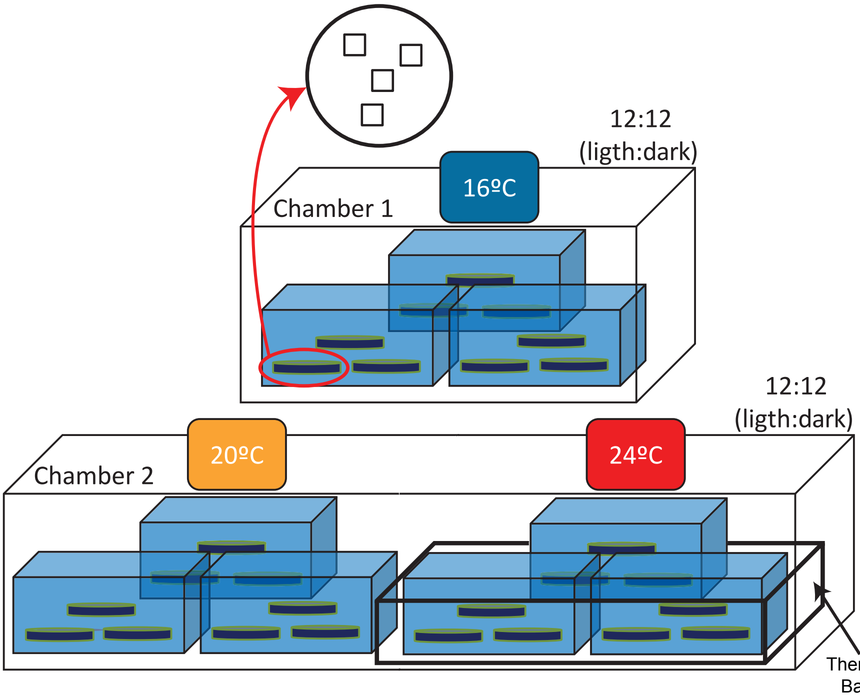

Figure D.2: Scheme of the experimental design used to estimate the effect of temperature on settlement and survival rate of zygotes.

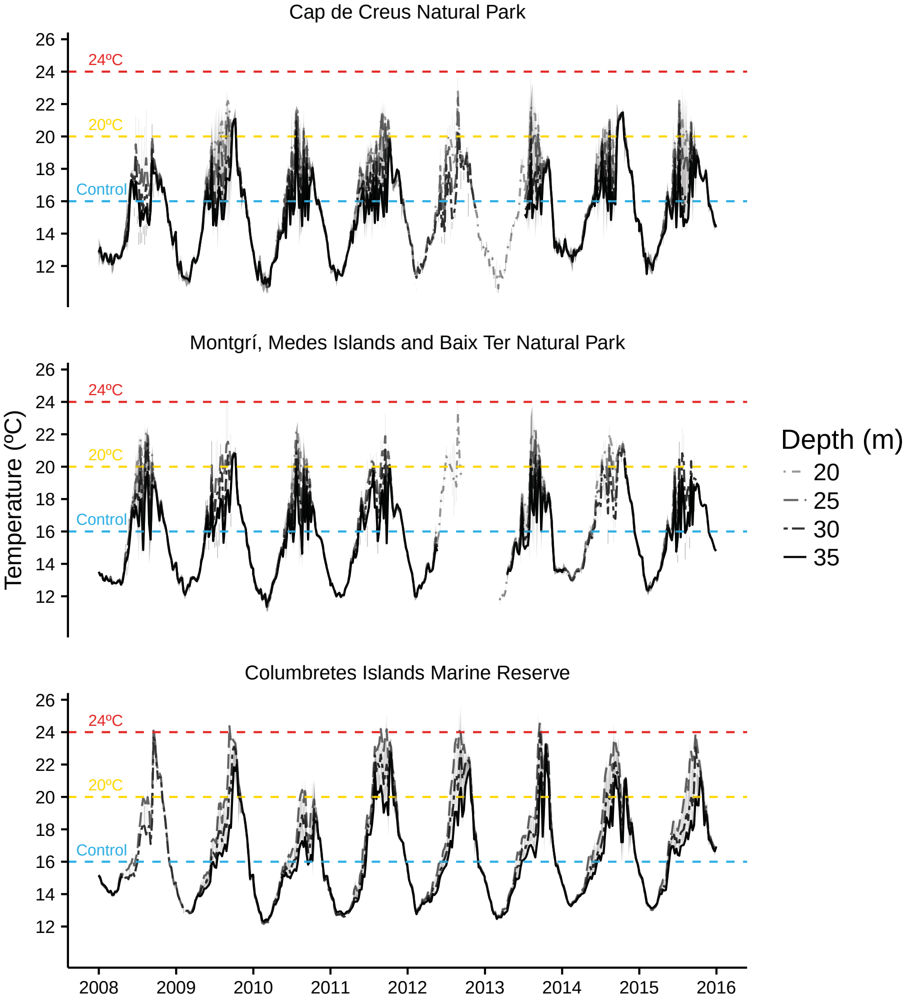

Figure D.3: Weekly mean temperature at the three different locations where our populations of *Cystoseira zosteroides* are monitored (Cap de Creus Natural Park, Montgrí, Medes Islands and Baix Ter Natural Park and Columbretes Islands Marine Reserve) at the respective depths (20, 25, 30, 35 m). Horizontal dashed lines indicate the treatments used in our experiment. Note that no data are available at 20 m depth for the Columbretes Islands population.

D.3 Details of the model formulation

Here we present the parametrization process of the Integral Projection Model (IPM, see main text in Chapter 5) used to model the life cycle and population dynamics of *Cystoseira zosteroides* (Figure D.4). We also show the overall structure and selection process of the survival and growth models (Table D.2). Finally, we present the different components of the reproductive model (Table D.3 and Figure D.5), including the details of the density dependent model (Table D.4).

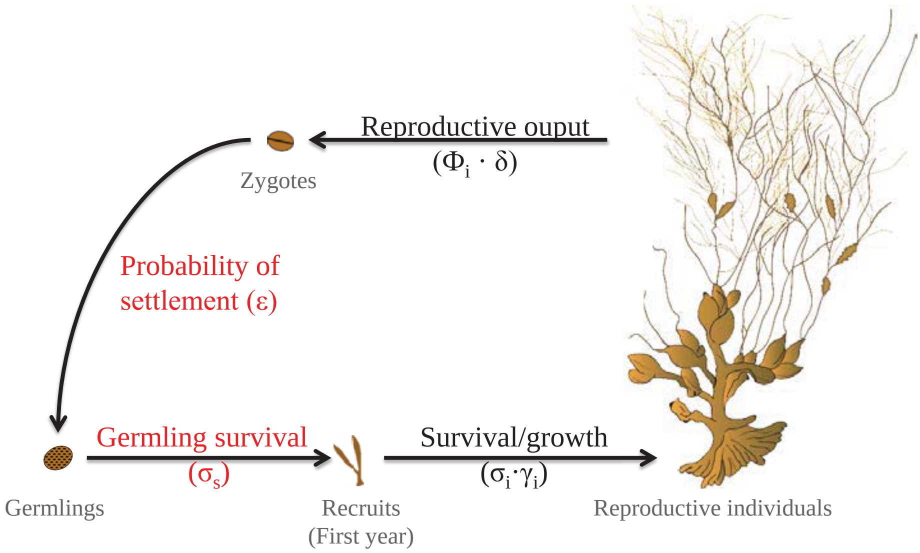

Figure D.4: Life cycle of *Cystoseira zosteroides*. Here are illustrated the possible fates of each of *C. zosteroides* life stages with special attention to the early phases. Once mature individuals reproduce ($\phi_i \times \sigma$), zygotes settle into the ground with a given probability (ϵ). Then these zygotes become germlings which must survive (σ_s), to become recruits. These two processes are colored in red because the effect of temperature has been quantified for both. Adult individual draw modified from Ballesteros (1990).

To model the population dynamics of *C. zosteroides* we used Integral Projection Models (IPMs). IPMs are a widespread mathematical approach to model the population dynamics of species (Easterling, 2000; Ellner and Rees, 2006). They are based on the premise that demographic rates are primarily influenced by a continuously varying measure (z; in *C. zosteroides* case individual size). This is analogous to matrix projection models but it has the main advantage that the IPM doesn't need to establish discrete classes.

In a mathematical sense, an IPM is function that describes the fate of an individual at time t of a given size/state and its offspring to time $t+1$, and generally follows D.1:

$$n(z', t+1) = \int_L^U K(z', z) n(z, t) dz \tag{D.1}$$

where $n(z', t+1)$ and $n(z, t)$ are the size distribution at time $t+1$ and t respectively. L and U in equation D.1 are the minimum and maximum empirically observed states over which vital rates are modelled. Here, $L = 0.25$ cm and $U = 16$ cm of *C. zosteroides* perennial thallus. $K(z', z)$ is the kernel, a function the fate of individuals and their descendants of size z at time t, to size z' and time $t+1$. This kernel includes two sub-kernels: (i) the survival sub-kernel P, describing the probability with which individuals survive and transition to a higher/same state along the continuous variable between time t and $t+1$; and (ii) the reproductive sub-kernel F, describing the per-capita sexual contribution of established individuals to new recruits.

Our IPM included six vital rates: survival (σ), growth (γ), fertility (ϕ), recruits per capita (δ), probability of settlement of recruits (ϵ) and early survival of recruits (σ_s). To parametrize the vital rate functions of survival and growth that integrate the IPM, we used data for each site and year. We fitted a set of candidate models to our data, and to evaluate their goodness-of-fit of and select the best-fitted to our data we used the Akaike Information Criterion (AIC; Akaike 1974), and to estimate the probability that the selected model was the best one given our data and the set of candidate models, we estimated the Akaike weights $w_i(AIC)$ (Burnham and Anderson, 2002) (see Table D.2).

The best fitted models for survival was a logistic mixed effects model (GLMM) including size as fixed factors and population nested in year as a random factor (Table D.2). Similarly, for growth the best fitted model was a linear mixed effect model (LMM), with size as fixed factor and population nested in year as random factor (Table D.2).

Table D.2: Results of AIC analysis for the eight competing survival and models fitted to our census data. Here are presented: the model formula, the AIC estimates and the rounded Akaike weights ($w_i(AIC)$). Models are ranked according to their goodness-of-fit, from best to worst fitted.

Vital rate	**Model formula**	**df**	**AIC**	$w_i(AIC)$
Survival (σ)	**Survival size + (1|Site/Any)**	**4**	**855.2**	**0.605**
	Survival Size + Density of adults + (1|Site/Year)	5	856.9	0.257
	Survival Size + (1|Site) + (1|Year)	4	858.8	0.098
	Survival Size + Density of adults + (1|Site) + (1|Year)	5	860.6	0.04
	Survival Size + (1|Year)	3	880.3	<0.001
	Survival Size + Density of adults + (1|Year)	4	881.9	<0.001
	Survival Size + (1|Site)	3	932	<0.001
	Survival Size + Density of adults + (1|Site)	4	933.4	<0.001
Growth (γ)	**Size t+1 Size t + (1|Site/Any)**	**5**	**2348.9**	**0.976**
	Size t+1 Size t + (1|Site)	4	2357.9	0.011
	Size t+1 Size t + Density of adults + (1|Site/Any)	6	2359.2	0.006
	Size t+1 Size t + (1|Site) + (1|Year)	5	2359.9	0.004
	Size t+1 Size t + Density of adults + (1|Site)	5	2367.4	<0.001
	Size t+1 Size t + Density of adults + (1|Site) + (1|Year)	6	2369.4	<0.001
	Size t+1 Size t + (1|Year)	4	2432.1	<0.001
	Size t+1 Size t + Density of adults + (1|Year)	5	2442.4	<0.001

The reproductive output of any species can be distilled into several processes (Caswell, 2001). In our case, reproductive kernel F is defined in equation D.2 as the product of the probability of being reproductive (ϕ),

$$F = \phi \times \delta \times \epsilon \times \sigma_s \tag{D.2}$$

Fertility (ϕ), the probability of being fertile for each size class, was estimated as the relation between reproductive status (reproductive vs. non-reproductive) and size with a binomial regression (Table S2.2). As recruitment is density-dependent in *C. zosteroides* (Chapter 2), recruitment per capita (δ) was incorporated into the IPM by modifying the recruit:adult ratio as a function of the adult density (Table D.3). To parametrize this part of the model we pooled all the data across all populations, including those impacted (Cap de Creus: 2010-2012; Medes: 2008-2011; Montgrí: 2008-2011; Columbretes I: 2010-2012; Columbretes 2: 2010-2012). To do so, we fitted a generalized linear model (GLM) with Poisson error distribution and a log-link function as follows:

$$\delta_t + 1 = 2.66 - 2.06 \times [adult \quad density \quad at \quad time \quad t] \tag{D.3}$$

Despite D.3, we considered that when adult density was 0, recruitment was null, assuming that the arrival of new individuals from other populations was negligible, as *Cystoseira* species present low dispersal abilities (Gianni et al., 2013; Mangialajo et al., 2012). Note that δ considers the number of adults at time t to predict the reproductive output at time $t + 1$.

Finally, the probability of settlement (ϵ) and early survival (σ_s) were estimated using our laboratory experiment data, considering also how they were affected by the two temperature treatments. Given that laboratory conditions could potentially over- or underestimate these taxes, we considered field data as a reference and we decreased the germling survival according to the attenuation levels, corresponding to the effect of temperature on survival in the fitted mixed model (see Settlement and survival statistical analysis section). The variation between these taxes was introduced in the model by means of sampling the mean effect of treatment and its confidence interval (95%CI) at each model iteration.

Table D.3: Binomial fertility model parameters relating the size of individuals with the probability of being fertile. Here we show the parameters of the model, intercept, and slope, as well as their Standard Error (SE) and their significance.

	Coefficient	**SE**	***P-value***
Intercept	-0.31	1.23	0.8
Size	0.62	0.27	0.02
Null deviance = 32.163			
Residual deviance= 25.01			

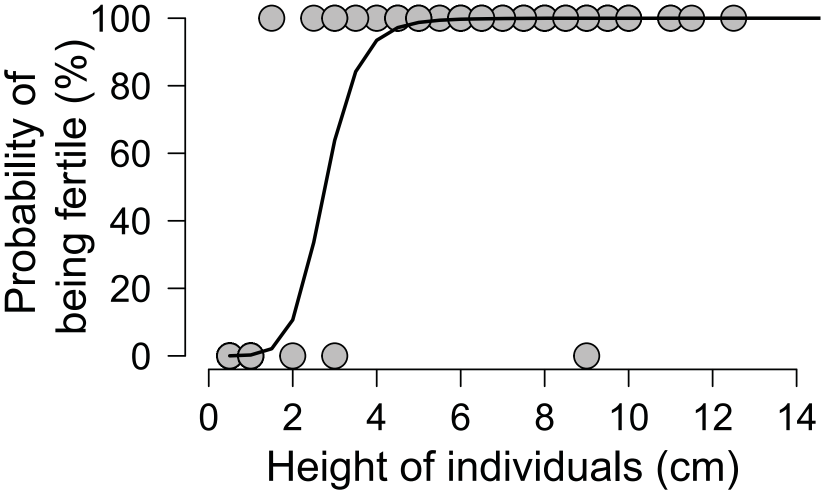

Figure D.5: The probability of being fertile as a function of the height of individuals (cm). Grey dots represent empirical data. The line represents the predicted probability according to the model showed at Table D.3

Table D.4: Generalized linear model with Poisson error distribution and a log-link function estimated for the density-dependent recruitment model. Here we show the parameters of the model, intercept, and slope, as well as their Standard Error (SE) and their significance

	Coefficient	**SE**	***P-value***
Intercept	2.66	0.07	<0.001
Adult/quadrat	-2.06	0.06	<0.001
Null deviance = 3079.6 **Residual deviance= 811.5**			

All analyses were performed using the statistical software R (R Development Core Team, 2014), mixed models were fitted using the function “glmer” and “lmer” from the lme4 package (Bates et al., 2014), the AIC and $w_i(AIC)$ were estimated using the function “AICtab” in the package bbmle (Bolker and R Development Core Team, 2016) and recruitment per capita and fertility functions were fitted using the “glm” function.

D.4 Complementary results to the main text

Here we present results from 1000 *Cystoseira zosteroides* population projections after a small disturbance of 10% mortality, over 100 years for each temperature scenario (Figure D.6).

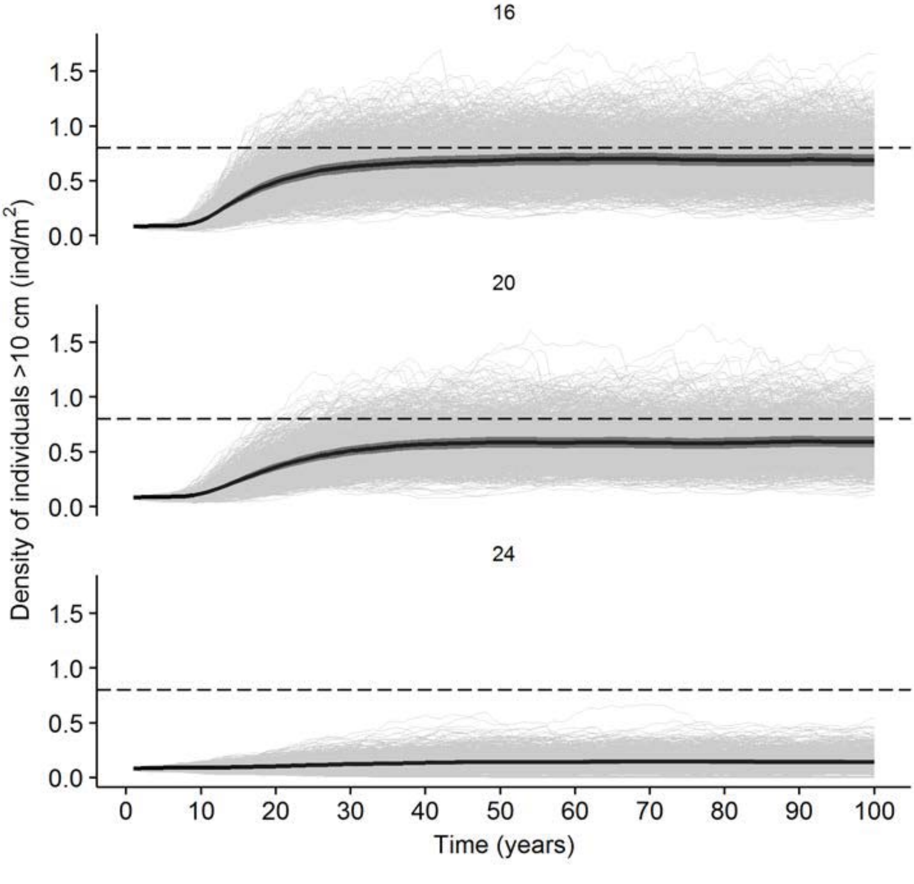

Figure D.6: Population trajectories (1000) projected over 100 years after a small (10%) mortality disturbance, for each of the temperature scenarios (16°C, 20°C and 24°C). Black line represents the mean value of all the projected populations, and the shadowed zone is the standard deviation. Grey lines are individual simulated populations. Dashed line represents our established threshold to consider a good conservation status

Appendix E

Published Chapters

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ORIGINAL PAPER

Recruitment patterns in the Mediterranean deep-water alga *Cystoseira zosteroides*

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Abstract Although recruitment is considered an essential process regulating populations of many marine species, there is still a lack of knowledge about the ultimate factors that influence it. This is especially true for seaweeds, where population dynamics studies are also lacking. The main objective of this study was to investigate the main mechanisms driving the recruitment patterns of an emblematic deep-water alga in the NW Mediterranean, *Cystoseira zosteroides*, and its influence on their population dynamics. Five *C. zosteroides* populations were monitored annually at different sites along the coast of Spain by using permanent transects over 3–4 years. Some of these populations suffered mass mortality events from natural or anthropogenic disturbances, allowing us to study the influence of such events. Our findings agreed with the expected results for a long-lived species. Under low frequency of disturbances, *C. zosteroides* populations displayed few fluctuations over time given the longevity of the adults, and they were poorly influenced by the dynamics of early life stages because of negative density-dependent control of conspecifics. Moreover, disturbances had a great influence on population dynamics because the removal of adults decreased the effects of density-dependent processes and enhanced the recruitment. Nonetheless, a high mortality was found for early life stages (~50 % year^{-1}), contrasting with the high survival of adults (~90 % year^{-1}). This study confirmed the slow population dynamics of these deep assemblages, demonstrated the influence of density in the *C. zosteroides* population dynamics and highlighted their vulnerability to the increase in natural and human-induced disturbances.

Introduction

Knowledge about key demographic processes is required to understand and predict the response of populations to environmental change (Caswell 2001; Smallegange and Coulson 2013). Recruitment is an essential process of regulating population abundance and dynamics (Caley et al. 1996; Hughes and Tanner 2000; Wright and Steinberg 2001). Nevertheless, factors controlling recruitment success are still poorly understood for most of marine organisms, mainly because of their small size during early life-history stages (Caley et al. 1996; Schiel and Foster 2006). Given the cumulative stressors to which marine ecosystems are exposed (Jackson et al. 2001; Harley et al. 2006; Halpern et al. 2008), understanding the dynamics of the early life-history stages of species is of great importance to assess their resistance and recover capacity.

Long-lived organisms often play an important role as foundation species creating unique habitats, providing biomass, producing biogenic structures, and enhancing biodiversity (Jones et al. 1994). These organisms usually exhibit low recruitment rates, and their populations are maintained by the long lifespan of the individuals (Åberg 1992). Thus, the slow dynamics of these species make them very vulnerable to the increase of perturbations. After disturbances, their recovery rate depends on both the supply of propagules to the disturbed site and their ability to colonize

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upon arrival (Dayton et al. 1992; Hughes and Tanner 2000; Reed et al. 2000). Macroalgae are important habitat-forming species in temperate rocky ecosystems (Schiel and Foster 2006); however, there are still few studies about population structure and dynamics on algae (Ang and De Wreede 1990; Åberg 1992; Chapman 1993; Wright and Steinberg 2001), and this is especially true for deep-water algal species (Flores-Moya et al. 1993; Spalding et al. 2003; Graham et al. 2007; Leichter et al. 2008).

Over the last decades, some efforts have been made to understand the drivers of early life stage dynamics in algae populations (reviewed in Vadas et al. 1992; Schiel and Foster 2006). From settlement until the juvenile stage, algae are likely to experience substantial mortality (Brawley and Johnson 1991; Dudgeon and Petraitis 2005; Schiel and Foster 2006). Density-dependent processes, such as intra- or interspecific competition, can play an important role in mediating settlement and recruitment success, with both positive and negative effects being possible (Reed 1990; Reed et al. 1991; Ang and De Wreede 1992; Steen and Scrosati 2004). Furthermore, early survival can be influenced by density-independent factors, such as light (Reed et al. 1991), microhabitat characteristics (Brawley and Johnson 1991; Benedetti-Cecchi and Cinelli 1992), sedimentation (Airoldi and Cinelli 1997; Irving et al. 2009), and herbivory (Dudgeon and Petraitis 2005; Araujo et al. 2012). Nevertheless, most studies of algal recruitment have been based on laboratory or in situ manipulative experiments, and few have been based on the observation of natural perturbations (Dayton et al. 1992).

In the Mediterranean Sea, the brown algae of the genus *Cystoseira* are considered important habitat-forming species. Because of their perennial thallus and canopy, they are very important for Mediterranean benthic communities, as they increase three-dimensional complexity, provide refuge and food for many species and harbour a high biodiversity of associated sessile invertebrates and algae (Ballesteros 1990; Ballesteros et al. 2009; Cheminée et al. 2013; Gianni et al. 2013). Nevertheless, some studies have shown evidence of the decline of *Cystoseira* assemblages over the last decades (Giaccone and Bruni 1973; Thibaut et al. 2005; Serio et al. 2006). Although the ultimate causes of this decline are not fully understood, several reasons have been proposed, including pollution (Sales et al. 2011), water turbidity (Cormaci and Furnari 1999), plucking from the bottom by fishing nets (Feldmann 1937; Thibaut et al. 2005), and episodic events, such as exceptional storms (Navarro et al. 2011).

Cystoseira zosteroides is an endemic and one of the most representative species of Mediterranean deep-water *Cystoseira* assemblages (Giaccone 1973; Ballesteros 1990; Ballesteros et al. 2009). Previous studies that focused on *C. zosteroides* populations showed that they were generally dominated by large organisms (which can be more than 50 years old) that displayed low recruitment and low growth rates (0.5 cm year^{-1}), and they were highly vulnerable to perturbations (Hereu et al. 2008; Ballesteros et al. 2009; Navarro et al. 2011). Given the limited information about the dynamics of this emblematic species and the paramount role of recruitment facing to increasing disturbances, the main objective of the present study was to assess the dynamics of the early life stages of this species and their influence on the population dynamics under disturbed and non-disturbed conditions.

Materials and methods

Study sites

Our study was performed on five *C. zosteroides* populations located at four localities in the NW Mediterranean Sea: Medes Islands Marine Reserve (Catalunya, Spain); Montgrí coast (Catalunya, Spain); Cap de Creus National Park (Catalunya, Spain) and two populations in Columbretes Islands Marine Reserve (Valencia, Spain) (Fig. 1; Table S1 Electronic Supplementary Material).

Sampling design

Permanent transects were installed in the summer of 2008 at Montgrí Coast and Medes Islands where 209 and 181 individuals were mapped, respectively. In addition, in May 2010, permanent transects were installed in Cap de Creus and in Columbretes (I and II), mapping 175, 124, and 130 individuals, respectively. Transects were monitored yearly during 4 years in Montgrí and Medes and during 3 years in Columbretes and Cap de Creus. Each transect was 1 m wide and 3 to 10 m long, depending on the morphology of each sampling zone (see Table S1 for details), and was partitioned using 50 × 50 cm^2 quadrats. Transects were placed between 20 and 28 m depth.

Cystoseira zosteroides is a perennial species with an erect thallus monopodically organized. The perennial part is the main axis (the stipe), and the tophules are reservoir vesicles which are situated at the top of stipe. In a previous study, Ballesteros et al. (2009) determined that the main axis was the best morphometric measurement to carry out underwater for size structure studies. Thus, in this study, we used the length of the main axis, as the distance between the apical part of the last tophule and the base of the axis insertion as the morphometric indicator. We did not measure the primary branches because of their deciduous character, they are formed annually at the beginning of spring (Ballesteros 1990). At each quadrat, all individuals were mapped, and the length of main axis was measured using a

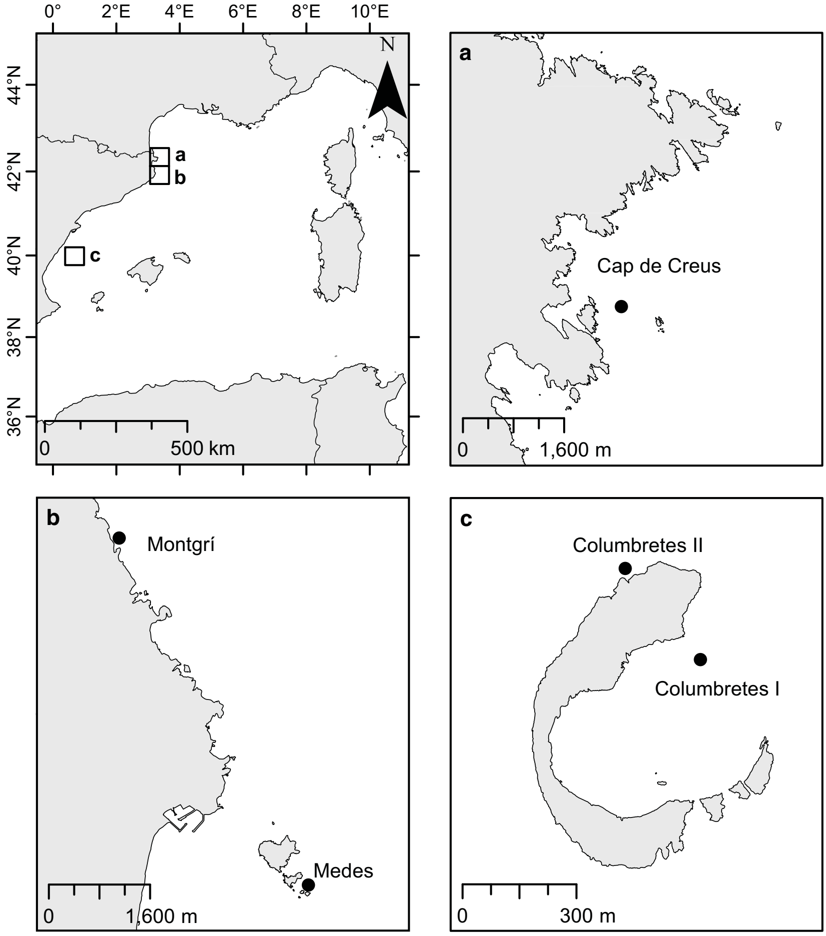


Fig. 1 Location of the study sites in the NW Mediterranean Sea. **a** Cap de Creus National Park (Catalunya, Spain). **b** Medes Islands Marine Reserve and Montgrí coast (Catalunya, Spain). **c** Columbretes Islands Marine Reserve (Valencia, Spain)

caliper with 1 mm accuracy. Recruits were identified as the new individuals appearing in the quadrats. During the first year of the census, recruits were considered those individuals with main axis length equal to or less than 0.5 cm long, based on our observations during the subsequent years of the study. Sampling was always performed by SCUBA diving at the beginning of the summer, between July and August, when *C. zosteroides* attain the highest seasonal biomass (Ballesteros 1990).

An unusual extreme easterly storm hit the Catalan coast (NW Mediterranean, Spain) on 26–27th December 2008 (Mateo and Garcia-Rubies 2012). This event was the largest recorded in the area and probably the most virulent one during the last decades. The most detrimental effect of the storm was the substrate movement which abraded and buried severely many shallow and deep benthic communities (Hereu et al. 2012; Sanchez-Vidal et al. 2012; Pagès et al. 2013). Damage on species depended on the exposure to wave action (latitude, orientation and depth), the type of surrounding substrate (continuous rock, boulders, sand), and the morphological traits of the organisms. The most affected region was the northern part of the Catalan coast (Costa Brava, NW Mediterranean), with winds of 20 m s^{-1}, maximum wave heights of 14 m and wave periods of 14 s (Jiménez 2012). Three of the studied *C. zosteroides* populations were situated in this northern region: Medes and Montgrí populations were observed to present 80 and 50 % mortality, respectively (Navarro et al. 2011); Cap de Creus population, situated at the northern part of the Catalan coast (Fig. 1), was probably also affected by the storm, though it was not previously reported.

The virulence of the storm progressively diminished as it moved to the southern part of the Catalan coast, where the wave power was only one-third of the recorded in the northernmost region (Jiménez 2012). Thus, there are no evidences that it affected to Columbretes populations situated 200 miles far from Medes Islands one of the most affected locations by the storm (Fig. 1). In addition, in 2009, an abandoned fishing net was found affecting the Montgrí population by eroding the bottom and plucking several *C. zosteroides* stands.

Data analysis

Population size structure was calculated by pooling individuals in size classes of 1 cm. Differences among populations and years in size-frequency distribution were tested using the nonparametric two-sample Kolmogorov–Smirnov test (K–S test; Legendre and Legendre 1998). Furthermore, Spearman's correlation (Wilcox 2003) was calculated between the number of recruits and adults per quadrat, and the number of recruits per quadrat and the mean size (length) of individuals inside the quadrat.

Generalized linear models (GLMs) were applied to explore the effect of different factors on the vital rates (recruitment and survival). Here, GLMs were used because they are mathematical extensions of linear models that do not force data into unnatural scales, and thereby, they enable to test differences between factors or explore relation between variables without assuming a normal error distribution or non-constant variance (McCullagh and Nelder 1989). A GLM with a binomial distribution and a logit link function was used to test the differences in survival (explanatory variable) between stages (adult/recruit), populations and years (factors). To explore the density dependence, we used a GLM with a negative binomial error distribution and a logit link function, because of the over-dispersion of the data. Number of recruits per quadrat was the explanatory variable, and factors were adult abundance per quadrat, site, and years. For parameter selection, in this case, we have tested different models with all different factors, and we tested the fitted-model factors using the Rao's score test in the survival test and the recruit model, because it is a good approximation when dealing with binomial or over-dispersed data (Lovison 2005).

All statistical analyses and the construction of the models were performed by using R software (R Development Core Team 2013).

Results

Size distribution

A shift to small individuals was observed in Medes population when it was affected by the 2008 storm (two-sample Kolmogorov–Smirnov test, $P < 0.001$, Table S2; Fig. 2) and in Montgrí population after the effect of the fishing net in 2009 (two-sample Kolmogorov–Smirnov test, $P < 0.001$, Table S2; Fig. 2). Conversely, the Columbretes I and Columbretes II populations were mostly dominated by large individuals without showing significant differences between consecutive years (Table S2; Fig. 2). In Cap de Creus, a greater proportion of small-sized individuals were observed, with a lower abundance of large individuals and no significant differences between years (Table S2; Fig. 2).

Density of individuals through time

Medes and Montgrí populations showed a decrease in density after the storm, in 2009; however, both populations showed contrasting recruitment dynamics. The Medes population displayed a high increase in recruit density in the years following the storm. In contrast, the density in Montgrí population notably decreased but not reaching the low-density values observed in Medes and exhibited no recruitment pulse; however, after the additional impact of an abandoned fishing net, density continued decreasing and recruit density increased slightly in 2010. On the other hand, Columbretes I and Columbretes II populations showed different dynamics, with almost no recruitment and a high density of non-recruit individuals with mild fluctuations over the years of study. Finally, the Cap de Creus population displayed intermediate values of adult density, with mild fluctuations and relatively high recruit density (Fig. 3). The number of recruits per quadrat was negatively correlated with the number of adults per quadrat (Spearman correlation: $\rho = -0.52$, $N = 997$, $P < 0.001$, Fig. 4a) and with the mean size of individuals inside the quadrat (Spearman correlation: $\rho = -0.82$, $N = 997$, $P < 0.001$, Fig. 4b). Mean size and adult density were positively correlated (Spearman correlation: $\rho = 0.61$, $N = 997$, $P < 0.001$). Thus, to test the influence of adult density on recruitment patterns across time and space, we applied a set of GLMs for the factors adult density, populations, and years. The Rao's score test showed that the only significant factors were adult density ($S1 = 249.25$, $P < 0.001$) and population ($S5 = 953.72$, $P < 0.001$) but not years ($S4 = 2.95$, $P = 0.566$), indicating a great variability on the recruitment between the studied places but not between overall years. The increase in adult density was negatively related to recruit abundance ($b = -0.205$, $P < 0.001$).

Temporal and spatial survival of recruits and adults

Survival was significantly higher for adults than for recruits ($S1 = 10.49$, $P = 0.001$), although a great variation between years ($S4 = 403.3$, $P < 0.001$) and populations ($S3 = 96.52$, $P < 0.01$) was observed. Mean adult survival

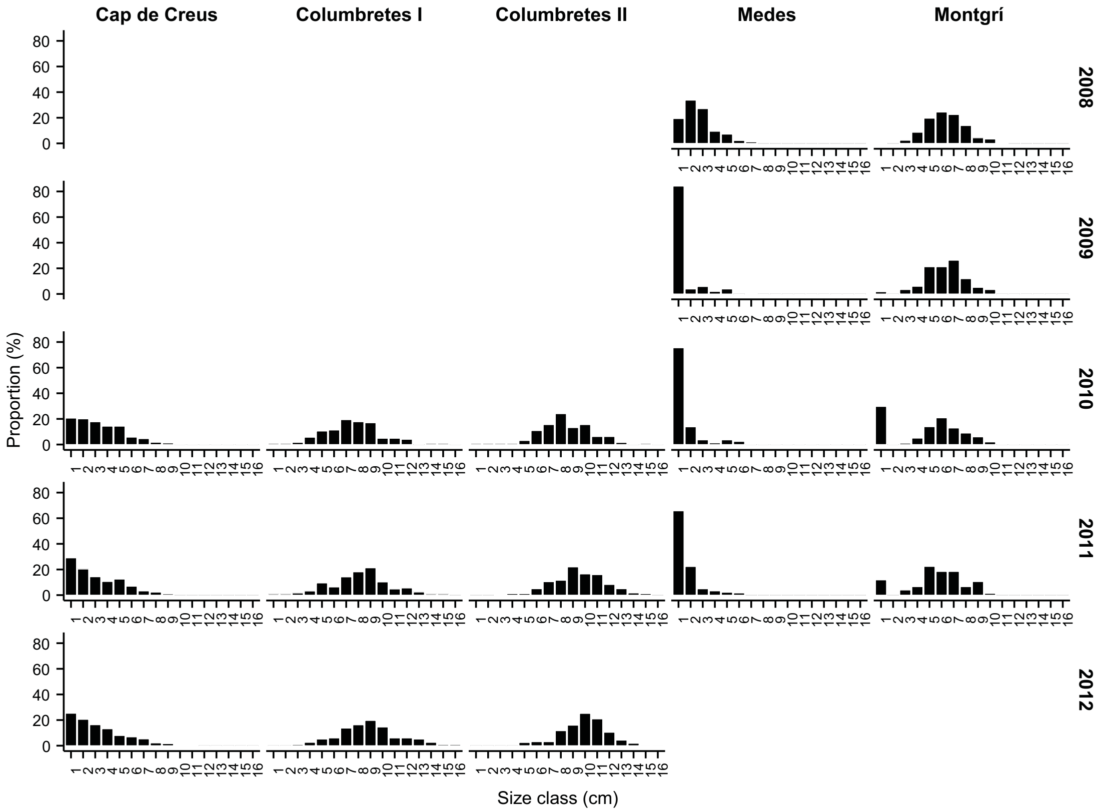
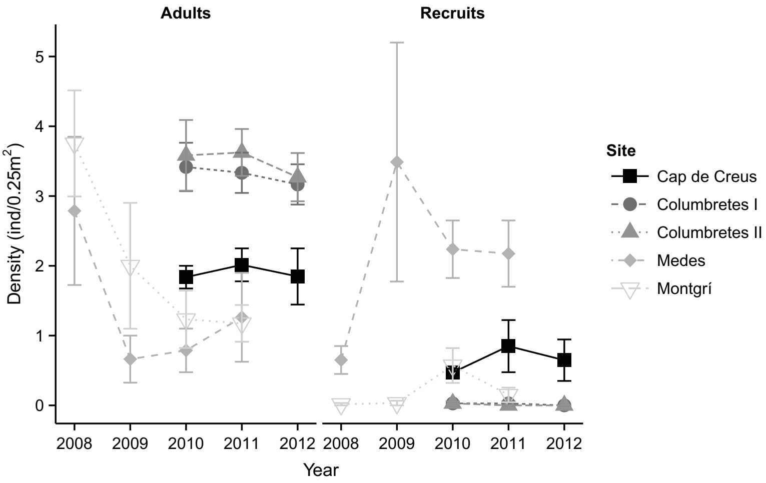


Fig. 2 Temporal evolution of size-frequency distribution of the length of the main axis (cm) for each studied population

Fig. 3 Density of recruits and adults (mean ± SE) over years for each studied population



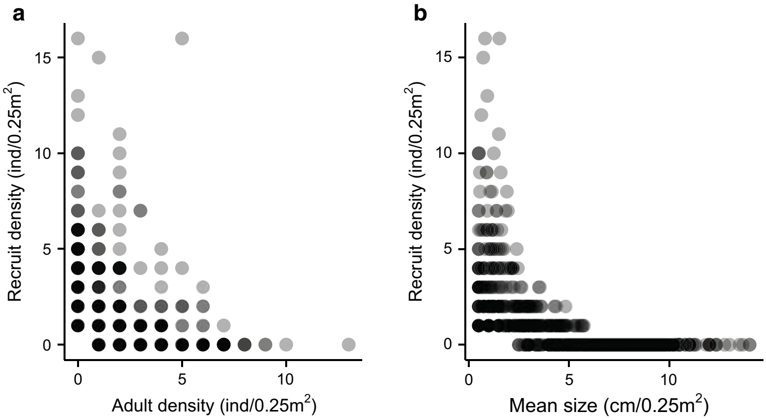


Fig. 4 Correlation between: **a** the number of recruits and the number of adults per quadrat (50 × 50 cm^2), **b** the number of recruits and the mean size of individuals at each quadrat. *Grey intensity of dots* is proportional to the number of quadrats

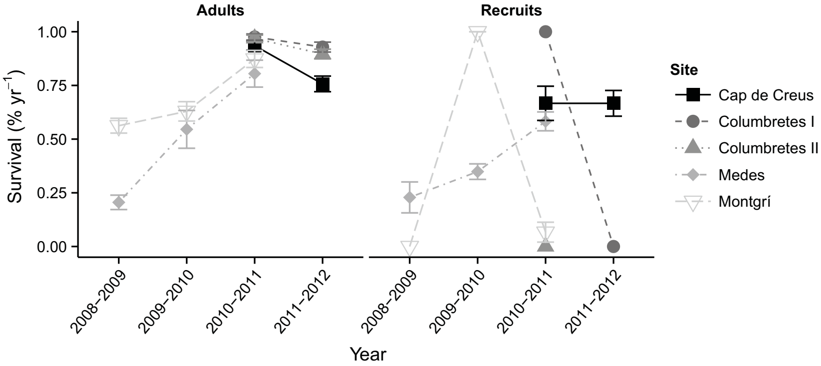


Fig. 5 Survival rates (mean ± SE) of recruits and adults estimated at each studied population and year

(±standard error) was 75.25 ± 1.13 % year^{-1} for adults and for recruits was 45.34 ± 2.29 % year^{-1}, but removing the years which populations were affected by disturbances mean survival values increased to 90.02 ± 0.97 % year^{-1} for adults and 55.21 ± 3.10 % year^{-1} for recruits. During the year of the storm, adult survival rates were lower than other years; however, there were differences between populations affected by the storm. Adult survival rates were lower in Medes (20.55 ± 3.35 % year^{-1}) in comparison with the Montgrí's population (56.25 ± 3.45 % year^{-1}). Both populations, Montgrí and Medes, showed an increase in the mean adult survival after the storm (Fig. 5), but in Montgrí population, this increase was less evident due to the impact of a fishing net (62.93 ± 4.50 % year^{-1}). In contrast, populations of Cap de Creus, Columbretes I and II showed higher adult survival rates, close to 90 % year^{-1} during the study period (Fig. 5). Recruit survival was highly variable among populations. In Cap de Creus and Medes, the populations with a higher abundance of recruits (Fig. 3), recruits showed survival values close to 50 % year^{-1}. In Medes, an increase in the survival of recruits in the following years after the storm was observed, as occurred for adults (Fig. 5). In contrast, recruit survival in Cap de Creus was very stable between the 2 years of study.

Discussion

Despite the paramount role of the genus *Cystoseira* as a habitat-forming species for Mediterranean communities, little attention has been paid to the population dynamics of these species, and this is especially true for deep-water species such as *C. zosteroides* (but see Hereu et al. 2008; Ballesteros et al. 2009; Navarro et al. 2011). To our knowledge, this is the first study regarding the dynamics of the early life stages of this species. Our studied populations displayed more contrasting size-frequency distributions than previously reported (Hereu et al. 2008; Ballesteros et al. 2009). It was observed a continuum of situations between populations dominated mainly by small individuals to others mainly dominated by large individuals with no recruits, showing a negative correlation between adult and recruit densities. Large disturbances seem to be the main factor explaining the contrasting dynamics of the studied populations. The impact of the storm in Medes and the fishing net in Montgrí caused an increase in recruitment rates, as a consequence of adult density reduction. In addition, Cap de Creus population, which was probably affected by the same storm, showed higher recruitment rates and lower adult density that the non-disturbed populations (Columbretes I and II). Hence, the contrasting size structure and recruitment dynamics suggested that this species was strongly influenced by density-driven responses, with adult canopy having a negative effect on the recruitment success.

Due to the scarcity of recruits in most of our studied populations, general survival patterns were difficult to observe. However, our results suggest that, on average, recruit survival was lower than for adults. In non-disturbed populations, adult survival was very close to 90 % year^{-1}, with similar values (98 % year^{-1}) that those reported by Ballesteros et al. (2009) for *C. zosteroides* populations from the Natural Reserve of Scandola (Corsica, France). Although adult survival rates in disturbed populations were notably lower during the impact year, they showed a tendency to increase from the disturbed year to the subsequent years. This suggests some delayed effects of these disturbances years after their impact. The investment of *C. zosteroides* in perennial thallus and reservoir vesicles (tophules) enhances their survival through years and enables them to persist during un-favourable seasons (Ballesteros 1990). Recruits do not have perennial thallus and tophules and then are probably more vulnerable than adults, which may explain their lower survival rates. This is commonly found in many perennial algal species, which display high mortality rates during their earlier stages [e.g. *Fucus disctichus*, Ang and De Wreede (1990); *Ascophyllum nodosum*, Åberg (1992); *Laminaria digitata*, Chapman (1993); *Delisea pulchra*, Wright and Steinberg (2001)], and it is also observed in other long-lived invertebrate species (Garrabou and Harmelin 2002; Linares et al. 2007; Teixidó et al. 2011; Kersting et al. 2014).

Previous authors observed no recruitment and low densities of small-sized individuals in *C. zosteroides* populations over long-time periods (Hereu et al. 2008; Ballesteros et al. 2009). Although we found higher recruitment rates in some *C. zosteroides* populations than previous studies, they are still much lower than the reported for other shallow *Cystoseira* species such as *C. barbata* (Perkol-Finkel and Airoldi 2010), *C. amantacea*, and *C. compressa* (Mangialajo et al. 2012). This is probably because of the paucity of the deep-water algae. Nonetheless, comparisons are difficult because most of studies about *Cystoseira* recruitment are based on manipulative or laboratory experiments rather than in natural rates (Benedetti-Cecchi and Cinelli 1992; Irving et al. 2009; Perkol-Finkel and Airoldi 2010; Mangialajo et al. 2012; Perkol-Finkel et al. 2012). Previous studies suggested that *C. zosteroides* is subjected to recruitment pulses promoted by occasional disturbances (Hereu et al. 2008; Ballesteros et al. 2009). Navarro et al. (2011) supported this hypothesis, as they found a pulse of recruitment after an extreme storm that caused mass mortality. Accordingly, we found that recruitment had little influence on the dynamic of populations under non-disturbed conditions. When adult densities decreased, due to mortality events (in our case), recruit densities increased rapidly. The recruit density was also negatively correlated with the mean size of individuals in the quadrat, as adult density was positively correlated with the mean size of individuals in the quadrat. This suggests that at high adult densities recruitment success is more limited due to intraspecific competition. In addition, due to the paucity of this species, the changes on the population dynamics remained several years after perturbations, as showed in Medes or in Cap de Creus 2 and 4 years after the storm (respectively).

Density-dependent processes influencing algal population structure have been very controversial, with studies showing both positive and negative effects (reviewed in Scrosati 2005). On one hand, some reproductive individuals are needed to provide new recruits (Dudgeon et al. 2001). Furthermore, in some species, it has been observed that adults can also provide protection against physical stress (Brawley and Johnson 1991) or grazing (Jenkins et al. 1999). Nonetheless, our results indicate that density of adults may have a strong negative influence on recruitment success in *C. zosteroides* populations, probably through intraspecific competition. Some studies suggest that dense algae stands can inhibit the survival of newly settled individuals in different ways, including by sweeping them (Vadas et al. 1992) or limiting light availability (Reed 1990). For example, experiments carried out by Cervin et al. (2005) showed that the shade effect of large canopies lowered the growth rate of *Ascophyllum* and *Fucus* recruits and prevented the development of mature plants. Light availability has a strong influence on the *Cystoseria* recruits development (Irving et al. 2009). Thus, light inhibition by adults could be a plausible explanation in our case, because of its scarcity under deep-water environments where *C. zosteroides* inhabits; however, data on light availability for the different study populations are not available.

Although most brown macroalgae species have a great reproductive potential, their greatest mortality occurs during microscopic stages (Schiel and Foster 2006), so very few eggs become settlers, and even less become visible recruits (Ang 1991; Champan 1995). Nevertheless, the processes influencing the step from spores to recruits are not fully understood for most of the algae species (the so called "black box", Schiel and Foster 2006). Many environmental factors have been suggested to influence recruitment patterns, such as sediment accumulation (Airoldi and Cinelli 1997; Irving et al. 2009), predation by herbivores (Dudgeon and Petraitis 2005; Araujo et al. 2012), habitat characteristics (Brawley and Johnson 1991; Benedetti-Cecchi and Cinelli 1992), or competition with other species (Blanchette 1996). *C. zosteroides* populations have been observed to present a high variability at small spatial scales (Hereu et al. 2008; Navarro et al. 2011), so the differences observed between our populations suggests that environmental factors may also have influenced recruitment success. For example, the limited recruitment observed in the population of Montgrí after disturbances could be related to their isolation in relation to other *C. zosteroides* populations (Hereu et al. 2010) and due to the limited dispersion ability of *Cystoseira* species (Gianni et al. 2013). Differences in the response to disturbances may also be explained by the type of substrate. Medes population was more affected by the storm than Montgrí, as the bottom of the former is formed by boulders, which were easily displaced by the effect of waves, generating more free space available for recruits. In contrast, Montgrí population was less affected by the storm as it thrives above hard rocky bottom, being a more stable substrate. Therefore, although our results suggest that conspecific density is an important factor determining recruitment success, the variability of environmental factors observed among populations point to that recruitment is influenced by several factors acting together.

Conclusions

Overall, our findings suggested that the scarcity of recruits in previously studied *C. zosteroides* populations (Hereu et al. 2008; Ballesteros et al. 2009) is related to post-settlement mortality and to negative effects of conspecifics on the recruitment success. During the absence of disturbances, *C. zosteroides* populations displayed few fluctuations over time because they are poorly influenced by the dynamic of early life stages, as observed in most long-lived plants (Åberg 1992; Adler et al. 2014). This stability was produced by the survival and longevity of large individuals, which established a ceiling for the smaller individuals through intraspecific competition. Disturbances acting at local or regional scales could alter the population dynamics of the species, decreasing the effects of density-dependent processes through the elimination of large individuals and through enhancing recruitment rates (Åberg 1992; Dayton et al. 1992; Engelen et al. 2005). These results suggested that these populations, similar to many other long-lived species, are conformed by intense pulses of recruitment, which produce cohorts that survive over long-time periods (Hughes and Tanner 2000; Ballesteros et al. 2009). Nonetheless, the high natural mortality during early life stages (as observed in this study) may limit the recovery capacity of this species facing the increase in natural and human-related perturbations.

Because of the high endangerment of deep-water *Cystoseira* assemblages throughout the Mediterranean (Thibaut et al. 2005; Serio et al. 2006), more efforts should be addressed to better understand their dynamics and the key processes shaping their populations. Our results have provided important knowledge about the population ecology of *C. zosteroides*, which is poorly understood for most of the deep-water algae species. This information helps to improve the predictive power of demographic models about future trends of these populations. In addition, a better understanding of demographic parameters, such as recruitment dynamics, may improve conservation initiatives (Perkol-Finkel et al. 2012; Gianni et al. 2013); however, there is still a need for more studies focused on the reproduction, the ecology of microscopic early life stages, and the dispersal ability of deep-water algae, what still remains an open question.

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Unravelling the natural dynamics and resilience patterns of underwater Mediterranean forests: insights from the demography of the brown alga *Cystoseira zosteroides*

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Summary

1. Despite being among the most important habitat-forming organisms in temperate seas almost nothing is known about the demography of many algal species. This limits our ability to understand the effects of global and local stressors and to predict future trends under ongoing environmental change, which in turn hinders conservation actions.

2. *Cystoseira* species develop important forest-like assemblages along the sublittoral zone in the Mediterranean Sea. In this study we investigated the natural population dynamics and resilience patterns of a deep-water brown and canopy-forming macroalga, *Cystoseira zosteroides*. We used density-dependent and stochastic matrix models to estimate its basic life-history and compare it with other relevant habitat-forming marine (brown algae) and terrestrial (plants) species. We also evaluated the consequences of increasing the disturbances caused by storms and the impact of lost fishing gear, and their interaction, on *C. zosteroides* population dynamics.

3. The population dynamics of *C. zosteroides* showed similar patterns to terrestrial long-lived species such as shrubs and trees, with high survival due to their investment in structural biomass. Our data and models suggest that this species is able to buffer mortality pulses by increasing the number of recruits (and probably recruit survival) due to the new space liberated and, therefore, lower intraspecific competition. Nevertheless, when storm disturbances were more frequent than once every 50 years, their populations collapsed, and this effect worsened when several stressors acted simultaneously.

4. Our results improve our understanding about the demography of algal forests, and highlight the fact that increases in local and global stressors may erode the resilience of macroalgae, resulting in a loss of structural complexity in the benthic communities of temperate seas.

5. *Synthesis*. Our findings reveal that deep-water *C. zosteroides* forests display slow population dynamics, similar to terrestrial perennials and trees. The increase in disturbance frequencies due to global and local stressors and their interaction will cause the decline of underwater macroalgal forests and may induce profound changes in their population and community dynamics.

Key-words: density dependence, disturbances, elasticity, life-history traits, lost fishing gear, macroalgae, matrix population models, population ecology, quasi-extinction, storms

Introduction

Understanding the relative importance of the demographic processes shaping populations is essential to answer relevant ecological and evolutionary questions (Metcalf & Pavard 2007) as well as to predict the response of species to ongoing environmental change (Smallegange & Coulson 2013). Despite the increased availability of demographic data (e.g. Salguero-Gómez *et al.* 2015), important biases exist towards studying terrestrial organisms over marine ones (Linares *et al.* 2007; Ripley & Caswell 2008). This is particularly worrying because coastal ecosystems are among the most ecologically and socioeconomically significant on the planet (Costanza *et al.* 1997; Harley *et al.* 2006).

Canopy-forming macroalgae, particularly large brown algae of the orders Laminariales, Tilopteridales and Fucales, have been historically considered the trees of marine temperate

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*Correspondence author. E-mail: pcapdevila.pc@gmail.com rocky ecosystems (Darwin 1839; Dayton 1985). Brown canopy-forming macroalgae are usually late-successional species (with some exceptions, e.g. *Pleurophycus gardneri*; Spalding, Foster & Heiine 2003), which increase the structural complexity where they live, providing shelter and food for many associated species (Steneck *et al.* 2002; Schiel & Foster 2006). Macroalgae can form important forests that extend from the littoral fringe (0 m depth) to deeper than 100 m (depending on species and region; e.g. Ballesteros 1990; Graham, Vásquez & Buschmann 2007; Marzinelli *et al.* 2015), and make important contributions to the benthic carbon cycle (Duarte & Cebrian 1996). Hence, the loss and/or reduction of canopy-forming algae has negative effects on the composition, structure and biodiversity of benthic assemblages (Steneck *et al.* 2002; Ling *et al.* 2015), which may impact the entire ecosystem functioning (Lotze *et al.* 2006; Worm *et al.* 2006; Smale *et al.* 2013).

Large natural disturbances (such as storms) play a major role in structuring macroalgal populations and communities (Steneck *et al.* 2002; Schiel & Foster 2006). These episodes can produce high mortality pulses, and macroalgal species are sometimes able to offset them through recruitment pulses (e.g. Dayton *et al.* 1992). Yet, the loss of dominant macroalgae can cause changes on the structure and dynamics of the community that can last for many years (Underwood 1999; Jenkins, Norton & Hawkins 2004). Regrettably, human-induced perturbations (e.g. fishing, lost fishing gear, eutrophication) are increasing in coastal areas (Halpern *et al.* 2008) and climate change is expected to augment the frequency and intensity of storms in marine environments (Harley *et al.* 2006; IPCC 2007; Kerr 2011). The increase in the recurrence of these stressors, or their combined effect, is suggested to be the main driver of canopy algae decline in temperate seas world-wide (Airoldi & Beck 2007; Strain *et al.* 2014; Mineur *et al.* 2015). However, a sound understanding of the demographic processes shaping macroalgal populations is still lacking, and this limits our ability to predict how they respond to disturbances (Åberg 1992a,b; Engelen *et al.* 2005; Svensson, Pavia & Åberg 2009) and hinders conservation actions (Perkol-Finkel *et al.* 2012; Campbell *et al.* 2014). Thus, understanding the population dynamics of these habitat-forming organisms and determining the population-level effects of changing disturbance regimes are crucial for preservation of the biodiversity that they harbour.

Due to the complexity of algal life cycles and the logistical challenges of tagging individuals in marine environments, demographic studies have generally neglected macroalgae (Schiel & Foster 2006). Most of the published studies are focused on easily accessible species located in shallow waters (e.g. Ang & De Wreede 1990; Engel *et al.* 2001; but see Spalding, Foster & Heiine 2003; Ballesteros *et al.* 2009) and assume that they are representative of other algal species. Nevertheless, community complexity (i.e. diversity and species richness) increases with depth, and community dynamics (i.e. productivity, turnover and growth rates) decrease (e.g. Ballesteros 1990; Garrabou, Ballesteros & Zabala 2002), as a consequence of the stabilization of physical restricting factors and light limitation. In addition, very few authors have modelled the effects of environmental stochasticity (but see Engelen *et al.* 2005; Engelen & Santos 2009; Svensson, Pavia & Åberg 2009) and, to our knowledge, none has included density dependence, despite the fact that these are important drivers of algal population dynamics (Schiel & Foster 2006).

In this study, we used high-resolution demographic data to build stochastic and density-dependent matrix models (Tuljapurkar & Caswell 1996; Caswell 2001) to study the population dynamics of a brown macroalga. As a model species, we used the Mediterranean alga *Cystoseira zosteroides* C. Agradh (Fucales, Ochrophyta; Fig. 1). This species is among the most long-lived macroalgae described to date, with a life span of up to 50 years (Ballesteros *et al.* 2009), and its populations are subjected to negative density dependence on recruitment (i.e. the negative effect of conspecifics on the recruitment success; Capdevila *et al.* 2015). Recent studies suggest that the distribution of *Cystoseira* spp. in the Mediterranean is shrinking mainly due to human disturbances including pollution (Sales *et al.* 2011), water turbidity (Cormaci & Furnari 1999), plucking from the bottom by lost fishing gear (Thibaut *et al.* 2005) and episodic events, such as storms (Navarro *et al.* 2011). Thus, the aims of this study were threefold: (i) to estimate basic life-history traits of *C. zosteroides*; (ii) to evaluate the relative importance of the different demographic processes and compare this species with other brown algae and terrestrial plants from the published literature; and (iii) to test its potential response to an increase in the recurrence of large, low-frequency disturbance events (storms) and of local impacts (lost fishing gear).

Materials and methods

STUDY SPECIES

In the Mediterranean Sea, *Cystoseira* species are the dominant macroalgae of the rocky benthic communities (Gianni *et al.* 2013). *Cystoseira zosteroides* inhabits rocky substrates from 15 to 50 m depth, with light levels ranging from 1% to 0.3% of surface irradiance

Fig. 1. Picture of a *Cystoseira zosteroides* canopy (Columbretes Islands, Spain). Photographic credit: Diego K. Kersting.

(Giaccone & Bruni 1973). Its distribution spans the western Mediterranean Sea with the exception of the Alboran Sea (Giaccone 1973); however, recent studies suggest that its distribution is shrinking mainly due to human disturbances (Thibaut *et al.* 2005 and references therein). This species is characterized by a perennial thallus with reservoir vesicles (tophules) at the top, from which primary branches originate. The deciduous parts of the algae (branches) develop on early spring and they fall at early autumn, so branches are renewed annually. Ballesteros *et al.* (2009) found that the length of the main axis (the perennial part) was the best morphological measure for the evaluation of the population structure independently of the season. Its populations are dominated by large individuals (Fig. 1), with low growth (0.5 cm year^{-1}) and high survival rates (Ballesteros *et al.* 2009; Navarro *et al.* 2011; Capdevila *et al.* 2015). *Cystoseira zosteroides* is monoecious with a diplontic and iteroparous life-history. Gametes are formed in reproductive structures (receptacles) located at the base of the primary branches (Ballesteros 1990).

DEMOGRAPHIC DATA

The demographic parameters used in this study are based on the data obtained in a previous study (Capdevila *et al.* 2015), in which five *C. zosteroides* populations were monitored at different localities across the NW Mediterranean (two populations of Columbretes Islands, one of the Montgrí coast, one of Medes Islands and one of Cap de Creus), during 3–4 years (2008–2011 in Montgrí and Medes and 2010–2012 in Columbretes and Cap de Creus).

For the model parameterization, survival and growth rates were obtained from the two undisturbed populations (Columbretes I 39°53′53.2″N 0°41′19.1″E and Columbretes II 39°54′02.2″N 0°41′11.6″E) located at the Columbretes Islands Marine Reserve (Castelló, Spain). Demographic data of survival and growth were obtained from annual monitoring of individuals from three permanent transects installed at two populations of Columbretes Islands, between 20 and 28 m depth in May 2010. Each transect was 1 m wide and 3 m long and was partitioned using 50 × 50 cm^2 quadrats. Sampling was always performed by scuba-diving, and transects were visited annually by the same experienced observers from 2010 to 2012 at the beginning of the summer (between July and August), when this species attains its highest seasonal biomass (Ballesteros 1990). A total of 254 *C. zosteroides* individuals were marked (124 in Columbretes I and 130 in Columbretes II). The size of individuals represents the maximum length of the primary perennial axis, which was measured using a calliper with 1 mm accuracy as the distance between the apical part of the axis and the base of the axis insertion of the last tophule (Ballesteros *et al.* 2009). For each individual, growth (difference in size between two consecutive censuses) and mortality (disappearance of individuals between censuses) were recorded. Recruits were identified as new individuals appearing in the quadrats.

To build the density-dependent recruitment model (see below and Appendix S1 in Supporting Information), we had to pool the data across all study locations (Columbretes but also Montgrí coast, Medes Islands and Cap de Creus; see Capdevila *et al.* 2015) to increase the statistical power in the estimation of recruitment at various population densities.

Given the difficulty of measuring fertility and fecundity rates *in situ*, these parameters were obtained by sampling 84 stands (outside the transect) covering a wide size range (1–12.5 cm) during the reproductive season (between early spring and summer). For these individuals, length was measured *in situ* and three secondary branches of each individual were collected to determine the presence or absence of receptacles in the laboratory. Fertility (the probability of an individual being reproductive) was estimated as the relation between reproductive status and size with a binomial regression (see Table S1). Fecundity, the number of seedlings produced per adult, was calculated as the product of fertility and the number of recruits *per capita* observed in the two study locations (the number of recruits at time $t + 1$ divided by the number of reproductive individuals at time t; Caswell 2001).

MODEL FORMULATION

Using these demographic parameters, a size-based matrix model was constructed with five size classes, based on the changes in survival and fertility *versus* size (Morris & Doak 2002). The first class represented recruits, individuals between 0.5 and 1 cm height, which are not fertile. The remaining classes were as follows: 1–4 cm, 4–6 cm, 6–10 cm and > 10 cm in height (Fig. S1 in Appendix S2). All these classes were chosen to have a significant number of individuals at each class. Transition matrices were built from the data obtained from each population and time interval (see Appendix S2). Transition probabilities between stages involved the following vital rates: s_i, the survival probability of an individual of class i; g_i, the probability that an individual of class i grows to class $i + 1$; and f_i, the reproductive output of individuals of class i. This species does not show clonal reproduction nor has a seed bank, so these were not included in the transition matrices.

Previous studies demonstrated that recruitment in *C. zosteroides* populations is subject to negative density-dependent processes (Capdevila *et al.* 2015). Consequently, density dependence was modelled using a generalized linear model (GLM) with Poisson error distribution and a log-link function using the data from Capdevila *et al.* (2015). Recruits per adult was negatively correlated with adult density ($b = -2.06$, $P < 0.001$; Table S2). Density dependence was incorporated into the matrix $\mathbf{A}_{N(t)}$ by setting f_i as a function of the density of adults:

$$\text{Recruits per adult} = 2.66 - 2.06 \times [\text{adult density}] \qquad \text{eqn 1}$$

When adult density was 0, recruitment was considered null, assuming that the arrival of new individuals from other populations was negligible, as *Cystoseira* species present low dispersal abilities (Mangialajo *et al.* 2012; Gianni *et al.* 2013 and references therein).

We constructed a mean matrix population model for *C. zosteroides* by averaging the survival and growth rates from the two populations studied. Further, for comparative analyses between our studied populations and other brown algal species (see below), we used our density-dependent model after setting it to stationarity ($\lambda = 1$) by iterating densities and changing the reproductive part of the matrix.

MODEL OUTPUTS

For each population and time interval, and for the mean density-dependent model, we calculated several demographic outputs. Yearly population growth rates were approximated as the dominant eigenvalue (λ) of each population and yearly matrix. The damping ratio (ρ), which is a measure of how quickly a population converges to its stable stage distribution, was also estimated (Caswell 2001). Finally, we estimated life expectancy based on the fundamental matrix approach described in Caswell (2001).

In order to compare the life-history traits of *C. zosteroides* with other brown algae and terrestrial plants, we compiled demographic data from the public data base COMPADRE (Salguero-Gómez *et al.* 2015) and for brown algae we added three species from the literature (see Appendix S3). For terrestrial plants, we compiled matrices with the same size range as for algae matrices (see Appendix S3), in order to avoid biases in the elasticity values of the different demographic processes due to matrix size (Salguero-Gómez & Plotkin 2010). Only matrices coming from non-disturbed populations were used, and for species studied at more than one site or year, mean matrices were used, thus obtaining only one matrix per species. This selection criterion excluded many annual and shrub species, yet we decided to follow it because analysing all groups of terrestrial plants was out of the scope of this study.

Once we obtained the transition matrix from different species, we calculated the matrix element elasticity values, which indicate how much a matrix element contributes to λ relative to the contribution of other elements (de Kroon *et al.* 1986; Caswell 2001). These were estimated for each species and for the density-dependent matrix $\mathbf{A}_{N(t)}$ of *C. zosteroides* at demographic equilibrium ($\lambda = 1$). Each matrix element was identified as a component of growth, survival or fecundity following Silvertown, Franco & McConway (1992). As the elasticities of all matrix elements sum to unity, we were able to standardize the values obtained from different species and compare them in a triangular ordination plot (Silvertown, Franco & McConway 1992; Silvertown *et al.* 1993). Elasticity matrix elements representing progression to the following size classes were assigned to growth, elements that represented stasis or shrinkage to smaller stages were assigned to survival, and elements representing reproduction were assigned to fecundity. As matrices came from different species, special care was taken to correctly assign elasticity values to the component for each species.

POPULATION PROJECTION AND DISTURBANCES RESPONSES

To study the dynamics of a population after a disturbance, we started by projecting a population for 50 years, multiplying the density-dependent transition matrix $\mathbf{A}_{N(t)}$ by a population vector n_t:

$$n_{t+1} = A_{N(t)} \times n_t \qquad \text{eqn 2}$$

where the initial $\mathrm{n_t}$ vector was taken from the stable stage obtained from the $\mathbf{A}_{N(t)}$ at equilibrium, and the matrix $\mathbf{A}_{N(t)}$ was updated at each time step to reflect density dependence in recruitment.

As explained above, large and low-frequency disturbances such as storms play a major role in the structure of macroalgal populations but these species are usually able to cope with these high mortalities through recruitment pulses. Nevertheless, climate change is expected to increase the frequency and intensity of storms and modelling is an essential tool to predict the future consequences of increasing disturbance frequency at population level. The consequences of the impact of a single large storm have been previously studied for *C. zosteroides*, and these data have been used to model this disturbance (Navarro *et al.* 2011). To do this, at year 10 of our simulations, we introduced the effect of a storm that caused 80% mortality in this species populations (Navarro *et al.* 2011).

We evaluated the effect of increasing annual frequency of extreme storms (from 0 to yearly) by simulating different disturbance

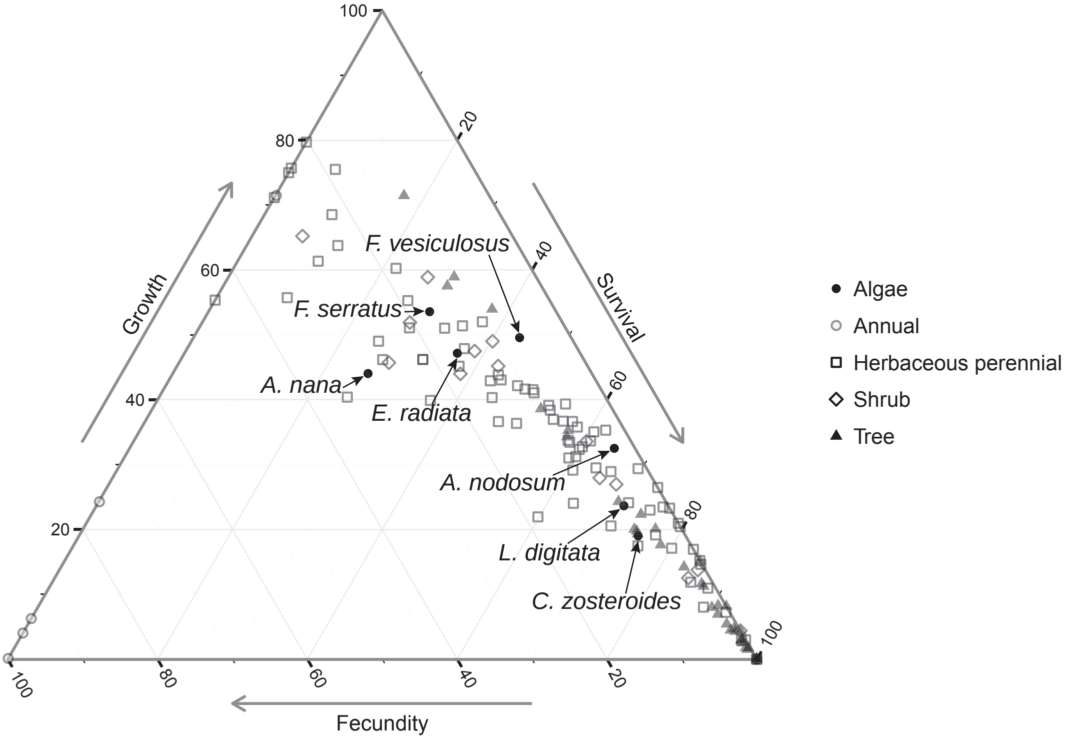

Fig. 2. Elasticity triangular plot of several brown algae and terrestrial species compiled from the literature.

frequencies (each causing 80% mortality) and projecting the population for up to 100 years with 10 000 iterations. In addition, to explore the consequences of the interaction between local and global stressors on the resilience of *C. zosteroides* populations, we used a similar approximation as Mandle, Ticktin & Zuidema (2015) by simulating different frequencies of mortalities caused by fishing nets (estimated to be about 60% of mortality in a previous study; see Capdevila *et al.* 2015) and storms. We did not model other disturbances, such as herbivory or competition, because their effect on this species is negligible (Vergés, Alcoverro & Ballesteros 2009) or unknown. For each storm recurrence, we calculated the mean matrix components elasticities (which were summed as contributions to survival, growth and fecundity) and the quasi-extinction probability, by using an extinction threshold of 10% of the initial population density. Quasi-extinction probability is the likelihood of a population falling below a minimum number of individuals below which the population is likely to be critically and immediately imperiled (Morris & Doak 2002). Furthermore, the mean lambda (λ) of the projected population was calculated for each simulation, as well as for the different combinations of disturbances.

All statistical analyses were performed using R software (R Core Team 2014). For the demographic estimates, we used the package 'POPBIO' (Stubben & Milligan 2007).

Results

CYSTOSEIRA ZOSTEROIDES LIFE-HISTORY

Our results show an increase in survival rates with size classes, ranging from 50 to 92% (Appendix S2), with a mean survival rate of 85%. Transitions between stages were quite constant (between 25 to 40%) but lower for the largest size class. We also observed an increase in the probability of being fertile with size (Appendix S2).

Deterministic growth rates (λ) for the two *C. zosteroides* populations varied between years and populations, ranging from 0.93 to 1 (Table 1). The damping ratio for all years and populations was between 1.12 and 1.33 (Table 1), indicating a very slow convergence to the stable structure. In accordance with the variability of lambda values, life span was very variable. While the population of Columbretes II showed values between 4 and 49 years, Columbretes I showed values between 71 and 76 years (Table 1), and for the population at equilibrium, it was calculated 64 years (Table 1).

The triangular plot resulting from the sum of the matrix elasticity components from the different species showed that most brown algae occupied the same region as perennial herbs, shrubs and trees, with high elasticity to survival and relatively little contribution to fecundity and growth (Fig. 2). Among the studied brown algae, *C. zosteroides* was the species with the largest contribution to survival (with a value of 75%) and occupied a position in the triangular plot in the vicinity of trees, shrubs and perennials. The algal species closest to *C. zosteroides* were *Laminaria digitata* and *Ascophyllum nodosum,* with elasticity survival values close to 70%. *Alaria nana*, *Ecklonia radiata, Fucus vesiculus* and *Fucus serratus* showed higher elasticities to growth.

Table 1. Basic demographic outputs for the studied undisturbed *Cystoseira zosteroides* populations and for the density-dependent model set at equilibrium. λ: eigenvalue of the matrix; ρ: damping ratio.

Population	Year	λ	ρ	Mean life expectancy
Columbretes I	2010–2011	0.94	1.12	76
	2011–2012	0.94	1.15	71
Columbretes II	2010–2011	1	1.33	4
	2011–2012	0.93	1.18	49
Density-dependent matrix at equilibrium	Mean	1	1.30	64

POPULATION PROJECTION AND RESPONSE TO DISTURBANCES

When simulating a large perturbation (with 80% mortality) on a natural population, striking changes occurred in its size-structure during the early phases of recovery (Fig. 3). After the reduction of large size classes' density, a recruitment pulse occurred. Then, a succession towards an increase in larger size classes until finally, after more than 20 years, the size-structure converged to a stage similar to that at equilibrium.

Cystoseira zosteroides populations are resistant to large disturbances if these occur at low frequencies (Fig. 4a). The intrinsic population growth rate (λ) slightly increased at intermediate frequencies of disturbance (one storm every 90–75 years) due to the positive effect on recruitment as a consequence of the removal of adults (Fig. 4a). Nonetheless, at values above one perturbation every 50 years, population growth rates fell below 1. Further, as the frequency of disturbances increased, populations showed a higher dependence on growth and fecundity than on the survival of individuals (Fig. 4b). Finally, increasing the frequency of disturbances also increased the quasi-extinction risk of this species, with probabilities higher than 90% in less than 40 years when disturbances occurred every 50 years (Fig. 5).

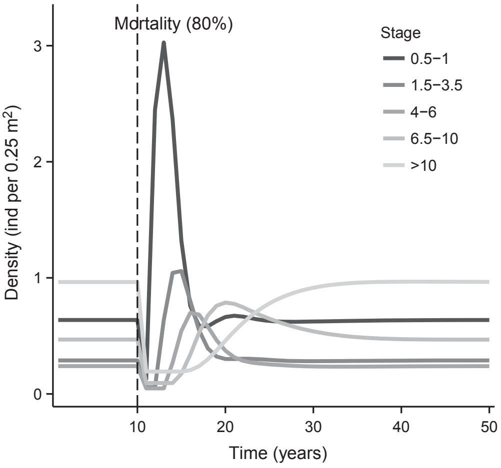

Fig. 3. Population projection over 50 years and response to a disturbance at year 10, causing a 80% mortality.

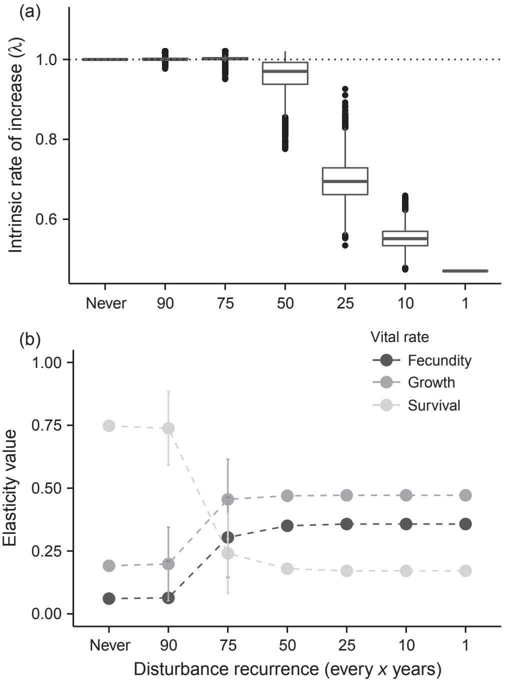

Fig. 4. Population response to an increase in the frequency of disturbances: (a) Response of lambda to increasing the probability of disturbances; (b) median and interquartile range of the different demographic components elasticity values (over 10 000 iterations and 100 years of simulation) for a range of yearly probabilities of undergoing a disturbance.

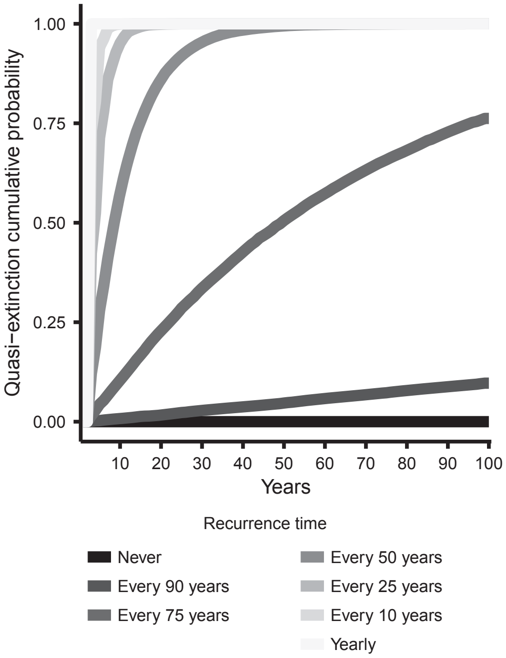

Fig. 5. Population quasi-extinction probability, with a quasi-extinction threshold of 10% the initial population, for a range of disturbance frequencies (as mean recurrence intervals in years). Grey intensities represent the frequency of storms (i.e. every 90 years).

Simulations showed that *C. zosteroides* was resilient to the impact of fishing nets maintaining growth rate values close to 1. As storm recurrence increased, population growth rates fell rapidly as explained above. The combined action of the two disturbances, lost fishing nets and storms, resulted in a higher decrease of population growth rates (reaching values below 0.3 in some cases) than when populations were affected by one single disturbance (Fig. 6).

Discussion

NATURAL DYNAMICS OF *CYSTOSEIRA ZOSTEROIDES*

All life-history characteristics found in this study place *C. zosteroides* among long-lived algae with slow population dynamics (i.e. slow growth rates and low mortality and recruitment rates; Ballesteros 1990; Ballesteros *et al.* 2009; Navarro *et al.* 2011). To our knowledge, this is the first study modelling the demography of a deep-water canopy-forming alga incorporating density dependence. *Cystoseira zosteroides* survival rates increased with size classes, with large individuals showing values higher than 90%, as reported in other long-term studies (Ballesteros *et al.* 2009). The life span estimates also agree with these previous studies, with values close to 50 years, despite presenting high variability. Population growth rates (λ) were close to 0.9, suggesting that these populations are decreasing, probably because this species is subjected to recruitment pulses (Ballesteros *et al.* 2009), which were not detected at the time scale of the study. The slow growth and low mortality rates result in low damping ratios, indicating slow convergence to stable size.

The distribution of species across the triangular plot is related to a successional sequence (Silvertown & Franco 1993). In our analysis, shallow-water algal species occupied the region of the plot mostly dominated by herb-like species (mid-successional stage), whereas the longest-lived species (*Ascophyllum nodosum*, *Laminaria digitata* and *C. zosteroides*; Åberg 1992a; Chapman 1993) occupied the region dominated by shrubs and trees (mid- to late-successional stage). *Cystoseira zosteroides* presented the highest elasticity values to survival, together with other deep-water species such as *L. digitata* (Chapman 1993). The high investment of these two deep-water species in a perennial thallus and, in *C. zosteroides*, reservoir vesicles (tophules; Ballesteros 1990) may ensure their survival through long time periods with low dependency on recruitment at the short term. In contrast, brown algae thriving on shallow bottoms showed a higher dependence on growth and reproduction, with the exception of the long-lived *A. nodosum*.

[Correction added after online publication 12 August 2016: *Czosteroides zosteroides* changed to *Cystoseira zosteroides*]

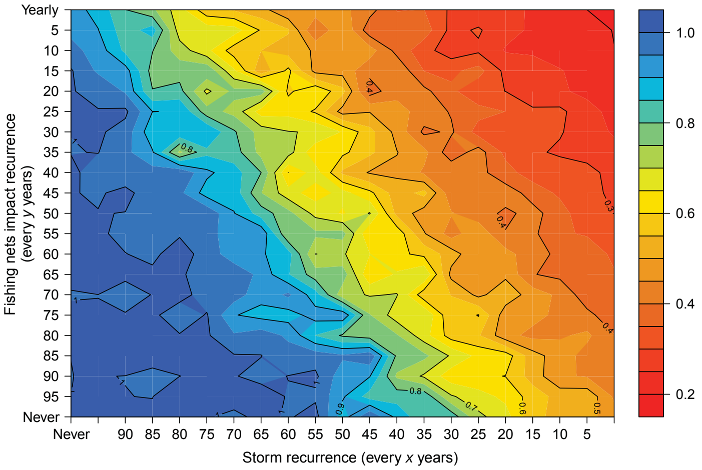

Fig. 6. Combined effects of increasing the recurrence of mortalities caused by a fishing net (*y*) and storms (*x*) on the projected population growth rates (λ) of *C. zosteroides*. Grey intensity indicates simulated population growth rate (λ) values for the projected populations for a range of disturbance frequencies.

Our findings agree with life-history theory, which predicts that species living in stable habitats and with limited resources (i.e. low nutrient concentrations and light availability) should present slow population dynamics and high rates of nutrient retention (Grime 1977; Silvertown, Franco & McConway 1992). In deep-water environments, subjected to light and nutrient limitations, increasing survival must be a good strategy to maintain populations. Besides, as depth increases, the risk of breakage diminishes due to the lower frequency of physical disturbances (Garrabou, Ballesteros & Zabala 2002) and decreased herbivory levels (Vergés, Alcoverro & Ballesteros 2009), thereby liberating resources that can be allocated to structural biomass to maximize survival. These patterns were also observed in a single species, *Sargassum polyceratium*, by Engelen *et al.* (2005) where shallow populations displayed higher elasticity to fertility, whereas deeper populations depended on the survival and persistence of individuals. Correspondingly, terrestrial habitat-forming species show high investments in structural biomass, increasing long-term survival at the expense of growth and reproduction (Adler *et al.* 2014). This also agrees with the high survival and structural biomass investment of other long-lived marine sessile and structural species such as gorgonians (Lasker 1991; Linares *et al.* 2007) or corals (Hughes & Tanner 2000; Garrabou & Harmelin 2002). Thus, despite the fundamental differences between algae and terrestrial plants, there exist similarities between the life-history strategies of these structural organisms independently of their marine or terrestrial origin which support the tree-like population dynamics of our studied alga *C. zosteroides*. Yet, data scarcity on algal demography limits the generalization of our results, so more data and in-depth studies are needed to infer general life-history patterns.

DISTURBANCE RESPONSES AND THE IMPORTANCE OF DENSITY DEPENDENCE

Density dependence is a stabilizing process for *C. zosteroides* populations (Capdevila *et al.* 2015). When this species was affected by mortality events, adult removal increased recruitment success, offsetting mortality pulses (Dayton *et al.* 1992) and maintaining the viability of populations (see Figs 4 and 5). This is because of the high ability of brown macroalgae to produce large amounts of spores and gametes with relatively little energetic cost (Schiel & Foster 2006; Gianni *et al.* 2013). Thus, low disturbance frequencies increased *C. zosteroides* populations' growth rates due to these compensatory responses.

High disturbance frequencies diminished the resilience of *C. zosteroides* populations. When disturbances occurred every 75 years, elasticity values for survival started to diminish, attaining their lowest values when disturbances occurred every 50 years. At this frequency of disturbance, when survival was the least important vital rate for the species, the long-term population growth rate started to significantly diminish. Yet, when disturbances became frequent, recruitment was not able to balance adult mortalities, displacing *C. zosteroides* from their dynamic equilibrium, and causing a large decrease in population growth taxes (λ) and higher extinction risks. This was mainly caused by the low survival and relatively late maturation of their recruits. In contrast to seeds and seed banks of terrestrial plants, early life phases of brown macroalgae are microscopic and free-living stages showing very low survival rates (Dudgeon *et al.* 2001; Gianni *et al.* 2013). Moreover, the combined effects of mortalities derived from fishing nets and storms reduced the population growth rates of *C. zosteroides* at lower frequencies than when only affected by extreme disturbances. Hence, local stressors can decrease macroalgae resilience and compromise their viability, exacerbating the effects of other natural stressors (such as storms), to which species are naturally adapted (e.g. Dayton *et al.* 1992; Navarro *et al.* 2011). This also supports the view that the compounded effect of increasing local and global stressors (Crain, Kroeker & Halpern 2008) must be one of the main reasons behind macroalgae declines (e.g. Wernberg *et al.* 2010).

Recurrent extreme disturbances also induced profound changes in *C. zosteroides* population dynamics. As disturbance frequency increased, a higher dependence on reproduction and growth was observed. Post-disturbed subtidal algal populations have been observed to present similar patterns (Engelen *et al.* 2005; Svensson, Pavia & Åberg 2009), but this is in contrast with the natural population dynamics of *C. zosteroides* and with what would be expected for a long-lived organism (e.g. Silvertown *et al.* 1993; Heppell, Caswell & Crowder 2000). This illustrates the importance of recruitment for the long-term persistence of long-lived species populations despite its small contribution at the short term. Besides the resilience loss of these species, these changes on population dynamics are likely to translate into alterations in community structure and dynamics (Agrawal *et al.* 2007). The loss of large individuals and the higher dependence on recruitment and growth in disturbed populations have the potential to reduce the structural complexity provided by these algal forests (Graham 2004; Jenkins, Norton & Hawkins 2004; Svensson, Pavia & Åberg 2009). Increasing disturbances will also produce the decline or loss of these habitat-forming organisms, leading to the demise of the species associated to them, with major consequences for the ecosystem functioning (Steneck *et al.* 2002; Graham 2004; Ling *et al.* 2015). Indeed, recent studies show that different fucoid species have reduced their abundance or even died-off in many regions of the Mediterranean Sea (Thibaut *et al.* 2005; Gianni *et al.* 2013) and in temperate seas worldwide (Airoldi & Beck 2007; Strain *et al.* 2014; Mineur *et al.* 2015). In addition, we predicted that several decades will be needed to fully recover the structure of natural populations and probably the habitat function of this species (Underwood 1999; Jenkins, Norton & Hawkins 2004).

Although our study confirm that the loss of dominant algae canopies has long-term consequences for their communities and can take many years to recover, our model assumptions limit the generalization of our results. Our model considers *C. zosteroides* populations to be closed; however, external sources of recruits, through natural reproduction of nearby populations or drifting adults, could enhance their recovery after disturbances. However, like many other fucoids, *Cystoseira* species have very restricted dispersal abilities (at the scale of metres), mainly due to their reproductive strategy and the size of their zygotes (Schiel & Foster 2006; Mangialajo *et al.* 2012; Gianni *et al.* 2013). For this reason, although our simulations suggest that one mass mortality event every 50 years could drive *C. zosteroides* populations to quasi-extinction in 40 years, this seems unlikely to apply to other macroalgal species which can disperse further than 1 km and regenerate quickly after storms (e.g. kelps; Dayton *et al.* 1992; Schiel & Foster 2006). In addition, due to the difficulties of sampling at the depth where *C. zosteroides* lives, our results come from a restricted sample size and time period (see Materials and methods), relative to the longevity of the studied species. For example, it cannot be expected that recruitment will be high at all populations and well maintained through time, because numerous local factors may limit recruitment rates (Schiel & Foster 2006).

Nevertheless, this work reveals the potential of studying the demography of canopy-forming algal forests, not only to understand their population dynamics but also for their conservation implications. Given the widespread collapse of macroalgae populations in many temperate reef ecosystems world-wide (e.g. due to sea urchin proliferation, Ling *et al.* 2015), future studies should consider including the impact of sea urchins when modelling macroalgae population dynamics to better predict their future trends and how these changes translate to community dynamics. Our findings highlight that underwater forests dominated by brown algae can display slow population dynamics, with life-history strategies similar to late-successional terrestrial species (such as shrubs or trees). It is likely that the increase in local stressors and in the frequency of extreme events will erode the resilience of macroalgae. Diminishing local stressors (such as fishing nets), which are more easily managed than global stressors, may improve the resilience of macroalgal forests to other disturbances (Strain *et al.* 2014, 2015). However, given the difficulty of conducting demographic surveys underwater, there still exist limitations to our understanding of algal demography. In our case, recruitment seems to be an effective method for *C. zosteroides* to replenish populations after disturbances, but very few studies have focused on their early life-history stages (Capdevila *et al.* 2015). For long-lived and deep-water algae, we suggest that the most effective management should target adult survival; however, conservation strategies should also consider favouring natural recruitment to ensure the long-term viability of these populations. More studies are needed to promote and develop conservation actions for these habitat-forming organisms but also to improve our understanding of general life-history patterns.

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Data accessibility

Data used in this study are available in Appendix S2.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Density-dependent recruitment model.

Table S1. Fertility model parameters.

Appendix S2. Transition matrices.

Appendix S3. Comparative analyses: terrestrial plant and algae species selected, and algae species not selected.