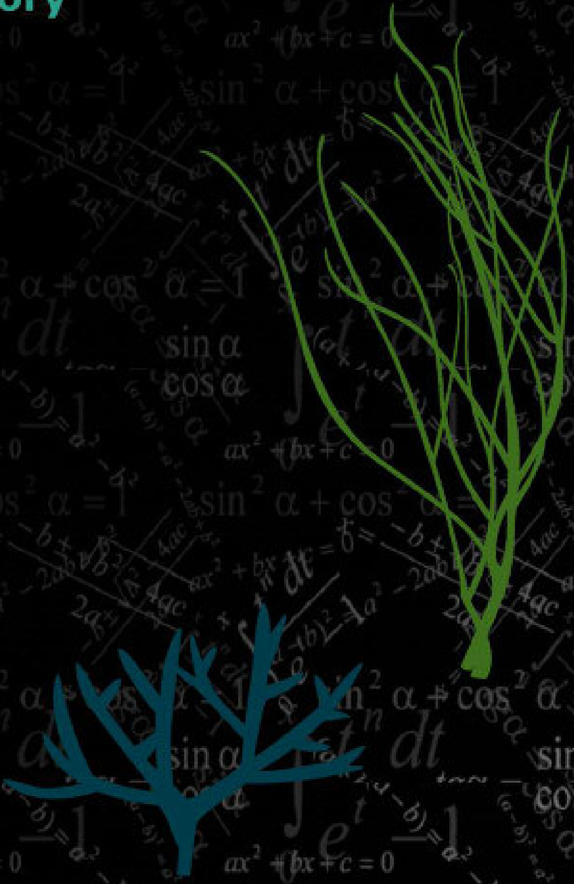
Resilience of Long-lived Mediterranean Gorgonians in a Changing World

Insights from Life History Theory and Quantitative Ecology



Ignasi Montero Serra

2018

Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
Doctorat en Ecologia, Ciències Ambientals i Fisiologia Vegetal

Resilience of Long-lived Mediterranean Gorgonians in a Changing World: Insights from Life History Theory and Quantitative Ecology

Memòria presentada per ***Ignasi Montero Serra*** *per optar*
al Grau de Doctor per la Universitat de Barcelona

Ignasi Montero Serra
Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
Universitat de Barcelona
Maig de 2018

Adivsor:	Adivsor:
Dra. Cristina Linares Prats	**Dr. Joaquim Garrabou**
Universitat de Barcelona	Institut de Ciències del Mar (ICM-CSIC)

A todas las que sueñan con un mundo mejor.

A Latinoamérica.

A Asun y Carlos.

AGRADECIMIENTOS

Echando la vista a atrás reconozco que, pese al estrés del día a día, este ha sido un largo camino de aprendizaje plagado de momentos buenos y alegrías. También ha habido momentos más difíciles, en los cuáles te enfrentas de cara a tus propias limitaciones, pero que te empujan a desarrollar nuevas capacidades y crecer.

Cierro esta etapa agradeciendo a toda la gente que la ha hecho posible, a las oportunidades recibidas, a las enseñanzas de l@s grandes científic@s que me han hecho vibrar en este mundo, al apoyo en los momentos más complicados, a las que me alegraron el día a día, a las que hacen que crea más en mí mismo y, sobre todo, a la gente buena que lucha para hacer de este mundo un lugar mejor y más justo. A tod@s os digo gracias!

GRACIAS! GRÀCIES! THANKS!

Advisors' report

Dra. Cristina Linares, professor at Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals (Universitat de Barcelona), and Dr. Joaquim Garrabou, research professor at the Institut de Ciències del Mar (ICM-CSIC), advisors of the PhD thesis entitled "**Resilience of long-lived Mediterranean gorgonians in a changing world: insights from life history theory and quantitative ecology**",

INFORM, that the research studies developed by **Ignasi Montero Serra** for his Doctoral Thesis have been organized in five chapters, which correspond to five scientific papers listed below: three are already published, one is under review, and the last one is to be submitted in the next months;

and CERTIFY, that the work has been carried out by Ignasi Montero Serra, participating actively in all the tasks: setting the objectives, conceiving and performing the analyses and writing the manuscripts.

Finally, we certify that the co-authors of the publications listed below and that conform this doctoral thesis, will not use these manuscripts in another PhD thesis.

Barcelona, 2 May 2018

Adivsor:
Dra. Cristina Linares Prats
Universitat de Barcelona

Adivsor:
Dr. Joaquim Garrabou
Institut de Ciències del Mar (ICM-CSIC)

List and publication status of the chapters of this thesis

CHAPTER I

Montero-Serra I[1], Linares C[1], Doak DF[2], Ledoux JB[3,4] & Garrabou J[3] (2018) Strong linkages between depth, longevity, and demographic stability. *Proceedings of the Royal Society B*. 285(1873), 20172688. 5-year Impact Factor (2016): 5.417

CHAPTER II

Montero-Serra I[1], Linares C[1], Garcia M[3], Pancaldi F[3], Frleta-Valic M[3], Ledoux JB[3,4], Zuberer F[5], Merad D[6], Drap P[6] & Garrabou J[3] (2015) Harvesting effects, recovery patterns and management strategies for a long-lived and structural precious coral. *PLoS ONE*. 10(2): e0117250. 5-year Impact Factor (2015): 3.535

CHAPTER III

Montero-Serra I[1], Garrabou J[3], Doak DF[2], Ledoux JB[3,4] & Linares C[1]. Marine protected areas enhance structural complexity but do not buffer the detrimental consequences of ocean warming for an overexploited precious coral. Under review at *Journal of Applied Ecology*. 5-year Impact Factor (2016): 5.989

CHAPTER IV

Montero-Serra I[1], Garrabou J[3], Doak DF[2], Figuerola L[1], Hereu B[1], Ledoux JB[3,4] & Linares C[1] (2018) Accounting for life-history strategies and timescales in marine restoration. *Conservation Letters.* 11(1), e12341. 5-year Impact Factor (2016): 7.316

CHAPTER V

Montero-Serra I[1], Linares C[1], Mumby PJ[7], D Macías D[8], Benoussan N[3] & Garrabou J[3]. Predicting depth-mediated impacts of ocean warming at the end 21st century in Mediterranean coastal ecosystems. In preparation.

AUTHOR'S AFFILIATION

1 Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Spain. **2** Environmental Studies Program, University of Colorado at Boulder, USA **3** Institut de Ciències del Mar, CSIC, Spain. **4** CIIMAR/CIMAR, Universidade do Porto, Portugal. **5** Institut Pytheas, UMS 3470, Station Marine d'Endoume, France **6** LSIS UMR CNRS 7296, Centre National de la Recherche Scientifique, France. **7** Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, Australia. **8** European Commission, Joint Research Centre, Directorate D - Sustainable Resources, Italy.

Contents

SUMMARY

Temperate benthic communities face cumulative impacts from multiple stressors acting both at local and global scales. Understanding how local management and ocean warming affect the dynamics and resilience of dominant habitat-forming species is central to marine conservation. In this thesis, we combined long-term demographic surveys and large-scale distribution datasets with innovative population and spatial modeling approaches, and meta-analyses to unravel the causes and consequences of extreme life-histories. The final goal was to understand resilience patterns and mechanisms, and to assess the effectiveness of widely used conservation tools such as fishing regulations, marine protected areas (MPAs), and active restoration.

A comparative analysis across marine sessile species revealed strong linkages between depth occurrence, longevity and demographic stability. These results demonstrated a fundamental role of environmental gradients in shaping the evolution of life-history strategies in the ocean and suggest that deep-sea benthic communities tend to be dominated by long-lived species that are very vulnerable to external sources of mortality. In addition, we demonstrate that life-history strategies play a role in important conservation issues such as recovery processes. For instance, recovery times after fishing or restoration actions for long-lived species can take several decades. Thus, accounting for the temporal dimension and life-history tradeoffs in conservation efforts is essential to avoid potential long-lasting impacts and enhance the recovery of damaged ecosystems.

Focusing on the Mediterranean red coral *Corallium rubrum*, an overharvested precious coral emblematic of coralligenous assemblages, we revealed an extremely slow life-history strategy characterized by low reproduction success, high natural survival, and extended longevity. These traits drive a general pattern of slow population dynamics and suggest low resilience to human-driven stressors.

We then show that local and global stressors such as overfishing and warming have strong impacts on different demographic processes of red coral populations.

Harvesting causes dramatic decreases in total biomass and strong shifts in size-class distribution towards populations dominated by small colonies. More broadly, MPAs strongly enhance structural complexity of red coral populations but, contrary to prior expectations, have little effect on their long-term viability and associated extinction risk. Population recovery after harvesting is a very slow process that can take decades. Interestingly, recovery is not driven by sexual reproduction but by the capacity of harvested colonies to survive and regrow new branches. This recovery mechanism may explain the persistence of this historically overexploited long-lived coral.

Unfortunately, novel impacts associated to climate change threat shallow red coral populations. Recurrent warming-driven mass mortality events had detrimental effects on affected populations, causing long-term declines and potential local extinction. While MPAs have been proposed to enhance the resilience of marine ecosystems to climate change, our simulations suggested that MPAs only have a weak buffering effect to climatic impacts. On the other hand, spatial analyses revealed that future climate change may cause extensive impacts on shallow populations of the red coral and the red gorgonian *Paramuricea clavata* (another emblematic species of coralligenous assemblages with an important structural role) across the Mediterranean Sea. Importantly, we found that the extent and severity of warming impacts is strongly dependent on depth and the global emissions scenarios. Altogether, our results demonstrate a high vulnerability and low demographic resilience of shallow red coral populations to climate change.

The results presented in this thesis suggest that, only by simultaneously acting at both local and global scales, we can we ensure the persistence and enhance the structural role of the long-lived Mediterranean red coral. Finally, this thesis also shows the potential of combining long-term large-scale field data, quantitative tools, and principles of life-history theory to provide new perspectives to advance marine conservation in a changing ocean.

RESUM

Els ecosistemes bentònics temperats estan exposats a diversos impactes derivats de l'activitat humana a escales locals i globals. Entendre com eines de gestió en l'àmbit local i els impactes derivats de l'escalfament dels oceans afecten a les dinàmiques i resiliència d'espècies estructurals marines és de vital importància per millorar la seva conservació. Al llarg d'aquesta tesi Doctoral, hem combinat seguiments demogràfics a llarg termini i dades de distribució d'espècies a gran escala amb innovadores tècniques de modelització i meta-anàlisis, per entendre les causes i les conseqüències derivades d'estratègies de vida molt longeves. L'objectiu final era explorar els patrons i mecanismes claus en la resiliència d'espècies estructurals longeves i avaluar l'eficàcia de diferents eines de conservació marina com són les regulacions de pesca, les àrees marines protegides i les accions de restauració ecològica.

Mitjançant una anàlisi comparativa d'espècies sèssils marines, vam observar una forta correlació positiva entre la fondària, la longevitat i l'estabilitat demogràfica. Aquests resultats demostren un paper fonamental dels gradients ambientals en els processos d'evolució de les històries de vida en els oceans i suggereixen que les comunitats bentòniques d'ecosistemes profunds tendeixen a ser dominades per espècies longeves i, per tant, molt vulnerables a pertorbacions externes que incrementen la mortalitat. A més, demostrem que la història de vida de les espècies juga un paper clau en temes importants relacionats amb la conservació com són els temps de recuperació de les poblacions. Per exemple, el temps de recuperació d'espècies longeves després de pesca o d'accions de restauració ecològica poden ser de l'ordre de dècades. Per tant, és important incorporar l'escala temporal i les històries de vida en les accions de conservació per tal de reduir possibles impactes amb conseqüències negatives a llarg termini i potenciar els processos de recuperació dels ecosistemes malmesos.

La tesi es va enfocar principalment en el corall vermell del Mediterrani, *Corallium rubrum*, com a espècies model, ja que és un corall emblemàtic i amb una funció estructural dintre de les comunitats del coral·ligen. Vam caracteritzar

la seva història de vida, amb un èxit reproductor molt limitat, una baixa mortalitat natural i una longevitat potencial de l'ordre de centenars d'anys. Aquests trets resulten en un patró general de dinàmiques poblacionals molt lentes que, a més, suggereixen una baixa resiliència del corall vermell enfront a pertorbacions externes. De fet, pertorbacions a escala local com és la pesca i a escala global com és l'escalfament dels oceans tenen un gran impacte en diferents aspectes de la dinàmica del corall vermell.

La pesca del corall vermell ha causat una gran davallada de la biomassa total i canvis en l'estructura de talles cap a poblacions dominades per colònies petites. A gran escala, les àrees marines protegides (AMPs) afavoreixen i incrementen la complexitat estructural de les poblacions de corall vermell però, contràriament a les hipòtesis inicials, les AMPs no afecten de manera significativa en la viabilitat poblacional a llarg termini ni en el risc d'extinció de les poblacions de corall vermell. La recuperació del corall després d'accions de pesca és un procés molt lent que pot trigar dècades. A més, vam demostrar que la recuperació no ve donada per mecanismes de reproducció sexual, sinó per una elevada taxa de supervivència de les colònies pescades i el rebroll de branques noves a partir de les bases de les colònies supervivents. Aquest mecanisme de recuperació podria explicar la persistència del corall vermell al Mediterrani després de mil·lennis de sobreexplotació.

Noves amenaces associades al canvi climàtic estan posant en risc algunes poblacions de poca fondària de coral vermell. Les darreres mortalitats en massa de corall vermell relacionades amb l'escalfament del mar tenen conseqüències molt negatives a llarg-termini, amb importants declivis poblacionals i increment del risc d'extinció local. Mentre les AMPs han estat proposades com a eina per augmentar la resiliència dels ecosistemes marins enfront a pertorbacions derivades del canvi global, malauradament, els nostres resultats mostren un paper molt limitat en l'atenuació impactes climàtics. Per altra banda, anàlisis predictives espacials suggereixen que, sota futurs escenaris climàtics, les poblacions de coral vermell i gorgònia vermella *Paramuricea clavata* (una altra espècie estructural i emblemàtica de les comunitats de coral·ligen) podrien patir impactes a gran escala a diverses regions del Mediterrani. Però el que és més interessant és que la intensitat i extensió dels impactes climàtics estan determinats en gran mesura amb els patrons globals d'emissions de gasos d'efecte hivernacle i amb la fondària a la qual es trobin les poblacions. Aquests resultats confirmen que les poblacions poc profundes de corall vermell són molt vulnerables a l'escalfament dels oceans i tenen una baixa resiliència demogràfica.

Al llarg de la present tesi hem mostrat com, només amb accions de gestió simultànies a escala local i global podrem assegurar la persistència i la funció estructural de les poblacions de corall vermell. Finalment, amb aquesta tesi també demostrem el gran interès de combinar dades de camp a llarg termini i a gran escala amb tècniques d'ecologia quantitativa i principis de la teoria d'històries de vida per tal de proporcionar noves perspectives i avançar en el camp de la conservació marina en un context de canvi global.

GENERAL INTRODUCTION

Marine biodiversity, functioning and habitat-forming species

Life in the oceans is incredibly diverse in shapes, forms and functions. The complexity of marine ecosystems has long fascinated ecologists and naturalists since ancient times. Besides fulfilling human curiosity, a deep understanding of ecological dynamics and underlying drivers is essential to develop sound evidence-based conservation strategies. A growing body of literature recognizes that biodiversity at all hierarchical levels, from genes to ecosystems, shapes key structural and dynamical properties such as primary productivity, nutrient cycling, functional diversity, trophic complexity, temporal stability, and resilience (Tilman et al. 1996, 2001; Cardinale et al. 2012, Duffy et al. 2016). Importantly, these processes underpin goods and services provide by marine ecosystems to a large proportion of world's human population (Worm et al. 2006, Palumbi et al. 2008, More et al. 2011, Hoegh-Guldberg et al. 2015).

In coastal marine ecosystems, dominant sessile organisms such as seagrass meadows and corals are considered habitat-forming species because of its structural role in providing three-dimensional properties to benthic habitats (Miller et al. 2018). They serve as shelter to several other species and enhance ecosystem services, including fishery productivity, sediment retention, and protection from physical disturbances (Mumby et al. 2004, Worms et al. 2006, Fourqurean et al. 2012, Serrano et al. 2017, Hoegh-Guldberg et al. 2015, Harris et al. 2018). Most habitat-forming species are slow-growing plants and sessile invertebrates that display low reproduction success and high longevity (Garrabou et al. 2002; Linares et al. 2007; Teixidó et al. 2011; Arnaud-Haond et al. 2012, Kersting et al. 2014). Organisms with such slow life-history strategies may be especially vulnerable to the cumulative effects of multiple stressors, including direct and indirect effects of overfishing, coastal pollution, and global change (Hughes & Tanner 2000, Carpenter et al. 2008, Linares & Doak 2010, Short et al. 2011).

Local and global threats to benthic ecosystems

Overexploitation

Humans influence all oceans (Halpern et al. 2008). Overexploitation of marine resources has been an historical major stressor to marine food webs and still impacts a large proportion of the global oceans (Kroodsma et al. 2018). According to FAO estimates, more than half of fish stocks are fully exploited and another third are over-exploited, or depleted (FAO 2014). Besides reported captures, widespread illegal, unreported and unregulated fishing further deplete fish and invertebrates' populations (Pauly et al. 2005, Pauly & Zeller 2016). Benthic habitats are especially vulnerable to destructive fishing practices such as bottom trawling, which can cause major and long-lasting damage to sessile communities (Hiddink et al. 2017).

Coastal ecosystems are further impacted by several local and regional stressors including pollution, coastal development, and global change (Halpern et al. 2008, 2015). Today, the cumulative effects of multiple threats have driven compositional changes, local extinctions, and wholesale destruction of many benthic ecosystems (Jackson et al. 2001, Airoldi & Beck 2007).

Global Change

Since the industrial revolution, the addition of large amounts of CO_2 and other greenhouse gases to the atmosphere is changing the Earth climatic system. The negative consequences of rising ocean temperatures are increasingly notorious at all levels of biological organization – from genes to ecosystems (Scheffers et al. 2016).

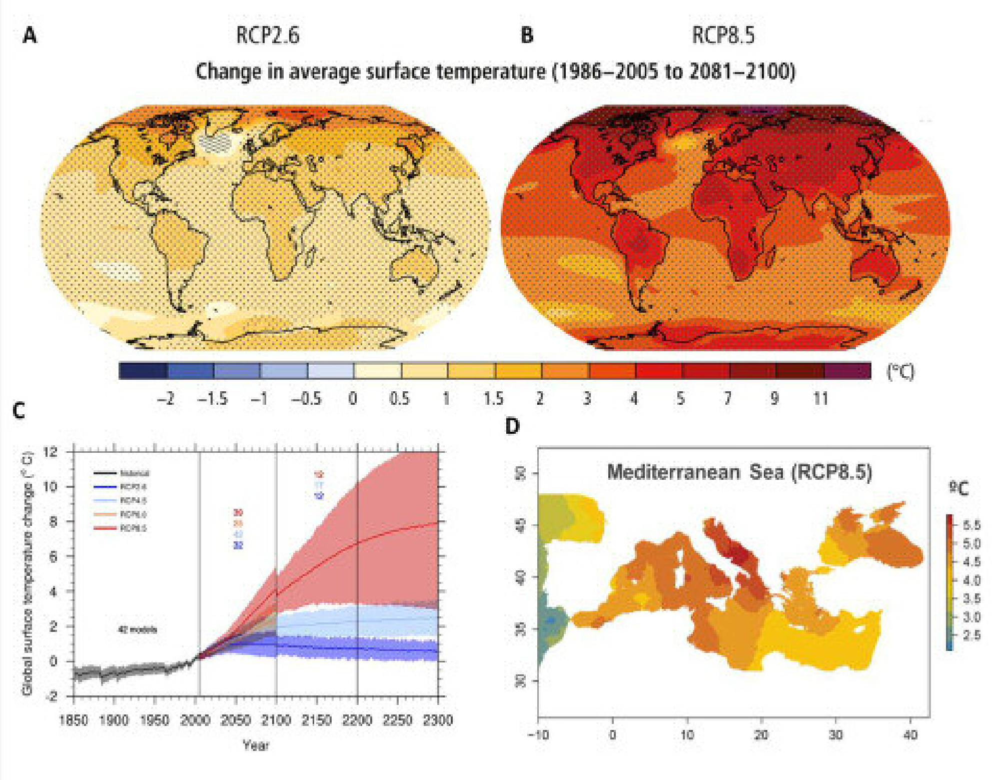
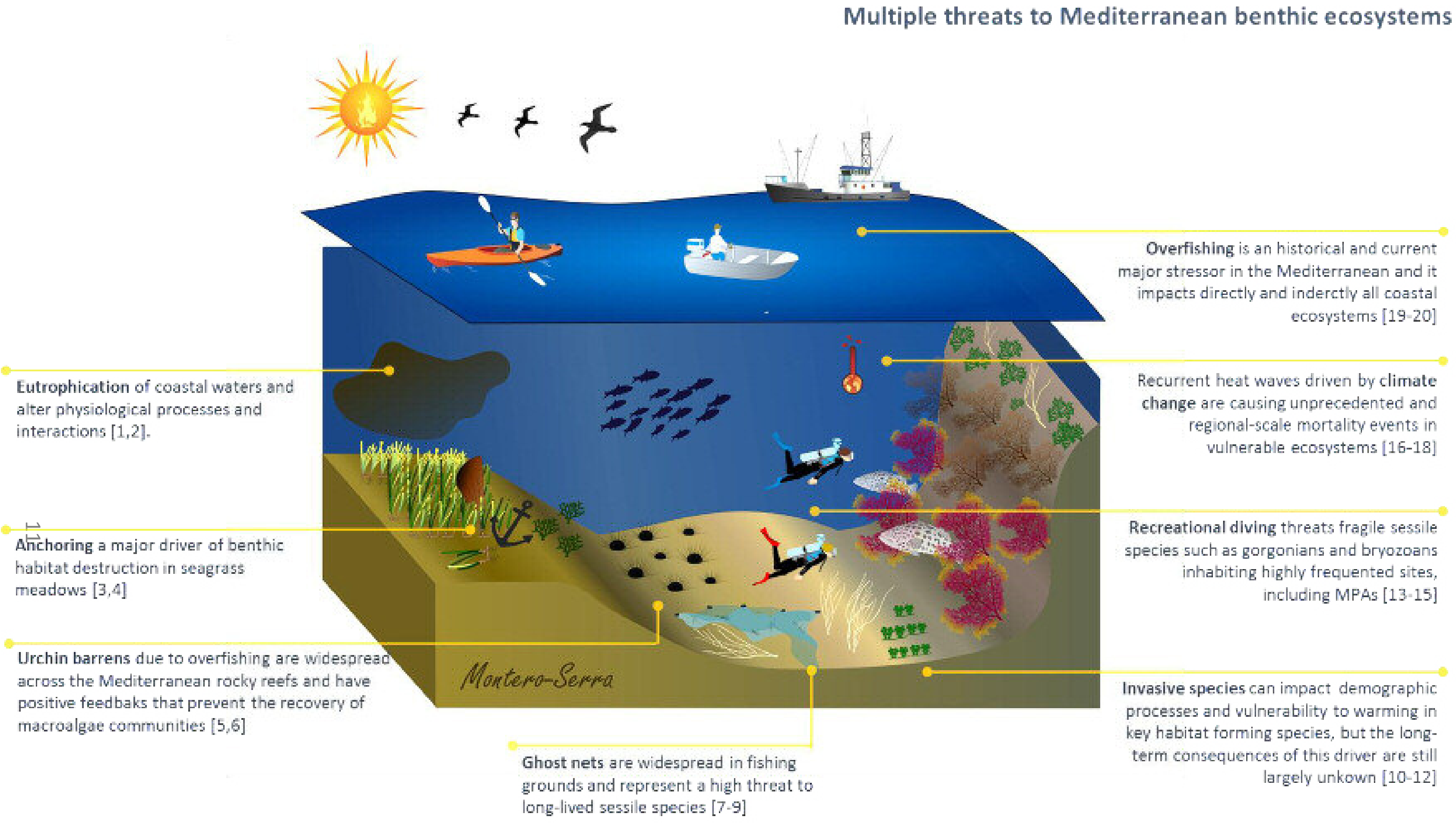


Figure 1. Projections on changes in average temperatures for the end of the 21st century according to IPCC5 scenarios: globally (a, b,c) and for the Mediterranean Sea (d).

Among many drivers linked to ongoing global change, steady increases in sea water temperature and recurrent heat-waves currently imperil structure, function and resilience of world's marine ecosystems (Hoegh-Guldberg & Bruno 2010, Ainsworth et al. 2016, Hughes et al. 2017b).

Widespread changes in the distribution and dynamics of marine organisms have been documented during past decades (Perry et al. 2005, Pinsky et al. 2013), and there is strong evidence that mobile organisms such as fish and invertebrates are tracking temperature trends over broad spatial scales (Pinsky et al. 2013, Montero-Serra et al. 2015). However, ecological responses to warming can be complex, and forecasting potential long-term consequences for habitat-forming species will require a deep understanding on how species-specific life-history, habitat requirements and community interactions shape their capacity to tolerate and adapt to new thermal environments (Sunday et al. 2015, Rutteford et al. 2015, Kortsch et al. 2015*)*. For instance, risks associated to ocean warming can be particularly high for sessile species with low larval dispersal and long-generation times because they cannot track suitable thermal conditions and thus may experience local population declines and local extinctions. Indeed, during the past three decades, large-scale mass bleaching and mortality events driven by heat waves have impacted iconic ecosystems such as tropical coral reefs (Graham et al. 2008, Hughes et al. 2016, 2017a, 2018); and temperate rocky reefs (Cerrano et al. 2001, Garrabou et al. 2009, Wernberg et al. 2016). These large-scale mortality events had notorious effects at the population and community level (Graham et al. 2016, Wernberg et al. 2016, Hughes et al. 2018a). Yet, for most species, the long-term consequences of recurrent heat-waves remain poorly understood. Worryingly, field data over large spatial scales suggest that these mortality events have already increased in their frequency and intensity during the past three decades (Hughes et al. 2018b), and there is strong evidence that they will maintain this trend (Oliver et al. 2018, Frölicher & Laufkötter 2018).



Multiple threats to Mediterranean benthic ecosystems

Overfishing is an historical and current major stressor in the Mediterranean and it impacts directly and inderctly all coastal ecosystems [19-20]

Recurrent heat waves driven by climate change are causing unprecedented and regional-scale mortality events in vulnerable ecosystems [16-18]

Recreational diving threats fragile sessile species such as gorgonians and bryozoans inhabiting highly frequented sites, including MPAs [13-15]

Invasive species can impact demographic processes and vulnerability to warming in key habitat forming species, but the long-term consequences of this driver are still largely unkown [10-12]

Eutrophication of coastal waters and alter physiological processes and interactions [1,2].

Anchoring a major driver of benthic habitat destruction in seagrass meadows [3,4]

Urchin barrens due to overfishing are widespread across the Mediterranean rocky reefs and have positive feedbaks that prevent the recovery of macroalgae communities [5,6]

Ghost nets are widespread in fishing grounds and represent a high threat to long-lived sessile species [7-9]

Figure 2. Conceptual example of a Mediterranean benthic ecosystem subjected to multiple local and global scale stressors. Original diagram that includes symbols from IAN Library of Symbols, University of Maryland. References are: [1] Delgado et al. 1999, [2] De'ath & Fabricius 2010, [3] Francour et al. 1999, [4] Montefalcone et a. 2008, [5] Sala et al. 2012, [6] Ling et al. 2015, [7] Ferrigno et al. 2017, [8] Bo et al. 2014, (9) Angiolillo et al. 2015, (10) Cebrian et al. 2012, (11) Kersting et al. 2015, (12) Kersting et al. 2014, (13) Garrabou et al 1998, [14)] Sala et al. 1996, [15] Barker & Roberts 2004, [16] Garrabou et al. 2009, [17] Cerrano et al. 2001, [18] Coa et al. 2009, [19] Coll et al. 2010, [20] Lejeusne et al. 2010.

Local management and resilience of benthic ecosystems: the role of marine protected areas

To cope with escalating effects of multiple stressors to marine ecosystems, conservation efforts at global and local scales are urgently needed (Kennedy et al. 2013). Locally, fishery regulations and marine protected areas (MPAs) can help to reduce or remove threats and are at the forefront of global biodiversity conservation strategies (Halpern 2003, Edgar et al. 2014).

MPAs are spatially explicit units where human uses of the ocean are regulated. This popular term is, however, very vague. Through this thesis, we use the term MPA to define areas where fishing is totally banned (i. e. no-take areas). However, artisanal fisheries could also be allowed in other types of MPA that either regulate specific gears or temporarily closures. In addition, several non-extractive human uses can also be managed within an MPA, including recreational activities such as scuba diving. Figure 3 represents a conceptual model of an MPA that has a gradient of protection levels, from

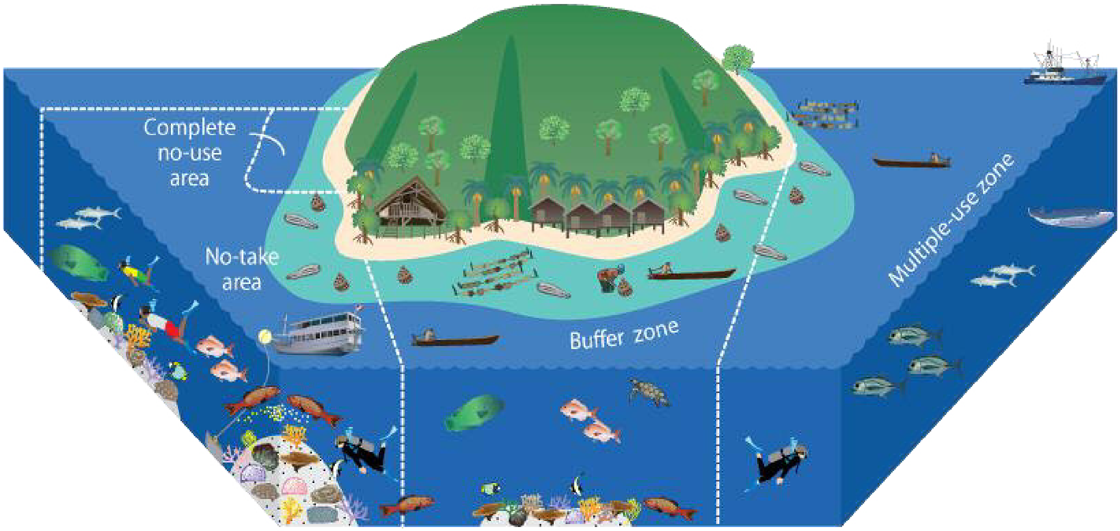


Figure 3. Schematic representation of a coastal marine protected area with different levels of protection. Source: IAN Symbols Library, University of Maryland.

buffering zones that restrict industrial fishing, to no-take areas that ban any type of extractive activity, to complete non-use zone or integral protection areas that prohibit any extractive or recreational activity.

MPAs were first used as a management tool to enhance fisheries productivity and ensure the long-term viability of fished stocks. Ecologists started recognizing community-level responses of fish assemblages to MPA implementations, either via direct trophic interactions or indirect cascading effects. In the 70's, James Estes and colleagues studied the dynamics of Eastern Pacific coastal ecosystems and demonstrated how protection lead to the recovery of sea otter populations and this cascaded into lower trophic levels, with a broad-scale recovery of kelp forests (Estes & Duggings 1995). Since then, ecosystem-level consequences of local protection have been observed in several tropical and temperate regions across the world. For instance, in tropical coral reefs, well enforced MPAs can rebuild parrotfish populations, enhance grazing intensity, and modulate coral-macroalgae interactions with potential implications for coral reef recruitment and resilience (Mumby et al. 2005, Hughes et al. 2007).

Based on these appealing experiences, MPAs have become a key global conservation tool, with most nations agreeing to commitments made at the World Summit on Sustainable Development in 2002, the fifth World Parks Congress in 2003, and the eighth Conference of the Parties (COP 8) in 2006 to set aside 10–30% of their waters in MPAs by 2012 (Sala et al. 2018).

Today, the perception of MPAs as a panacea that can save vulnerable ecosystems from any stressor is widely embraced. However, empirical evidences that also underscored some limitations of relying on MPAs to protect habitat-forming marine species (Sala et al. 2012, Christiansen et al. 2014, Toth et al. 2014).

In this context, ecologists should provide sound evidence-based frameworks to understand and predict the positive effects of MPAs, but also to identify their potential limitations to protecting marine biodiversity from stressors that cannot be managed locally. There are several important aspects to consider and unknowns that should be scientifically addressed to advance towards the design of sound scientific and effective management strategies.

A well-developed theory based on empirical studies states that MPAs are most effective at rebuilding depleted populations of targeted fish when all fishing is prohibited, enforcement is strong, and marine reserves are large, old, and isolated (Halpern 2003, Edgar et al. 2014, Gil et al. 2017). For habitat-forming species that are targeted for exploitation, such as the case of precious corals, oysters, clams or sponges, the same principles of design and enforcement of MPAs may apply (Michelli et al. 2010), although in some cases the time periods needed can be of the order of decades (Linares et al. 2010, 2012, Keiser et al. 2018).

The catastrophic consequences of ongoing climate change push for a critical debate in marine conservation to assess when MPAs can enhance resilience on structural benthic species. MPAs can remove several local threats and, in some cases, we may expect some buffering capacity via indirect mechanisms, including changes in population size-structures (Linares et al. 2010), portfolio effects (Bernhard & Leslie 2013), and competition release. For instance, in tropical coral reefs, enhanced herbivory within reserves plays a crucial role in facilitating coral recruitment and recovery (Mumby et al. 2007). However, in many cases, these mechanisms are not clear and current evidences of large scale bleaching events suggest that MPAs may not provide increased resistance in affected benthic communities (Hughes et al. 2017a). Under which circumstances protected reefs can show increased resistance and recovery is a major research question that needs to be addressed.

How does this thesis contribute to current challenges? Insights from quantitative tools and life-history theory

Principles of life-history theory

Life-history strategies define lifetime patterns of energy allocation to growth, reproduction and maintenance of individuals. These traits can differ in their relative magnitude and timing, and their combination determines the overall fitness at the population level, which is subjected to natural selection and drives evolution (Stearns 1977, 1989). Life history theory studies mechanisms underlying the great diversity of strategies coexisting on Earth. Despite a longstanding interest from ecologists and evolutionary biologists to disentangle what drives life-history variation, some fundamental questions remain partially unresolved. In addition, the potential for life-history principles to address marine conservation issues is generally overlocked.

Besides its crucial role in linking individual traits to population-level fitness and providing insights into evolutionary process, life-history theory can play a crucial role as a framework to address conservation challenges (Griffith et al. 2016). In particular, the demographic differences that arise from life history tradeoffs can shape responses to conservation efforts, including the effectiveness of management strategies (Morris & Doak 2002), likelihood of biological

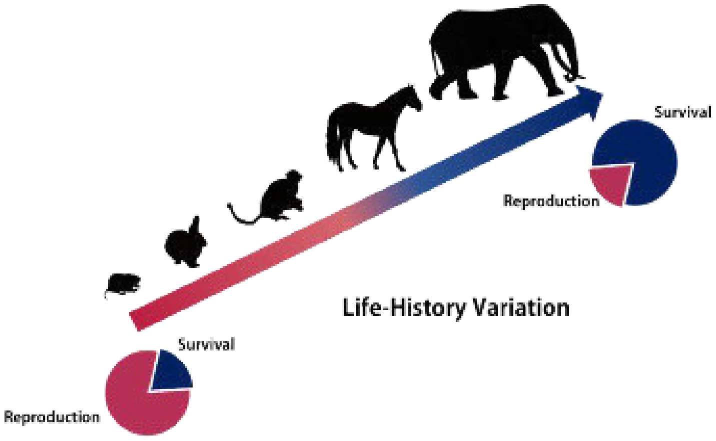


Figure 4. Example of life-history variation along the *fast-slow continuum* in mammal species.

invasions (Kerr et al. 2016), and the responses of species to global change (Jiguet et al. 2007, Linares and Doak 2010, Salguero-Gomez et al. 2012).

In the present thesis, we provide new insights into the role of the environment in life-history evolution and explore potential applications of life-history theory to inform conservation issues, including assessments of the effectiveness of marine protected areas, ecological restoration actions, and anticipating recovery periods.

Quantitative Ecology

Quantitative ecology is a growing field that focuses on statistical and computational methods for addressing questions in fundamental and applied ecology. It differs from theoretical ecology which focuses on simpler mechanistic models and aims to find general rules across model biological systems. Rather, quantitative ecology tools are fitted to empirical data and often used to address specific environmental issues. Common examples of their application include modeling dynamics of natural populations, forecasting the potential impacts climatic change, and predicting the spread of invasive species. Will an exotic species thrive in a new territory? What are the best management options to eradicate invasive species or to facilitate population recovery? Those are examples of important questions that population modeling can help to answer.

Population models

Population models are flexible quantitative tools with multiple relevant applications (Griffith et al. 2016). The basic rationale behind them is that populations experience a net growth resulting from a balance between the entrance of new individuals to the population by reproduction and immigration, and the reduction of individuals by death or emigration. However, often individuals show divergent traits and populations are best modeled when individuals are classified into age, size or physiological state. A structured population model tracks the dynamics not only of total population size, but also the distribution of the variables that differentiate individuals. The choice of the suitable stages depends on the type of organism and should be informed by biological knowledge. In corals, for instance, stages are generally best determined by size rather than age, because they often exhibit size-dependent fecundity, growth and mortality rates (Hall & Hughes 1996, Tsounis et al. 2006), but also due to the challenges associated to age-determination in clonal organisms (Hughes & Jackson 1090, Hughes 1984).

Matrix population models

Matrix population models are a specific type of population model that uses transition matrices, which are a form of algebraic representation for synthetizing a larger number of often repetitious algebraic computations. The matrix describes all the ways that an individual in one stage class at present time can contribute to another stage class in the next year (or any time step defined in the model). Matrix models are very popular in ecology because they are relatively simple, easy to construct and provide useful information. For instance, elasticity analysis of matrix models is an important tool in conservation biology, allowing quantifying the relative contribution of each vital rate to the overall population growth, and this can be highly informative to assess conservation priorities (Morris & Doak 2002).

The main intrinsic limitation of the matrix models comes from discretizing individual states into a finite list of options. All individuals within a given stage therefore are assumed to be identical, in terms of their possible fates and the odds for each possible fate. Sometimes this is reasonable but for many sessile species can include arbitrary decisions. For instance, for organisms often described according to a continuous variable such as size, like plants or corals, defining discrete classes can be arbitrary and potentially misleading (Hughes et al. 1984, Merow et al. 2014).

Integral Projection Models

Dealing with this issue requires models that can accommodate a continuous individual-level state variable (Fig.5). Easterling (2000) show how to construct such an Integral Projection

Model (IPM), using continuous stage classes and discrete time, and provides sensitivity and elasticity formulas analogous to those for matrix models. While the change to a continuous structuring variable has very little impact on the behavior of the model, IPMs retain much of the analytical machinery that makes the matrix model appealing (Ellner & Rees 2005). In this thesis, we fitted integral projection models to long-term demographic data on the red coral *Corallium rubrum* to describe his life-history and vulnerability to local and global stressors, and provide novel potential applications of these models to anticipate expected recovery times after fishing and active restoration actions.

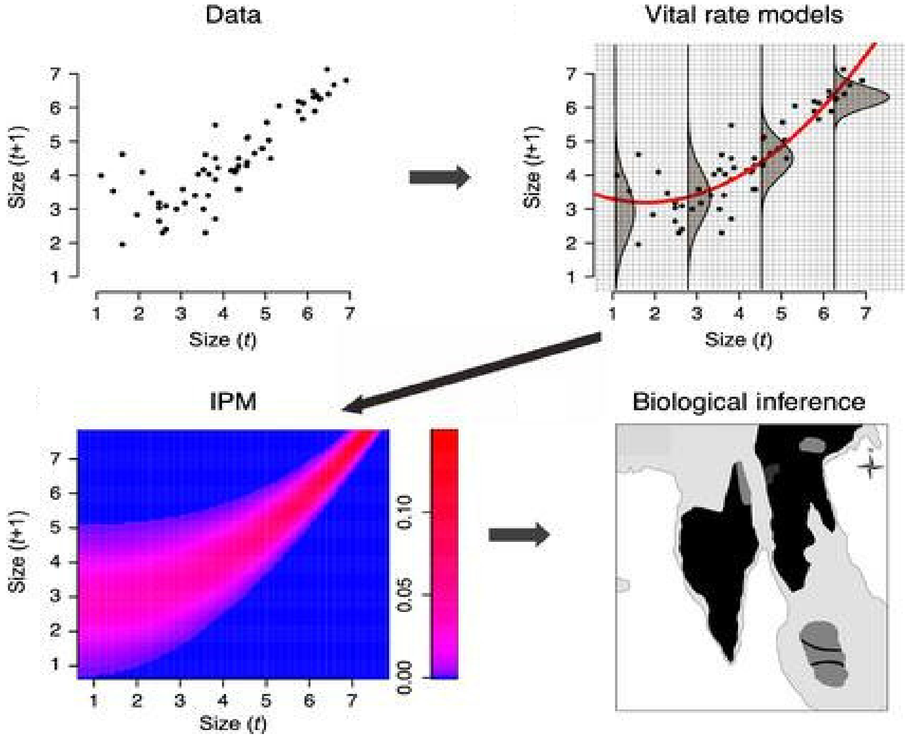


Figure 5. Integral projection models allow integrating continuous size-based individual data to perform a way arrange of biological inference (Merow et al. 2014).

Study system and model species

Mediterranean Sea

The Mediterranean Sea hosts high levels of biodiversity and sustain coastal economies providing ecosystem services to 143 million of people from 21 countries (Coll et al. 2010, NOAA 2015). Mediterranean marine habitats have been historically damaged by the cumulative action of multiple stressors such as overfishing, habitat destruction, pollution and invasive species (Lejeusne et al. 2010, Claudet & Fraschetti 2010). In addition, temperate regions are global hotspots of present and future climate change (Oliver et al. 2018). Due to its geographic position and semi-enclosed configuration, the Mediterranean is warming at much faster rates than the observed mean trends for the global oceans (Vargas-Yanez et al. 2008) and the occurrence of hot extremes has increased by more than two-fold (Oliver et al. 2017). These heat waves had impacted Mediterranean benthic communities at broad-scales, triggering widespread mass mortality events across vulnerable ecosystems such as seagrass meadows or coralligenous habitats (Garrabou et al. 2009).

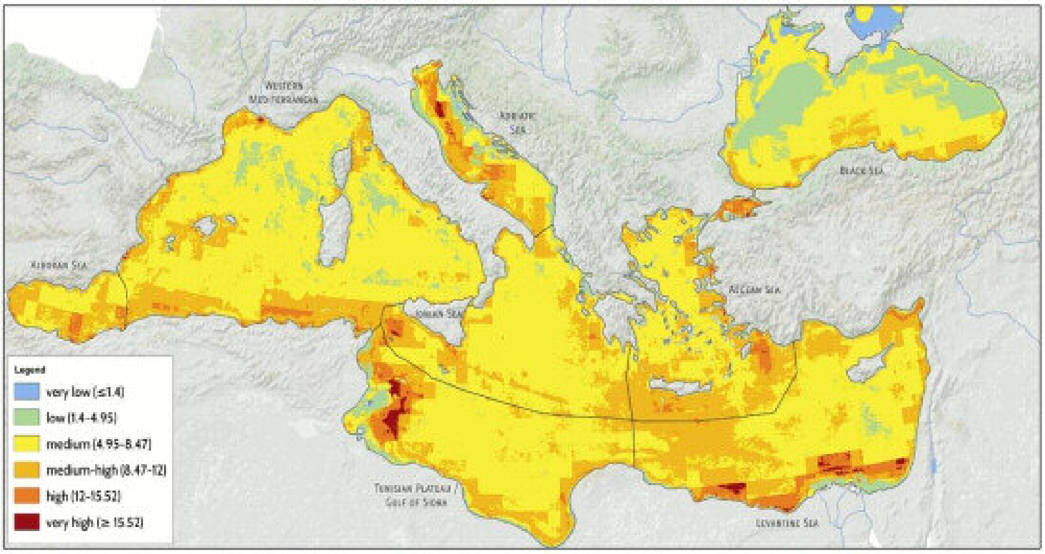


Figure 6. Cumulative stressors on Mediterranean marine ecosystems (Micheli et al. 2013)

Mediterranean coralligenous habitats

Coralligenous habitats are bioconstructions formed by the accumulation of calcareous encrusting algae growing at low irradiance levels. They are highly diverse assemblages that harbor more than 1600 species (Ballesteros 2006). These communities are dominated by long-lived algae and sessile invertebrates, which exhibit low dynamics and belong to a variety of taxonomic groups including anthozoans, porifera, bryozoans and tunicates (Teixidó et al. 2011). Coralligenous habitats can be found in hard bottoms across all Mediterranean coasts and have a bathymetrical distribution ranging from 20 to 120 m depth depending on the local environmental variables (Ballesteros 2006, Martin et al. 2014).

Mediterranean anthozoans are among the most charismatic and ecological important species found in coralligenous habitats. They form relatively dense populations that provide structural complexity to benthic habitats and enhance biodiversity (Ponti et al. 2014, 2016). In this dissertation, we will focus on the Mediterranean red coral *Corallium rubrum,* which is a long-lived octocoral with an important cultural and ecological role in the Mediterranean Sea. The red coral as well as other coralligenous species are affected by several disturbances affect the Mediterranean red coral populations. Destructive fishing practices, ghost fishing, anchoring, over-frequent recreational diving, mucilaginous algal aggregates and algal invasions. More recently, several mass mortalities related to positive seawater temperature anomalies have been reported across NW Mediterranean populations (Cerrano et al. 2001, Garrabou et al. 2001, 2009).

Mediterranean red coral

The red coral, *Corallium rubrum* (Linnaeus 1758) is an emblematic precious coral endemic to the Mediterranean and adjacent Atlantic waters. Precious corals are cnidarian of the anthozoan group (animals with plant-like shape) that build an internal hard carbonate-skeleton which is very appreciated for jewelry. They are completely azooxanthellate and mostly feed on detrital organic matter and zooplankton (Tsounis et al. 2006, Picciano & Ferrier-Pagès 2007).

Red coral populations are patchily distributed in crevices, overhangs or cave entrances (Riedl 1984, Fig. 7). The bathymetrical distribution varies considerably in different areas, from shallow water populations formed in some nutrient-rich locations in the NW Mediterranean, up to a maximum of 1000m depth, as it has been recently discovered in Maltese waters (Carpine & Grasshoff 1975, Riedl 1984, Rossi et al. 2008, Costantini et al. 2010, Knittweis et al. 2016).

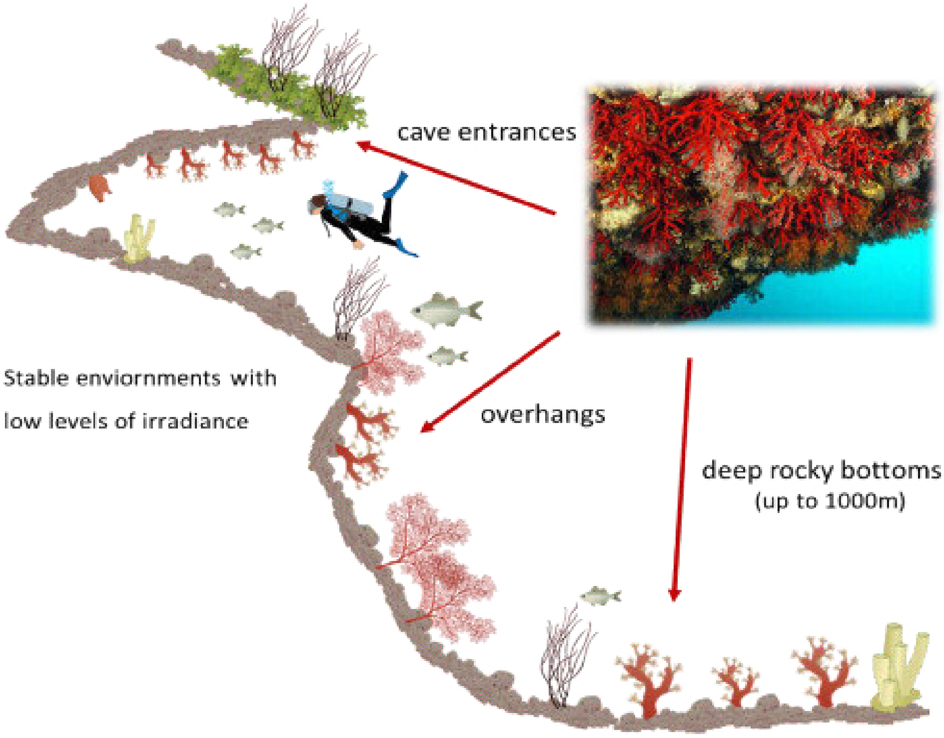


Figure 7. Habitats and bathymetric distribution of the Mediterranean red coral.

The red coral is a gonochoric internal brooder. Females brood larvae internally and then release them from late June and throughout July (Tsounis et al. 2006, Torrents & Garrabou 2011). *C. rubrum* reaches sexual maturity at relatively small sizes (about 2 mm in diameter and 3 cm in height) which corresponds to ages between 7 and 10 years old (Torrents et al. 2005, Gallmetzer et al. 2010). As commonly observed for marine sessile invertebrates, red coral colony sizes are correlated to reproductive outputs: the number of polyps per colony increases exponentially with size and large colonies also show higher proportion of gravid polyps (Torrents et al. 2005, Tsounis et al. 2006).

Population genetic studies revealed a very restricted gene flow (effective dispersal was estimated in 22 and 32 cm) (Ledoux et al. 2010a). Thus, red coral populations are mainly closed at ecological timescales and recovery from larvae coming from external sources is limited (Costantini et al. 2007, Ledoux et al., 2010a,b).

Due to historical overexploitation and present widespread unsustainable fishing practices, most red coral shallow populations are depleted and can be considered functionally impaired or even ecologically extinct (Bruckner 2009, Garrabou et al. 2017a).

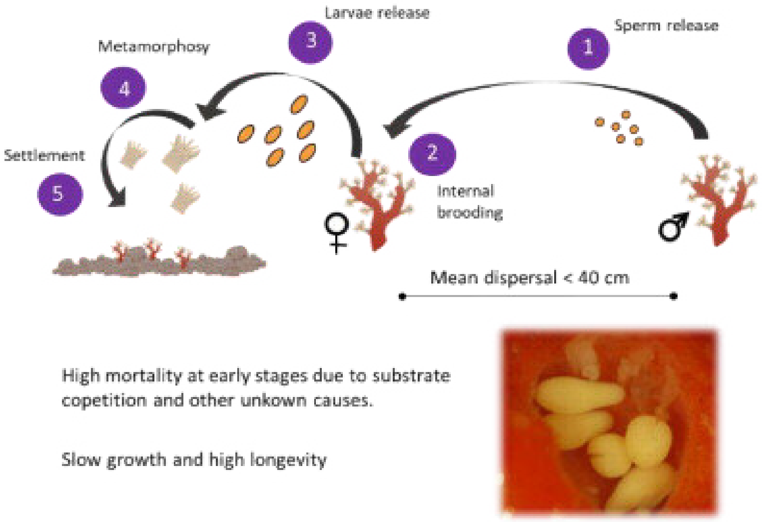


Figure 8. Life-cycle and reproduction in the Mediterranean red coral.

Aims and outline of the thesis

The present Doctoral Dissertation aims to implement cutting-edge modeling tools to address several issues in fundamental and applied ecology. In particular, we combine population and spatial models, long-term datasets, and global meta-analyses to unravel drivers in life-history evolution and their demographic consequences. Focusing on the long-lived red coral, we explore demographic consequences of harvesting and population recovery mechanisms, the long-term consequences of recurrent climatic disturbances and assess the effectiveness of local management tools such as marine protect areas in the face of local and global threats. We then investigate how lie-history theory can shape the outcomes of active restoration efforts, and show how population models can be used to anticipate a crucial aspect of conservation actions such as the expected recovery times. Finally, we develop novel spatial modeling approaches to explore how depth will mediate the expected impacts of present and future climate change in two main gorgonian species across the Mediterranean Sea. This thesis provides a broad overview on the demographic drivers of resilience for the Mediterranean red coral and other long-lived invertebrates to local and global stressors and shows how quantitative tools can be used assess the effectiveness of current marine conservation efforts in a changing environment.

The present Doctoral Dissertation has been conceived as a whole; however, the topics have been structured in five chapters intended for publication in international peer-reviewed scientific journals. Chapters 1, 2, and 4 are already published, but the format has been unified here to preserve the consistency of the present document. All figures, tables and text have been preserved as appear in the published papers. Cited literature has been unified and appears at the end of the document.

Chapter I: Strong linkages between depth, longevity, and demographic stability across marine sessile species

A comparative analysis across more than 200 marine sessile species revealed strong linkages between depth occurrence, longevity and demographic stability. These results demonstrated a fundamental role of environmental gradients in shaping the evolution of life-history strategies in the ocean. On the other hand, we showed that high longevity lead to dampened population dynamics. Focusing on the Mediterranean red coral, *Corallium rubrum*, which is an emblematic and highly overfished precious coral, we quantified the extremely slow life-history strategy of this species and the high vulnerability to external mortality sources of these strategies.

Chapter II: Harvesting effects, recovery patterns and management strategies for a long-lived and structural precious coral

Like other precious corals worldwide, the red coral *Corallium rubrum* has been historically overfished and its conservation is currently a worldwide concern. However, the processes underlying their recovery after fishing remain poorly understood. We examined harvesting effects and recovery mechanisms on red coral populations and revealed high impacts with large decreases in biomass and strong size-class distribution shifts towards populations dominated by small colonies. The observed general pattern of low recruitment and high mortality of new recruits demonstrated limited effects of sexual reproduction on population recovery. Adversely, low mortality of partially harvested adults and a large proportion of colonies showing new branches highlighted the importance of re-growth in the recovery process. The demographic projections obtained through stochastic models confirmed that the recovery rates of *C. rubrum* can be strongly modulated depending on harvesting procedures.

Chapter III: Marine protected areas enhance structural complexity but do not buffer the detrimental consequences of climate change for an overexploited precious coral

We used long-term data on multiple red coral populations and Integral Projection Models to show that local management and warming-induced mass mortality events have different demographic consequences. Warming-driven mass mortality events had detrimental effects on the viability of red coral populations, causing long-term declines and leading to a potential local extinction. On the other hand, removal of local stressors through MPAs strongly enhanced the structural complexity of protected coral populations. Contrary to our expectations, however, local management had little effect on the long-term viability and associated extinction risk of coral populations. Simulations combining the effects of both global warming and harvesting under multiple climatic scenarios, revealed that MPAs have a weak buffering effect to extreme climatic impacts.

Chapter IV: Accounting for life-history strategies and timescales in marine restoration

Understanding the drivers of restoration success is a central issue for marine conservation. Here, we explored the role of life-history strategies of sessile marine species in shaping restoration outcomes and their associated timescales. A transplantation experiment for the red coral *C. rubrum* was highly successful over a relatively short term due to high survival and reproductive potential of the transplanted colonies. However, demographic projections predict that from 30 to 40 years may be required for fully functional *C. rubrum* populations to develop. More broadly, a comprehensive meta-analysis revealed a negative correlation between survival after transplanting and growth rates among sessile species. As a result, simulated dynamics for a range of marine sessile invertebrates predict that minimum recovery times are positively associated with survival rates. These results demonstrate a tradeoff between initial transplantation efforts and the speed of recovery.

Chapter V: Predicting depth-mediated impacts of ocean warming at the end 21st century in Mediterranean coastal ecosystems

Understanding the effects of global warming on the biogeography and vertical distribution of marine organisms remains challenging. Here, using a 3D ocean model, we show that present and future climate shapes the bathymetrical distribution of two dominant gorgonians of the Mediterranean Sea: *Paramuricea clavata* and *Corallium rubrum*. Under present conditions, local temperatures are negatively correlated to the upper distribution ranges of both species. In the future, using Bioclimatic Envelope Models, we predict a large decrease in habitat suitability based on 21st century climate change scenarios. The frequency and intensity of climatic impacts, however, will strongly depend on depth, basin (Western vs. Eastern Mediterranean), and emissions scenario. Overall, gorgonian populations will be highly impacted at shallow depths from 5 to 25m, but there will be regional differences: in the warmer Eastern Mediterranean Sea, the impacts will be extensive and reach deeper habitats; and in the generally colder Western basin, there will be heterogeneous patterns of warming across space and depth.

CHAPTER I

Strong linkages between depth, longevity and demographic stability across marine sessile species

Ignasi Montero-Serra, Cristina Linares, Daniel F. Doak,
Jean-Baptiste Ledoux and Joaquim Garrabou

INTRODUCTION

From sequoias to small desert shrubs to naked mole rats, the study of species with unusually long lifespans has long fascinated evolutionary ecologists (Buffenstein 2005, Baudisch et al. 2013, Jones et al. 2014, Colchero et al. 2017). Understanding the conditions where extreme life histories dominate and the potential consequences of these singular strategies for the dynamics of natural populations is central to ecology and evolution, and may also have important implications for conservation biology (Griffith et al. 2016). However, to date ecologists have only found weak correlations between extrinsic factors and longevity, and we still have relatively few full demographic descriptions for extremely long-lived species.

In terrestrial landscapes, high longevities are common in relatively inhospitable environments characterized by low availability of resources, such as desert and alpine ecosystems (Vasek 1980, Forbis & Doak 2004, Garcia et al. 2011). However, some species of extreme longevity inhabit highly productive habitats (e.g, the coastal redwood), and climate or habitat factors generally provide only weak predictions of life history traits (Stearns 1977, McIntyre et al. 1995, Morrison & Hero 2003, Moles et al. 2007). The marine realm is perhaps a more promising setting to examine the external factors driving life history variation than are terrestrial habitats, due to the set of physical-chemical properties that lead to strong and predictable depth-related gradients at smaller spatial scales than are observed in other systems (Garrabou et al. 2002). The main abiotic factors controlling bottom-up processes in marine communities (light, food availability, temperature, and disturbance intensity) all generally decrease with depth (e.g., Sanders 1968, Barnes & Hughes 1999, Smith & Brown 2002); these factors are also often invoked as likely selective agents favoring short or long lifespans (Munch & Salinas 2009). If environment plays a role in shaping the evolution of longevity, we therefore expect an increase of lifespan along depth gradients. Yet, quantitative analyses addressing this hypothesis are scarce.

In this study, we first explore longevity patterns of marine habitat-forming species, asking how predictable longevity is across depths and whether there are consistent consequences of individual longevity for population dynamics. We discuss these results in the light of similar analyses for terrestrial plant species. Next, we conduct a focused analysis of the iconic Mediterranean red coral, examining aspects of population biology of an extremely long-lived species that may be general for high-longevity species. Our findings represent an important step towards a better understanding on the role of environmental conditions as drivers of the evolution and mainenaince of longevity and have implications for the conservation of dominant structural species found at deep habitats, where demographic data are scarce.

METHODS

Review of demographic studies

Life history strategies are complex combinations of multiple traits that describe the timing and magnitude of the species' reproduction, growth, and survival, which in turn generate life history metrics such as longevity, generation time, and net reproductive rate. For two reasons, we have focused here on longevity as a proxy for this broader diversity in life history strategies. First, several comparative demography studies have shown that longevity is highly correlated to many other demographic traits; in particular, longevity is positively correlated to age at maturity and generation time and negatively correlated to reproductive output and growth (Gaillard et al. 2016, Salguero-Gomez et al. 2016). Second, unlike many complicated life history traits that require detailed demographic study to estimate, longevity can be estimated in quite simple ways and is widely reported, making it especially suited to broad-scale comparisons.

To construct our dataset, we searched the literature for studies reporting longevity estimates and demographic data by using several combinations of keywords. We restricted our analysis to marine sessile species and used the terms “marine sessile”, “coral”, “hexacoral”, “octocoral”, “macroalgae”, “seaweed”, “bivalve” and “bryozoan”. These were combined with either “demographic model” and “matrix model” or “longevity” and “lifespan” in the Web of Knowledge. We found 144 suitable studies reporting data for 241 species (Table S9). We include studies of polycheates that form cemented tubes, and thus are effectively sessile, as well as studies of bivalves that are and are not strictly sessile.

Maximum longevity is estimated through different methodologies. Some studies directly report estimates of maximum observed lifespan using growth rings or geochemical analysis or both. Others report standard demographic data in the form of a matrix model or annual survival rates of adult individuals or colonies. The latter were used to derive potential maximum lifespan based on demographic simulations using the same methodology as for the red coral (see Section on Demographic analysis below). When demographic data were based on non-annual transitions, annual lifespan was calculated as $L_{ann} = L*12/T$, where L_{ann} is the annual lifespan, L is the non-corrected lifespan value, and T is the period described by each transition in months.

As a proxy for habitat, we used depth of occurrence, quantified by the maximum depth reported for the species. While mean or median depth would be more informative, accurate information on these central depths is not available for a wide range of species. Maximum depth is more commonly reported and likely to be correlated with a species’ characteristic depth range. Maximum depths were obtained by searching in the literature including the keywords “depth”, “depth range” and “maximum depth” combined to the species scientific name (Table S9).

Demographic variability using matrix population models

To quantify temporal variance in population growth, we used stochastic demographic models based on at least 5-year study periods (4 annual transition matrices) for marine sessile species (n = 9) and terrestrial plants (n = 25) (Table S10). For each species, we simulated the fate of 1000 initial individuals for 1000 years, assuming equal probabilities for each reported annual transition, and computed changes in population size by dividing the total number of individuals at each time (t) by the previous number (t-1). We then log-transformed these realized annual lambda values and computed their variance. Two long-term demographic studies on bivalve species reported only observed annual lambdas, thus we computed variance in population growth directly from these observed lambdas after a log-transformation.

Statistical analysis

We used Pearson and Spearman’s rank correlations and linear models to assess the relationships between depth and longevity as well as longevity and population growth variability. We also explored multiple combinations of potential predictors and their interactions by fitting a set of multiple linear models and using Aikaike Information Criteria corrected for small sample sizes (AICc) to select the best models. First, a set of linear models was fitted to the whole longevity dataset to test for effects of depth while accounting for different methodological differences in longevity calculations and also to explore potential significant interactions between depth and taxonomic class. We also ran seperate set of models to test for other taxomonic levels (Phylum or Order) had more explanatory power or shifted the results. A second set of models was fit using only the species for which estimates were based on demographic models. For these species, we explored which longevity definition (see section on Demographic Analysis) had a better fit with maximum depth. Finally, to assess the effect of longevity on demographic variability, a third set of models was fit to sessile species for which four or more annual transition models were available, setting variance in population growth as a response variable and maximum longevity, habitat, and their interaction as potential predictors. In these and all other statistical tests, longevity was log-transformed for analysis to achieve more linear results.

Study Case: The Mediterranean red coral *Corallium rubrum*

Natural history

Precious corals are long-lived species found in several seas across the world. The red coral *Corallium rubrum* is a long-lived octocoral of the Mediterranean Sea. It is a depth-generalist species commonly observed in the NW Mediterranean at shallower depths in overhangs and caves but its bathymetrical distribution can reach up to 1000m deep (Knittweis et al. 2016). Due to the high value of its carbonate skeleton for the ornamental jewlary industry, *C. rubrum* has been intensively harvested for millennia. Exploitation - both legal and illegal - as well as ongoing climate change are current threats to this species (Garrabou et al. 2001, 2009, 2017, Linares et al. 2012, Bramanti et al. 2013, Montero-Serra et al. 2015).

Study area and demographic monitoring

A total of 1144 coral colonies from eight *C. rubrum* populations along the North-Western Mediterranean region were individually monitored using photographic techniques (n = 30 photoquadrats of 20x20cm at each population) over periods ranging from 3 to 10 years between 2003 and 2011 (Table S1, see Montero-Serra et al. 2018 for detailed information).

Demographic Analysis

Based on the photographic time-series data, we could estimate size-dependent annual survival, fecundity and growth rates. We used a set of Generalized Mixed Effects Models (GLMMs) to describe annual survival and fecundity rates. Because the goal was to describe the general life-history of the red coral, population and year were included in the models as random factors. Growth rates are extremely low for this species (Garrabou & Harmelin 2002, Marschal et al. 2004), thus a non-linear growth/shrinkage model was fit to data of initial and final colony sizes measured for 247 colonies in two populations over periods of 7-8 years. Due to relatively rare ‘extreme shrinkage’ of some colonies, we divided the growth/shrinkage process into normal growth and extreme retrogression, each with their own mean change of size (see SI). The growth/shrinkage rates model and the fixed effects from the survival and reproduction GLMMs, which included colony size as a fixed effect and population and year as random factors, were then used to construct a deterministic Integral Projection Model (hereafter IPM). We analyzed this model as a large matrix based on 80 colony size classes (see Montero-Serra et al. 2018, and Supplementary Methods for a full description on model construction).

Maximum potential lifespan was estimated by deterministic simulations using the demographic IPMs. Specifically, we simulated the fate of 100 individuals starting at the same stage and recording the number of years until 50% (mean lifespan) and 5% (maximum potential lifespan) of individuals were still alive. To explore the expected mean and maximum lifespan conditional on starting at different life-stages, we run three set of simulations: starting with 100 recruits, starting with 100 of the smallest size-class adults (first reproductive individuals, Torrents et al. 2005), and starting with 100 largest size-class adults. In all results reported in main text, we use adult maximum longevity. To explore how robust these longevity metrics are to changes in the dimension of the transition matrix derived from the IPMs, we computed all these metrics using matrices constructed with 10 to 200 size classes.

To assess the elasticity of deterministic population growth to each vital rate, we performed a perturbation analysis of size-dependent survival, fecundity, and mean normal growth and mean extreme shrinkage, using an 80 size-class model. Each size-dependent vital rate was separately increased or decreased (by 1% and 5%). A mean demographic model was derived that included each perturbation and its deterministic population growth rate (dominant eigenvalue) was computed. Finally, the size dependent elasticity of each vital rate to lambda was calculated using:

$$\frac{\;}{\;}\quad\frac{\;\;}{\;\;}$$

Where *a* is the vital rate, *j* the size-specific interval, *λ* the deterministic population growth, and e_{aj} is the elasticity for vital rate a_j. Since underlying vital rates were perturbed separately (e.g, mean growth, mean extreme shrinkage, and survival), no compensation to control for shifting effects on other vital rates was required (see approach 4 in Griffith et al. 2017).

We calculated mean age-specific survival and fecundity rates by simulating a cohort of 1000 new recruits and computing at each time step the survival rate (N_t/N_{t-1}) and the fecundity (R_t/N_{t-1}) where N is the total adult abundance and R is the total number of recruits.

RESULTS

Depth, longevity and population stability

The comparison of maximum lifespan revealed a great diversity of life histories across marine sessile species (Fig. 1). Hydrozoans, bryozoans, cirripeds and polychaetes displayed the shortest lifespans, ranging from weeks to several decades. These generally short-lived taxa have received significantly less attention in the literature compared to other major taxa such as bivalves and corals. The other groups had a

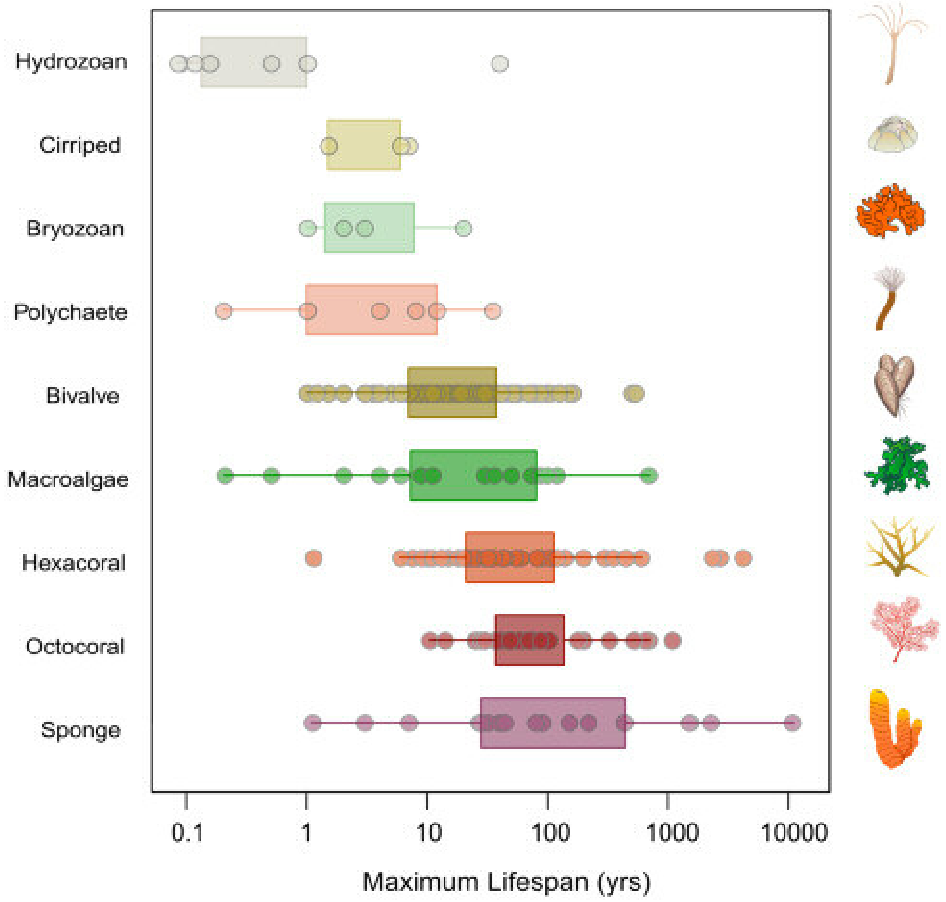


Figure 1. Longevity patterns across marine sessile species (n = 241). Data were obtained from the literature and correspond to the maximum potential lifespan reported for each species for the main marine sessile taxa. See Table S9 for specific species data.

great range of lifespans, up to hundreds of years for some calcareous macroalgae and bivalves and to thousands of years for cnidarians and sponges. Most macroalgae species ranged from less than one year to several decades, but an outlier with exceptional longevity is the Antarctic calcareous algae *Clathromorphum nereostratum*. Marine bivalve's lifespans ranged from less than 1 yr to more than 500 yrs for the antarctic scallop *Arctica islandica* and the giant deep-sea oyster *Neopycnodonte zibrowii*, which is the longest-lived known non-clonal animal. Modular and structural taxa such octocorals, hexacorals and sponges were dominated by longer lived species. Extreme cases were the deep-sea coral *Gerardia sp.,* found in Hawaii, with an estimated age of 4700 yrs and the longest-lived known marine species, the sponge *Monorhaphis chuni*, observed at 1000m depth with an estimated age of 11000 yrs (Roark et al. 2009; Jochum et al. 2012).

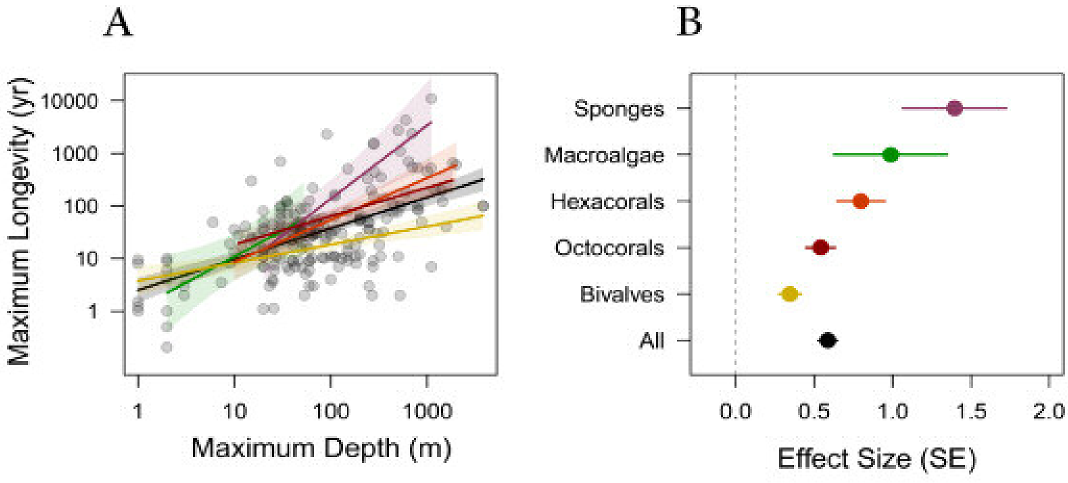


Figure 2. Relationship between maximum depth of occurrence and maximum longevity across marine sessile species. Colors correspond to the labels in panel B, and lines show the best fit linear model for each taxon. Black line shows the linear relationship for all taxa. Shaded areas represent standard errors. B. Slope corresponds to the estimated slope of maximum depth on maximum longevity for each taxon, with error bars showing ± 1 standard error.

We correlated log(maximum lifespan) with log(maximum depth) and found strong positive relationships in the five main taxa for which enough data were available to perform meaningful analyses: octocorals (Spearman's ρ = 0.673; P < 0.001; n = 35), hexacorals (Spearman's ρ = 0.592; P < 0.001; n = 40), sponges (Spearman's ρ = 0.647; P < 0.001; n = 17), macroalgae (Spearman's ρ = 0.600; P = 0.023; n = 14), and bivalves (Spearman's ρ = 0.491; P < 0.001; n = 93) (Fig. 2, Table S2). The positive relationship between depth and lifespan was consistent across different measures of longevity, although adult maximum longevity showed the strongest relatioships with depth (Table S3). This relationship is also consistent when accounting for taxon or matrix dimension; the best supported model includes an interaction between depth and taxon, with significantly larger slopes for sponges (P = 0.0131) and macroalge (P = 0.0308) than for the other taxa (Table S4) (Table S4; overall model statistics: $R^2 = 0.511$; F = 18.12; df = 185; P < 0.001). Use of other taxonomic levels does not change this qualitative result, and model fit is best for Class (Table S5). We also ran quantile regressions between log(depth) and log(longgevity) to see if depth is a more powerful regulator of extreme life history values, but found no significant differences in the slope of the depth ~ longevity relationship for 10% up to 90% quantiles (Table S6).

To assess population consequences of longevity, we regressed variance in realized log-lambda on longevity across marine sessile invertebrates and terrestrial plants and found a similar, strongly negative relationship for both. Short-lived species displayed higher variability in population growth over time than did longer lived species (n = 34; Spearman rho = -0.73; P < 0.001). The pattern was consistent in terrestrial plants (n = 25, Spearman rho = -0.68; P = 0.0002) and marine sessile invertebrates (n = 9; Spearman rho = -0.67, P = 0.0214) (Fig. 3, Table S7).

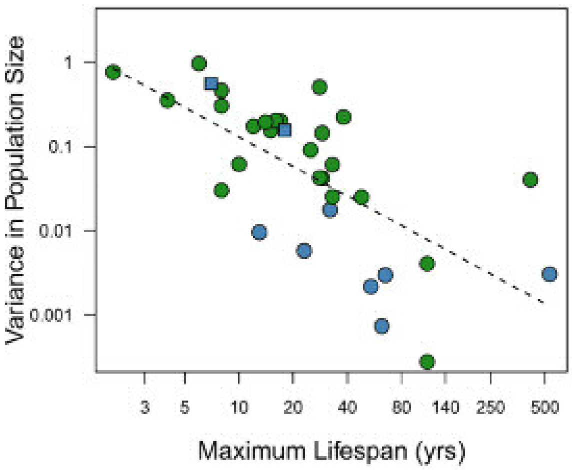


Figure 3. Relationship between temporal variability in population growth and maximum longevity in terrestrial plants (green, n = 25, Spearman rho = -0.68; P = 0.0002) and marine sessile (blue, n = 9; Spearman rho = -0.67, P = 0.0214) species, and overall (n = 34; Spearman rho = -0.73; P < 0.0001). Squared blue dots correspond to two bivalve species whose variance was computed directly from observed annual lambdas.

The extreme life-history of *C. rubrum* and its population dynamics

The red coral *C. rubrum* displayed slow dynamics over the eight populations studied along the NW Mediterranean (Fig. S1), a pattern driven by extremely high adult survival, ranging between 98.05% and 99.76% from the smallest to the largest reproductive *C. rubrum* colonies (Fig. 4a). Monitoring of post-recruitment survival revealed that relative to later survival rates, annual survival is low during the first years after recruitment with a mean of 69.5% (Fig. 4c). However, by the age of four, young colonies already displayed a high survival probability of 92.2%. Overall, mortality rates decreased rapidly during the early stages of the red coral lifetime, following a Type III survivorship curve, and then decreased steadily, more similar to Type II survivorship (Fig. 5a). Recruitment was very limited; from 246 quadrats (about 30 per population) individually monitored for recruitment at the eight studied populations, 83.7% showed no annual recruitment. The remaining 16.3% of quadrats were divided into 10.7% with only a single recruit present, 5.1% with 2-44 recruits, and only 0.5 with five or more recruits (Fig. 4b, 4d). Mean annual per capita recruitment, weighted by the relative abundance of differnet sized individuals, was 0.077. This is considerably lower than the average per capita recruitment for a range of marine sessile invertebrates for whichthere standard demographic data was available (n = 28, Median = 0.547-

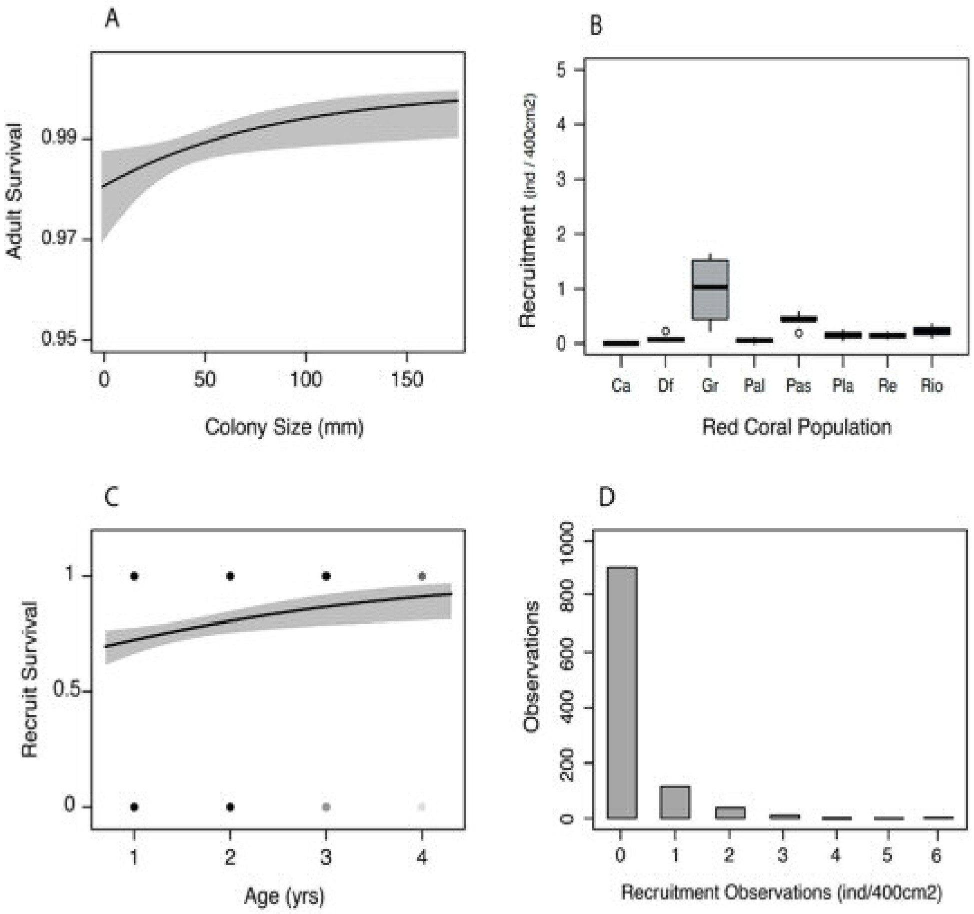


Figure 4. Long-term demographic traits of the red coral *Corallium rubrum*. A. Adult survival probability depending on colony size. The line represents a logistic Generalized Linear Mixed Effects Model including population and year as random effects and colony size as a fixed effect. B. Mean recruitment rates in eight C. rubrum populations. C. Age-dependent post-recruitment survival probability. D. Frequency of annual recruitment observations in eight *C. rubrum* populations. In A and C, grey areas show ± 1 standard error.

0.727, Mean = 5.14 ± 4.02 (SD), Table S8), although higher than the same estimate for 6 other species (Table S8).

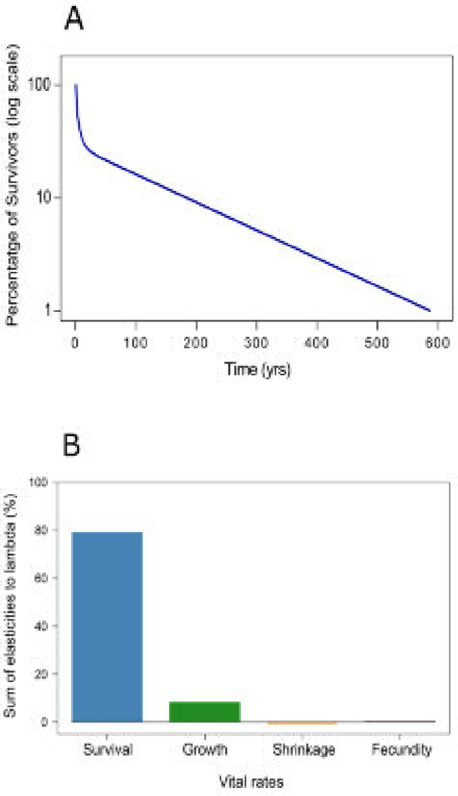


Figure 5. Demographic analyses for the red coral Corallium rubrum. A. Survivorship curve based on a determinstic simulation of 100 individuals. B. Patterns of elasticity to the asymptotic population growth rates of different vital rates, with each bar indicating elasticity summed across all size classes. Other vital rates have even lower elasticities (Fig. S4).

Demographic simulations revealed high maximum potential future longevity for *C. rubrum* colonies, ranging from 501 to 532 yrs for small and large adult respectively (Fig. 5a, S2). The mean expected lifespan was also relatively high for adult red coral colonies and ranged from 98 yrs for small adult colonies to 129 yrs for the larger red coral colonies. Our simulations also revealed potential artefacts due to matrix dimensionality. When using relatively small transition matrices (<60 size classes) simulations underestimated values of maximum and mean longevity, the values stabilized around 60 to 80 size-classes and were consistent thereafter (Fig. S2).

Perturbation analysis revealed a disproportionately large influence of survival rates on asymptotic population growth (Fig. 5b). Elasticity of lambda to fecundity, mean growth and mean extreme shrinkage, as well as all other vital rates, was markedly lower (Fig. S4). Model fitting of age or size dependent fecundity and survival showed no evidence of senescence (Fig. S3).

DISCUSSION

Demography is a powerful tool to understand the evolution of life histories and has provided important insights into plant, mammal, and bird's strategies (Griffith et al. 2016, McDonald et al. 2017). However, a lack of long-term and broad spatial scale data on the dominant species of marine ecosystems, particularly those living at deeper depths, hinders our understanding of the processes shaping the dynamics of these threatened ecosystems (Donovaro et al. 2017). In this study, we analyzed the long-term dynamics of the long-lived red coral *Corallium rubrum* and published data for a broad range of marine sessile invertebrates and macroalgae. The results revealed strong positive relationships between depth, longevity and demographic stability, showing strong habitat-determined predictability of key demographic processes in marine ecosystems.

Marine sessile species have a wide range of maximum lifespans across taxa and habitats, ranging from weeks in some intertidal species to hundreds of years for the red coral *C. rubrum,* and several thousands of years for some deep-sea corals and sponges (Fig. 1). Our most striking finding was that maximum lifespan was strongly and positively correlated with a species' maximum depth occurrence in hexacorals, octocorals, sponges, and although weaker, also in bivalves (Fig. 2). These results demonstrate a strong role of habitat features at shaping the distribution of longevity patterns.

In the shallowest waters, short-lived species dominate (Fig. 2), perhaps due to high disturbance rates and competition in high-energy environments where fast-growing species have a distinct advantage. In contrast, species displaying diverse life-history strategies coexist at intermediate depths, including short-lived invertebrates that also occur intertidally and longer-lived massive corals, macroalgae and seagrasses

(Arnaud-Haond et al. 2012; Darling et al. 2012). The high energy availability due to constant solar irradiation may allow the presence of a large spectrum of life-history strategies that have diversified to occupy multiple niches, following analogous processes than those shaping tropical rainforest plant communities (Connell 1978). Finally, in deeper waters, environmental constraints seem to favor the dominance of slower life-histories and longer lifespans. Depth gradient determines changes in environmental factors such as light and food availability, temperature, and disturbance intensities. In turn, these factors are likely to control the evolution of lifespans through several mechanisms. First, deeper habitats are generally less productive, limiting food supply for consumers and favoring slow growth and longer lifespans (Larson 2001). Empirical studies exploring physiological tradeoffs have shown that the elevated metabolic costs of fast strategies can be detrimental in the absence of high availability of resources (Reznick et al. 2000). Also, as light is strongly depth-dependent, organisms dwelling at deeper habitats may experience a "competition release", mainly by the absence of macroalgae and other fast-growing autotroph organisms that are constrained to the photic zone (Zabala & Ballesteros 1989). Similarly, deeper habitats are less diverse and thus organisms could face less predation pressure, pushing selective forces to favour somatic maintenance and therefore life extension (Healy et al. 2014). Finally, the relative predictability of deep environments may enable species to survive with lower reproductive and mortality rates. Shallow habitats are more exposed to external sources of mortality due extreme physical disturbances (i. e. hurricanes and storms) and temperature fluctuations (Garrabou et al. 2002; Bridge et al. 2013), making them less suitable for organisms whose long-term success relay on extremely high survival of adult stocks (Linares et al. 2007).

Previous anecdotal data on longevity in sessile and mobile marine organisms support our findings. For instance, the highest longevity reported to date corresponds to the sponge *Monorhaphis chuni*, found at 1000m depth with an estimated age of 11000 yrs (Jochum et al. 2012). A similar pattern has been also observed in marine fish (Cailliet et al. 2001). Indeed, a recent study based on radiocarbon dating on eye tissue revealed that, the deep-resident Greenland shark *Somniosus microcephalus*, which can live up to 400 yrs, may be the longest-lived vertebrate on Earth (Nielsen et al. 2016). Overall, these results demonstrate a strong role of depth-related environmental gradients in shaping life-history strategies across marine taxa. The strength of this pattern is striking and contrasts with the weak environmental correlates of longevity or other life history traits that seem typcial in terrestrial systems (Stearns 1977, McIntyre et al. 1995, Morrison & Hero 2003, Moles et al. 2007). Nonetheless, our findings open new questions regarding the existence of potentially analogous processes driving the evolution of life-history strategies along elevation and/or productivity gradients in terrestrial landscapes. Further analyses exploring the relationship between depth and different environmental paramters could provide a more mechanistic understanding of this general pattern of increasing species maximum longevity towards deeper marine waters.

At least three demographic mechanims may contribute to the strong relationship observed between depth and longevity in marine sessile organisms. First, species may show relatively indiscriminate settlement. Under this scenario, the longevity pattern may arise because faster-growing, shorter-lived species out-compete slow species in productive, shallow sites, while at deeper sites only slow-growing species with high longevity may persist. Second, species may have evolved specific settlement cues so that larvae of long-lived species preferentially settle in either deep or shallow sites. Finally, to some extent these life history patterns could result from demographic compensation, reflecting phenotypic plasticity in life histories (i. e. fecundity, growth or survival rates) as a function of local constraints on population growth rates (Villellas et al. 2015). In reality, all three mechanisms are likely to contrbute to this matching of life history to environment.

The extreme life-history features of the red coral *Corallium rubrum*

While our survey shows that mesophotic and deep-sea ecosystems are predictably inhabited by species of extreme longevity, we have few detailed studies of the population ecology of these taxa. We found that *C. rubrum,* a widely distributed Mediterranean red coral, showed a consistent pattern of slow population dynamics driven by extremely high survival, recruitment limitation, and apparently negligible senescence (Fig. 5 & S3a). The species revealed a maximum potential longevity up to 532 yrs, overlapping with lifespan ranges of other deep-sea organisms. Although previous research had shown that *C. rubrum* settlement can be highly heterogeneous (Bramanti et al. 2005, Santangelo et al. 2012), in this study we observed a much more homogenous pattern of low recruitment in the long term (Fig 4b, 4d, Table S8). Recruitment limitation has been observed in other long-lived temperate invertebrates (Grigg 1988, Teixidó et al. 2011, Kersting et al. 2014) and can seriously hinder the ability of populations to recover after intense perturbations (Hughes & Tanner 2000).

For species with limited recruitment, adult survival becomes of paramount importance to ensure their persistence (Linares et al. 2007). We found extremely high survival for *C. rubrum* (Figs. 4a & 5a), with estimated mortality even lower than found in previous experimental studies (Garrabou & Harmelin 2002, Teixidó et al. 2011). In agreement with previous observations in long-lived gorgonians (Linares et al. 2007), perturbation analysis supported that survival is the vital rate demonstrating the highest effect on population growth in *C. rubrum* (Fig. 5b). The absence of detectable senescence is common in sessile marine species and terrestrial plants (Tanner 2001, Baudisch et al. 2013), and may be related to high investments in structural tissues, although some authors have suggested that modularity may also play an important role (Tanner 2001). It should also be noted that our data, like that for most other studies of extremely long-lived species, lack the precision necessary to carefully test for senescence. Precious corals build an energetically demanding hard carbonate skeleton; while preventing a fast rate of colony growth, it may provide the structural basis that allows for an extremely high survival.

The shallow occurrences of the monitored populations of this long-lived species could seem to make it an outlier in the depth-longevity pattern. However, this coral is distributed from shallow to deep waters up to 1000m depth (Knittweis et al. 2016) and its shallow occurrences are exclusively found in dim-light and dark habitats where it cannot be outcompeted by fast-growing organisms (Zabala & Ballesteros 1989). Given the overall pattern observed for marine species, the dynamics of red coral populations dwelling at deeper habitats are likely to be even slower and more dependent on adult survival. However, we must be cautious with these extrapolations and note that demographic data on deeper locations is not available due to logistical constraints. Exceptional shallow presence has been also observed in other important cold-water corals, such as *Lophelia pertusa*, which can occur at 25m in sediment laden fjords where light attenuation reduces the abundances of autotroph organisms, and thus competition; while at the other end of the scale this species may be found as deep as 3300m (Squires 1959).

Population-level consequences of extreme life-histories

As important as unraveling the drivers of extreme longevities are the implications of these strategies for dynamics of natural populations. We show that maximum longevity strongly predicts temporal stability in population growth across terrestrial and marine sessile species (Fig. 3). This finding agrees with previous studies suggesting that long-lived species can strongly buffer environmental stochasticity (Morris et al. 2008, García et al. 2008). As observed for the red coral *C. rubrum*, this buffering capacity relies on high adult survival and low reproductive success. While confering stability under natural conditions, this extreme life history will also hinder the ability of long-lived species to overcome increased mortality rates, but whether these species will be able to cope with rapidly changing perturbation regimes driven by the ongoing global change is still unclear. For instance, while the red coral has persisted after millennia of historical overharvesting due to the combination of consistent survival of partially harvested colonies (Montero-Serra et al. 2015) and small size at maturity (Torrents et al. 2005), new human-related stressors such as global warming have increased mortality rates and put some shallow populations at risk (Cerrano et al. 2000, Garrabou et al. 2001, 2009). Worryingly, although declines may already be driving populations of some long-lived species towards collapse, in some cases, these trajectories may be too subtle to be noticed by ecologists and managers (Hughes et al. 2013). The consistent depth relationship for longevity also implies greater sensitivity of species and communities occuring at greater depths to human perturbations, amplifying recent calls to better monitor and protect these vulnerable ecosystems (Danovaro et al. 2017).

AKNOWLEDGEMENTS

We thank K. Kaplan, M. Pages, A. Griffith and one anonymous reviewer for their valuable comments on early versions of this manuscript. This study was partially funded by the Spanish Ministry of Economy and Innovation Biorock project (CTM2009-08045), the Smart project (CGL2012-32194), the TOTAL Foundation Perfect Project and the European Union’s Horizon 2020 research and innovation programme under grant agreement No 689518 (MERCES). This output reflects only the author’s view and the European Union cannot be held responsible for any use that may be made of the information contained therein. IMS was supported by a FPI grant (BES-2013-066150), CL by a Ramon y Cajal (RyC-2011-08134), and JBL by a Postdoctoral grant (SFRH/BPD/74400/2010) from the Portuguese Foundation for Science and Technology. Support for DFD came from National Science Foundation awards 1340024 and 1242355. IMS, CL, JBL and JG are part of the Marine Conservation research group (2014 SGR 1297) from the Generalitat de Catalunya.

CHAPTER II

Harvesting effects, recovery mechanisms, and management strategies for a long-lived and structural precious coral

Ignasi Montero-Serra, Cristina Linares, Marina García, Francesca Pancaldi, Maša Frleta-Valić, Jean-Baptiste Ledoux, Frederic Zuberer, Djamel Merad, Pierre Drap and Joaquim Garrabou

INTRODUCTION

Overfishing is a major threat to the integrity of world's marine ecosystems. Historical exploitation of marine resources has resulted in drastic population declines, species extinctions and the general simplification of marine food webs (Pauly et al. 1988, Jackson et al. 2001). This structural impoverishment has also hindered the resilience of marine populations, lowering their ability to recover after recurrent natural and human disturbances (Hughes 1994, Hughes et al. 2003). Understanding the ecological consequences of different extractive practices on the structure and function of populations, especially of those organisms exhibiting a long life span and slow dynamics, is therefore one of the greatest challenges in conservation biology (Lotze et al. 2011).

Precious corals have been harvested and traded worldwide since ancient times due to the high economic value of their carbonate axial skeleton (Grigg 2008, Bruckner 2009, Tsounis et al 2010). These sessile invertebrates are considered habitat forming species with a keystone role on coastal systems because they provide structural complexity and host high levels of biodiversity (Gili & Coma 1998). Additionally, they can enhance fisheries by providing shelter during early stages for some commercially important species of rock fishes, shrimps and crabs (Husebø et al. 2002). The red coral *Corallium rubrum* is a precious octocoral endemic to the Mediterranean rocky bottoms and adjacent Atlantic waters. Available data showed recent large declines in the Mediterranean yields, suggesting that this fishery is unsustainably managed following boom and bust cycles (Tsounis et al. 2007, Bruckner 2009). Intensive harvesting has resulted in significant shifts in the size structure of current *C. rubrum* populations (Santangelo et al. 1993, Bruckner 2009) causing a decrease in biomass and mean and maximum colony size (Garrabou & Harmelin 2002, Linares et al. 2010).

Moreover, current warming and acidification trends associated to global change are major threats for shallow red coral populations (Garrabou et al. 2001, 2009, Bramanti et al. 2013, Cerrano et al. 2013). Consequently, there is a growing concern for the conservation of *C. rubrum* and the rest of the precious corals worldwide as evidenced by the recent struggle to include the Genus *Corallium* in the Appendix II of Cites (Bruckner 2009, 2010, 2013, Tsounis et al. 2013).

The need for a responsible fishery for *C. rubrum* and the negative effects of current practices are widely accepted (Tsounis et al. 2007, 2010, Cau et al. 2013). However, given the fragility and vulnerability to different threats of this species, all studies addressing harvesting effects and recovery have been carried out by comparing size-class distribution of different populations and periods (Tsounis et al. 2007, García-Rodriguez & Massó 1986, Abbiati et al. 1992, Bavestrello et al. 2015). To date, biomass reduction has been only quantified once after a poaching event (Linares et al. 2012). Beyond the reported shifts in size structures of *C. rubrum* populations (Tsounis et al. 2007, Abbiati et al. 1992), sound field and experimental data on the effects of different extractive practices and the recovery process are essentially lacking in the literature.

Due to their low population dynamics and limited dispersal capacities (Ledoux et al. 2010a, 2010b) precious corals are considered to have low resilience to disturbances that cause high adult mortality such as harvesting. Paradoxically, *C. rubrum* has not undergone extinction despite being exposed to intensive harvesting since ancient times. In fact, the biological processes underlying coral populations' persistence are largely unknown. The early maturity of *C. rubrum* (2.4 cm in height) corresponding to an age of 6-10 yr (Torrents et al. 2005, Gallmetzer et al. 2010), could partially explain this persistence. It allows the colonies to contribute to reproductive output before they reach the size of interest for harvesters. On the other hand, colonial organisms have the capacity to recover after events of partial mortality (e.g. breakage of a branch). Indeed, red coral colonies with signs of breakage and recent re-growth of new branches have been observed (Torrents et al. 2005, Hereu et al. 1999). The resilience to harvesting will therefore depend on two main mechanisms: (1) re-growth or clonal growth of colonies suffering partial mortality (i. e. when leaving the basal section) and (2) recruitment by sexual or asexual reproduction (i. e. when eradicating the whole colony). Yet, there is no assessment on the relative contribution to recovery of these two mechanisms from a long-term perspective. This assessment would provide a scientific basis for new management measures that enhance the sustainability of this natural resource.

In this study, we examined harvesting effects and the recovery processes of *C. rubrum* using 5-7 years photographic series on two populations located on the coast of Marseilles (France, NW Mediterranean). Fishermen unexpectedly harvested two *C. rubrum* populations that were already being studied by our research team and this represented a unique opportunity to establish before / after comparisons as well as to explore directly the recovery mechanisms by following individually affected as well as unaffected *C. rubrum* colonies. Our overall goal was to elucidate the demographic process underlying the recovery of *C. rubrum* after harvesting events with a particular focus on the relative contribution of re-growth of harvested colonies and reproduction. More precisely we quantified (1) survival and re-growth rates of harvested colonies, (2) survival of non-affected colonies and (3) recruitment rates and survival of recruits. Based on these data, we developed biomass projections to compare population trajectories under different harvesting practices. We contend that the results provide meaningful insights to inform new legislation measures to promote resilience and ensure the conservation of this threatened species and other precious corals also at deeper depths, where most of fishing efforts are concentrated and this type of data is more difficult to obtain.

METHODS

Study Area

We monitored two Mediterranean red coral populations located along the rocky coast of Massif des Calanques in the SE of Marseilles, France. Due to the specific habitat characteristics of the area, such as submerged cavities and overhangs, along with instability of the water column during summer (Bensoussan et al. 2010), the development of red coral populations at shallow depths (15-22m) is favored. The studied populations are located in a vertical wall at Riou Island (43° 10' 23.47"

Figure 1. Harvesting effects on red coral populations. Partial mortality at Riou is shown a) before and b) after a harvesting event. c) Detail of re-growth of new branches on a partially harvested colony.

N i 5° 23' 13.24" E) (hereafter Riou) and in a cave-like tunnel at Maire Island (43°12'32.34"N; 5°20' 14.01"E) (hereafter Maire).

Coral Population Monitoring

In each population we monitored 30 quadrants (20 x 20 cm) by setting up 2 permanent plots using PVC screws fixed to holes in the rocky substratum. Each plot was variable in length, depending on the complexity of the substratum, and 40 cm wide. In each sampling, a cord was deployed between the screws and quadrats assembled with a scale were sequentially positioned and photographed above and below the cord throughout the length of each transect. Two photographs from each quadrat (using 2 slightly different angles, ~30°) were used for analysis with photogrammetric techniques which allowed measuring the height of colonies (Drap et al. 2013). Transects were photographed using a NIKON D70 with a housing and 2 electronic strobes.

At Maire, permanent plots were installed at 15 m after a harvesting event was observed during June 2002 and monitored till 2009 but due to logistic constraints, pictures were not taken during 2007 and 2008. Colonies that suffered partial mortality were evident because fishermen remove the branches leaving a wide colony basis, short in height with injuries (naked tissue), that unequivocally belongs to an older red coral colony that was recently pruned. In contrast, at Riou the permanent plots were installed in 2005 just before the harvesting event. Between April and June 2006 fishermen were observed in the area and subsequent surveys clearly detected their impact in the permanent plots (Fig. 1).

Our study did not involve any sampling of or damage to red coral colonies. The authors had all the permits provided by the French authority Affaire Maritimes to perform scientific surveys in the study area.

Demographic parameters

From the photographic series, the harvested and non-harvested colonies were individually identified and compared year to year to estimate mortality rates, number of branches and colony height. We also estimated adult population density (colonies number per 400 cm^2) and recruitment rates. We considered a recruit the new button like colonies observed ranging from a minimum detection size of 2 mm to 10 mm in height. Annual recruitment rates were estimated as the number of recruits appearing for the first time in a photoquadrat and post-recruitment mortality were estimated by following these recruits through the study period.

With this dataset we were able to assess:

3.1 Changes in size-structure. To assess population size-structure changes and the recovery process, we measured maximum height of all colonies and classified them into five size classes (0-30mm; 30-60mm; 60-90mm; 90-120mm, >120mm). Riou population was measured before harvesting (2005), right after (2006) and four years after (2009). Maire population was measured right after harvesting (2002) and seven years after (2009). Biomass variations were estimated by applying a height-weight polynomial equation to height data. The equation was previously calculated from height and weight data measured on 300 dead red coral colonies collected in previous studies in the same region (Torrents 2007), and from different poaching events (Linares et al. 2012). The resulting curve was: Weight (g) = 0.001(Height, mm)^2 + 0.096(Height, mm) - 4.010 ($R^2 = 0.868$, $P < 0.001$) (Fig. S1).

3.2 Recovery mechanisms.
We quantified the cumulative survival probability of non-harvested adults, harvested adults, and new recruits based on annual mortality rates, calculated as follows:

(1)

$$m = \frac{\left(1 - \frac{N_t}{N_0}\right)}{\Delta_t}$$

where *m* is the annual mortality rate of *C. rubrum* colonies, N is the total number of colonies, and Δt is the duration of the study period. In addition, we assessed the degree of recovery of affected colonies by quantifying the frequency of colonies showing new branches and the number of branches per colony during the study period.

4 Simulations of recovery process under different harvesting practices

To analyze whether recovery rates depend on harvesting practices in the long-term, we developed a set of basic stochastic demographic models under two different scenarios with contrasting levels of total (TM) and partial mortality (PM): a) removal of almost all colonies causing 90% TM and 10% PM; b) leaving the basal section in almost all colonies causing 10% TM and 90% PM. The second scenario was based on the observed mortality values at Riou (see results). The two scenarios were calculated by setting initial population densities according to the corresponding levels of total mortality. To run the model we used demographic parameters (adult density, annual recruitment rates, adult and post-recruitment mortality, and biomass increase rates per colony) obtained from the two monitored populations during the study period. The two harvesting scenarios were projected by running 100 stochastic simulations during 30 years according to the following steps:

First, we estimated the changes in the number of colonies following the next formulation:

(2)

$$N_{T(t)} = N_{R(t)} + N_{A(t)}$$

$$N_{R(t)} = N_{R(t-1)} (1 - g) (1 - m_R) + r$$

$$N_{A(t)} = N_{A(t-1)} (1 - m_A) + N_{R(t-1)} g (1 - m_R)$$

where N_T is total population, N_R is total number of recruits, N_A is the total number of adults, m_R and m_A are annual mortality rate of recruits and adults respectively, r is the annual recruitment rate and g is the proportion of recruits growing to the adult stage:

(3)

$$g = \frac{G}{h_{\max} - h_{\min}}$$

where G is the recruit growth rate (2.5 mm · yr $^{-1}$ in height, from Bramanti et al. (2005)), $h_{\min}$ and $h_{\max}$ are the lower and upper height intervals for recruits.

Secondly, we estimated the evolution of biomass recovery using the biomass increases (ΔB) per colony and abundance values from the demographic models previously described. Mean (SD) biomass increases were estimated according to the next equations applied to colonies suffering partial mortality at Riou (n = 57) and Maire (n = 67) right after harvesting and 4 and 7 years after respectively:

(4)

$$\Delta B = \frac{1}{N}\sum_{i=1}^{N}\left(\frac{B_f - B_0}{\Delta_t}\right)_i$$

(5)

$$B_{(t)} = NT_{(t)} \cdot \Delta B$$

where B_0 is the colony biomass right after harvesting, B_f is the total biomass at the end of the study period, Δt is the number of years, and NT is the total number of colonies in each population.

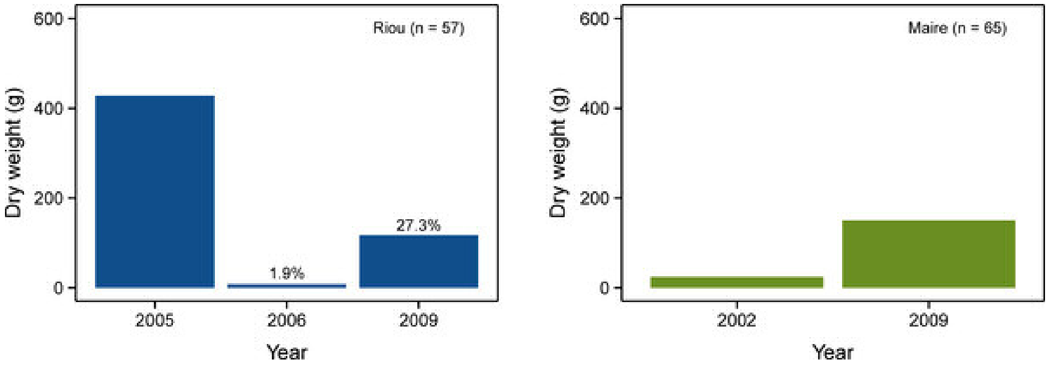


Figure 2. Biomass changes during the study period at Riou (left) and Maire (right).

RESULTS

Harvesting effects

Harvesting affected 30.1% of the colonies at Riou (n = 209) and 49.6% of the colonies at Maire (n = 139). At Riou, total mortality was around 9.5% and partial mortality was 90.5%, causing a large biomass loss with a 98.5% of reduction in total dry weight (Fig. 2). Harvesting targeted mainly medium and large colonies, triggering a dramatic size-distribution shift toward populations characterized by a large proportion of small colonies (Fig. 1 and 3a). At Maire, because the monitoring started after the harvesting event, we could not determine the loss of biomass nor the size-class distribution shift. Nonetheless, the same size-distribution pattern was observed after the harvesting event with no large colonies present and a

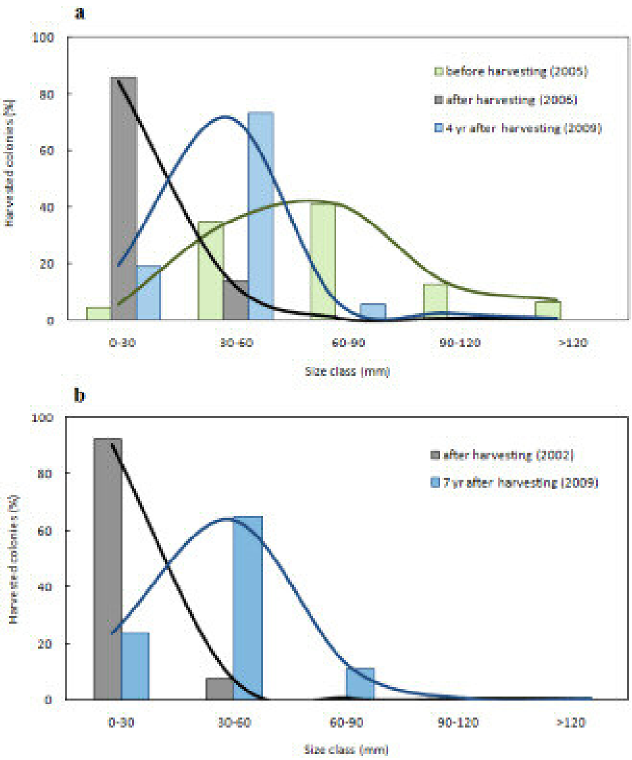


Figure 3. Size-distribution changes on harvested red coral populations. a) Size-distribution at Riou before harvesting, after harvesting, and four years after harvesting. b) Size-distribution at Maire after harvesting and seven years after harvesting.

great proportion of small-size colonies (Fig. 3b).

Temporal trends

Demographic parameters did not show large differences among sites. Mean annual density was 12.26 ± 0.80 colonies · 400 cm^{-2} at Riou (n = 30) and 11.36 ± 0.52 colonies · 400 cm^{-2} at Maire (n = 30). Densities were quite stable during the study period (Fig. S2), and recruitment

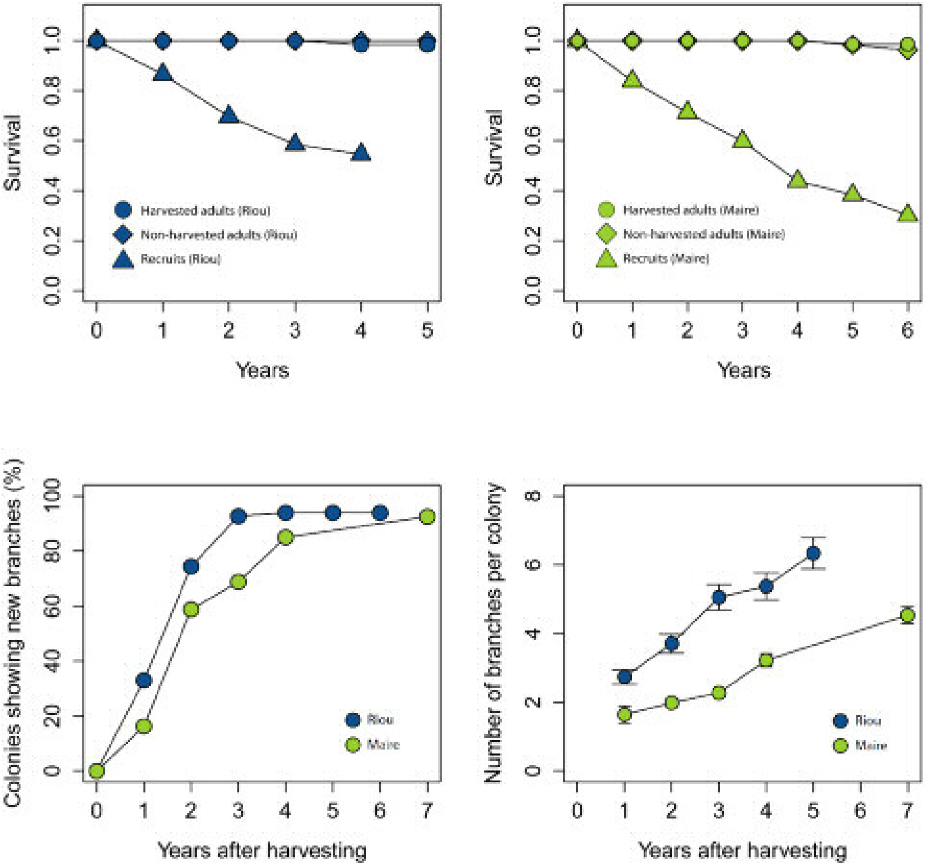


Figure 4. Demographic parameters estimated during the study period at Maire and Riou populations. Cumulative survival probability estimated at Riou (a) and Maire (b) for non-harvested colonies, harvested colonies, and recruits. (c) Temporal variation on the proportion of colonies showing new branches after fishing. (d) Temporal variation of mean (± SD) number of branches after harvesting.

rates were low at both sites: 0.98 ± 1.40 (SD) colonies · 400 cm^{-2} at Maire and 0.21± 0.53 (SD) colonies · 400 cm^{-2} · yr^{-1} at Riou. Harvested colonies suffering from severe partial mortality did not show a differential "post affection" survival as they showed similar high values than unaffected colonies (Fig. 4a, 4b). This could explain the observed stability in adult density in both populations throughout the study

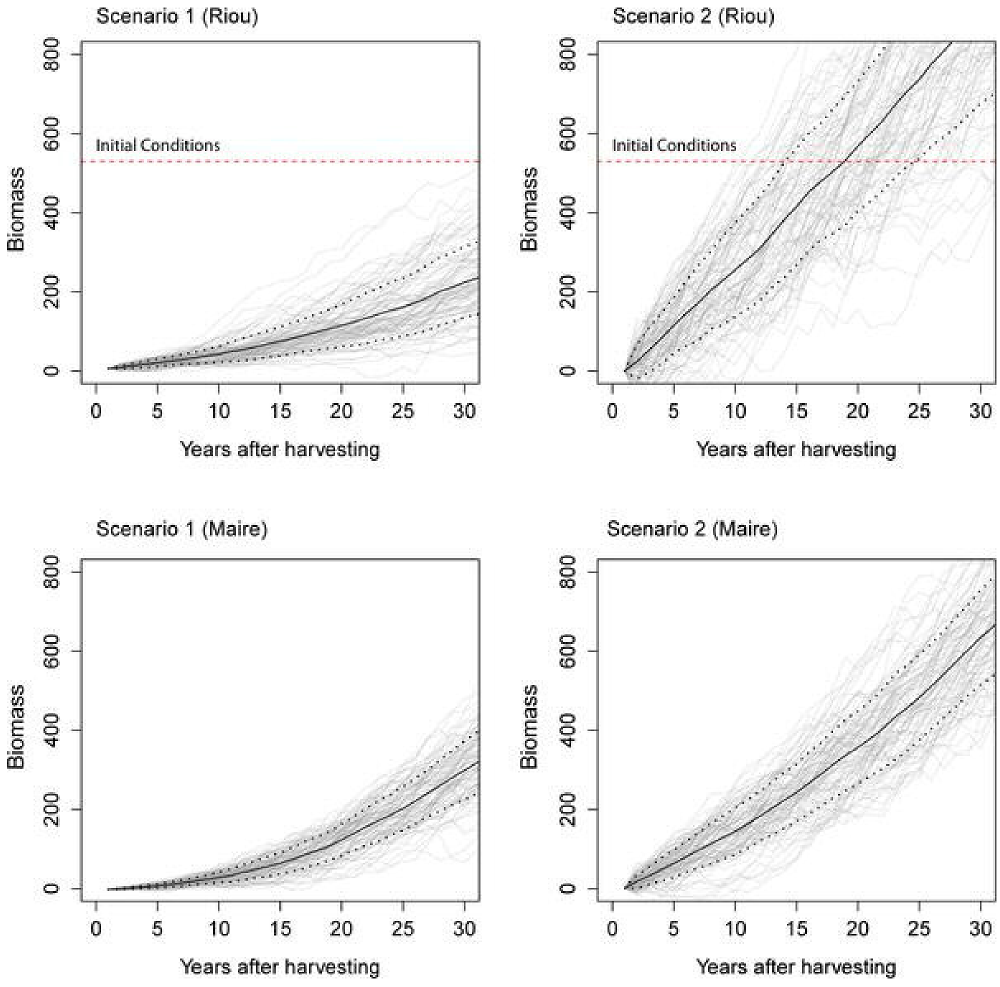


Figure 5. Biomass projections of red coral populations to compare different harvesting scenarios. Scenario 1) 90% total mortality and 10% partial mortality. Scenario 2) 10% total mortality and 90% partial mortality. Horizontal broken lines show initial conditions at Riou. Black lines represent the mean trend and dot lines the standard deviation (n = 100).

period (Fig. S1.2). Conversely, survival of recruits was very low and decreased rapidly at both populations (Fig. 4a and 4b).

Rate of recovery

The two studied red coral populations demonstrated very low rate of recovery. A small increase of biomass was observed at Riou after four years, representing 22% of the initial biomass recorded prior to the harvesting event (Fig. 2). A slight recovery was also observed by comparing size-class distribution from Riou and Maire populations after four and seven years respectively (Fig. 3). Despite a general increase in the proportion of medium size-classes, there was no recovery of the largest sizes (>100mm) and very little of colonies >80mm at Riou. At the end of the study, small colonies (0 - 60 mm) still represented a large proportion of the whole population (92% at Riou and 89% at Maire). Re-growth was observed in more than 75% of the harvested colonies after two years at Riou and four years at Maire (Fig. 4c). Mean number of branches in harvested colonies also increased quickly in both populations (Fig. 4d).

Recovery process simulations

Biomass simulations based on demographic projections showed that harvesting practices strongly influence the recovery process of *C. rubrum* populations. Harvesting practices in which the colony basis remains attached showed recovery times from 15 to 25 yr, whereas events causing total mortality (eradicating the whole colony) slowed down the recovery process, preventing the populations from recovering to initial conditions even 30 years after being harvested (Fig. 5). Riou population showed a slightly higher recovery rate than Maire population. However, the influence of harvesting practices at slowing down the recovery rate when increasing total mortality was consistent for both populations (Fig. 5).

DISCUSSION

This study provides new insights into the recovery mechanisms of a heavily exploited precious coral and illustrates how different harvesting practices can strongly modulate the recovery of affected populations. Our results also highlighted the detrimental effects of harvesting and the low rate of recovery displayed by these long-lived invertebrates.

Harvesting heavily impacted red coral populations has led to drastic reductions of biomass and size-structure shifts towards populations dominated by small colonies. Although both populations still persisted at the end of the study period (after 4 and 7 years), they were far from initial conditions in terms of biomass and sizes. The slow recovery processes reported here confirms the long-lasting negative consequences of harvesting on slow-growing sessile organisms and indicates that extractive practices under the current legal framework are not sustainable from a long-term perspective (Lotze et al. 2011).

We investigated the relative contribution of reproduction and re-growth of harvested colonies as drivers of recovery of red coral populations. The high survival of harvested colonies suffering partial mortality and fast growth of new branches demonstrated that re-growth plays a key role in recovery and persistence of *C. rubrum* (Fig. 4c, 4d). Similar to previous long-term studies conducted in French and Spanish localities (Garrabou & Harmelin 2002, Linares et al. 2012), the observed low recruitment rates and very low survival probability of new recruits suggest that recovery through reproduction is very limited (Fig. 4a, 4b). This demographic strategy is shared by other temperate gorgonians (Linares et al. 2007), and is concordant with life-history theory, which states that adult survival is inversely proportional to reproductive success (Heppell et al. 2000). Indeed, biomass simulations developed to compare different harvesting practices showed that when the whole colony is removed and thus reproduction is the main recovery mechanism, the process is much slower and it can take much more than 30 years to return to initial conditions pervious to harvesting. Conversely, when fishermen leave the basal section of the colonies recovery is enhanced through re-growth of new branches (Fig. 5). The biological reference point used in this study (size-class distributions at Riou prior to harvesting) does not represent an undisturbed population; therefore, recovery leading to pristine conditions would take longer periods than those reported here. Further, we must note that the models used here do not completely account for the complexity of demographic processes in long lived species. *C. rubrum* is characterized by a low dispersal that leads its populations to be generally self-seeding (Costantini et al. 2007, Ledoux et al. 2010a), and breeding units seem also to be restricted in space, suggesting that density may play an important role in the reproduction of this species (Ledoux et al. 2010b). Thus, events causing total mortality on adult colonies could lower the potential for recovery even more through reproduction (Lasker 2013). Alternatively, negative density-dependent processes affecting recruitment and post-recruitment survival were also reported in corals due to intra-specific competition and resources limitation (i. e. availability of suitable substrate to settle) (Vermeij & Sandin 2008). Further research should therefore address these questions by applying more complex modeling techniques to long-term experimental data. However, the observed large and consistent differences on population trajectories depending on harvesting procedures revealed by our study represent an important first step in the characterization of the ecological consequences of different harvesting practices on *C. rubrum* populations.

Reported recent declines on the Mediterranean yields sparked a wide debate about the conservation status of *C. rubrum*. This discussion raised questions about the sustainability of this fishery and if this species should be categorized as threatened (Bruckner 2009, 2010, 2014, Santangelo & Bramanti 2010). Our results show that populations demonstrate a high degree of persistence in terms of density due to high survival of affected colonies. This may explain the existence of red coral populations despite intensive harvesting during the past few centuries. Nevertheless, we emphasize the large reduction of biomass and the size-distribution shifts toward populations dominated by small colonies likely hindered their structural function. A general simplification of benthic communities may also have negative consequences for multiple trophic levels that use these habitats as shelter during early life-stages (Jones et al. 1994, Husebø et al. 2002), This finding should be especially relevant for policymakers. Indeed, abundance is a parameter commonly used by international organizations such as IUCN or CITES to categorize vulnerability levels in commercial species (Brucner 2009, UICN 2014). However, our results challenge the suitability of abundance-based metrics to assess the conservation status of clonal (modular) organisms by showing that large declines in biomass due to partial mortality of colonies can remain masked. Furthermore, abundance measures do not reflect the reduction in reproductive potential caused by harvesting colonial organisms, which exhibit a size-based exponential increase in reproductive output (Santangelo et al. 2003). The development of a new metric focused on size and biomass parameters is crucial to assess the conservation status of precious corals and to develop sustainable fisheries management plans.

On the other hand, benthic communities are currently facing multiple perturbations derived from the ongoing global change such as warming and ocean acidification

(Garrabou et al. 2001, 2009, Coma et al. 2009, Cerrano et al. 2013). The precautionary principle accounting for potential synergistic effects of fishing and climate warming should thus be considered in these new regulations (Garrabou et al. 2001, 2009, Torrents et al. 2008). While climatic perturbations are generally diffuse and difficult to minimize, fishing restrictions on no-take areas can be useful tools at a local scale to enhance the resilience of sessile invertebrates through increased larval production of large individuals (Micheli et al. 2013). MPAs also enhance the recovery of exploited populations in terms of biomass and size-structure (Linares et al. 2010, 2012). However, given the low recruitment rates and limited dispersal of gorgonian larvae (Ledoux et al. 2010a), it is unlikely that protected populations act as a source to exploited populations ensuring their long-term persistence. Further, poaching and diving activities hinder the enhancement of coral populations' recovery within MPAs when regulations are not enforced (Hereu et al. 1999). Therefore, we should not just consider improving the actual network of MPAs but also moving towards a more restrictive legal framework outside of the protected areas. Several new regulations have been proposed during the last decades to improve *C. rubrum* fisheries, including the establishment of annual quotas and minimum harvesting sizes and the ban on using dredges. However, these current guidelines are still largely based on untested assumptions and have failed to improve the sustainability of coral fisheries (Bruckner 2014). For instance, a significant step was the recent recommendation on total ban on harvesting of *C. rubrum* populations under 50m depth (Cau et al. 2013), although poaching in shallow waters is still widespread and individual countries may avoid this prohibition by developing specific management plans. Rotating systems were also proposed for precious corals fisheries in the Pacific and the Mediterranean though there still is a large uncertainty around the recovery periods of affected populations (Bruckner 2014). Here, we show how red coral populations may take much more than three decades to recover and that total removal of colonies can significantly slow down this process further. Our approximations are consistent with previous studies conducted within French and Spanish MPAs where populations showed only partial recovery after 20 to 30 yrs of protection (Tsounis et al. 2007, Linares et al. 2010). Additionally, there has been a recent development of new jewelry manufacturing processes that allow using small pieces of coral that can be ground to powder and mixed with epoxy or other substances (Cau et al. 2013). This development worsens the effects of harvesting by targeting whole size ranges and including entire colonies. Recovery of populations affected by these new practices might be even more jeopardized since re-growth mechanisms are dramatically limited. Finally, this study highlights the importance of long-term ecological monitoring programs because they provide reliable data on key ecological processes such as the recovery patterns of natural populations after human-induced disturbances and enable the improvement of conservation strategies.

ACKNOWLEDGEMENTS

We acknowledge the support of all the people that helped us with the photographic surveys during all the years. The authors are part of the Marine Conservation Research Group (2009 SGR 1174) from the Generalitat de Catalunya.

CHAPTER III

Marine protected areas enhance structural complexity but do not buffer the detrimental consequences of ocean warming for an overexploited precious coral

Ignasi Montero-Serra, Joaquim Garrabou, Daniel F. Doak,

Jean-Baptiste Ledoux and Cristina Linares

INTRODUCTION

The cumulative effects of multiple stressors acting at both local and global scales threaten the integrity and resilience of virtually all ecosystems, and have been particularly of concern for marine ecosystems and their associated services (Halpern et al. 2008, Worm et al. 2006, Ainsworth et al. 2016). The rapid rate of marine biodiversity loss because of overexploitation and climate change is raising major concerns about the effectiveness of current conservation strategies (Hughes et al., 2017). Global policy agreements to reduce greenhouse gas emissions are urgently needed to slow down the current rate of warming and other associated impacts of global change such as ocean acidification (Kennedy et al., 2013, Anthony et al. 2015). Nonetheless, at local scales, conservation management tools such as fishing restrictions and marine protected areas (MPAs) may enhance ecosystem function and resilience to global change (Bozec et al. 2016, Mumby & Harbone 2010, Mellin et al. 2016, Wolff et al. 2018). Given this dichotomy, there are multiple calls for the use of enhanced local conservation efforts to compensate for delayed and ineffective efforts to slow or reverse climate change impacts (Hughes et al. 2010, Roberts et al. 2017).

At a global scale, climate-induced mass bleaching and mortality events are among the greatest threats faced by tropical and temperate marine benthic ecosystems (Garrabou et al., 2009, Wernberg et al., 2016, Hughes et al., 2018). Several comprehensive studies have reported the immediate detrimental impacts of positive thermal anomalies on habitat-forming species such as corals and sponges (Garrabou et al. 2009, Hughes et al. 2017), but much less is known about the long-term consequences of these recurrent events. Individual-based demographic data and modeling tools such as structured population models can improve predictions of the effects of global warming, as well as provide a framework to understand how these effects interact with other stressors.

In a context of rapid environmental change, a critical uncertainty is how effective local management tools such as no-take marine protected areas (MPAs) are in enhancing the resilience of benthic ecosystems to recurrent warming impacts. Some studies suggest positive effects of MPAs on coral cover and complexity (Linares et al. 2010, Selig & Bruno 2010), recruitment (Mumby et al. 2007) and resilience (Michelli et al. 2012, Olds et al 2014, Mellin et al. 2016). But null (Toth et al. 2014, Bruno & Valdivia 2016, Cox et al. 2016) or even negative relationships between local protection and resistance to climatic disturbances have also been reported (Graham et al. 2008, McClanahan 2008, Hughes et al. 2017).

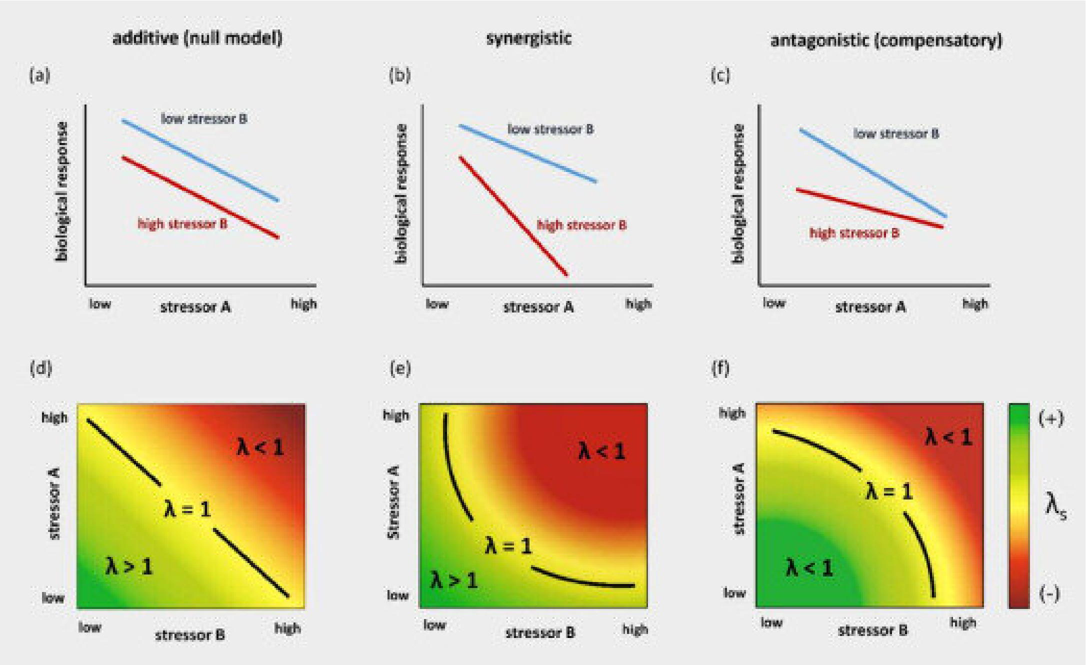


Figure 1. Conceptual models for two interacting stressors. Potential interactions can be additive (left), in which the total impact is equivalent to the sum of the two individual stressors, synergistic (center), when the combined effect leads to a higher impact than the expected addition of the two individual stressors, and antagonistic or compensatory (right), when the combined effects of the two stressors lead to a lower impact than the expected sum of the two individual stressors.

Developing better methods to assess how local management shapes the stochastic dynamics and structural complexity of habitat-forming species is thus a key research need.

The success of local conservation efforts in effectively mitigating for climate change effects will depend on the extent to which different impacts are additive, synergistic or compensatory in their combined effects (Fig. 1). In marine coastal systems, ecological synergies between fishing and climate change have been commonly hypothesized, but meta-analyses and empirical evaluations have suggested that they are less frequent than expected (Darling et al. 2008, Côté et al., 2016). However, most prior work has been carried out through correlational approaches, preventing a clear dissection of the effects of individual drivers. For example, losses of percent cover in corals, or many other easy to monitor measures of impact, can arise from different processes and lead to counter-intuitive interactions between stressors (Darling et al. 2010). Thus, we still need better mechanistic frameworks for understanding how multiple stressors interact to mitigate or exacerbate their negative consequences on vulnerable ecosystems (Côté et al. 2016). While there are different levels of mechanistic analysis, one that can uncover at least some synergies or other interactions is demographic modeling, which tries to tie stressors to impacts on particular vital rates. Unfortunately, obtaining individual-based demographic data can be methodologically challenging in the marine realm, and there are few long-term datasets that allow for an in-depth exploration of the interactive effects of multiple drivers. Here, we apply a demographic analysis to look at the impact of two major threats – ocean warming and fishing– to populations of a long-lived octocoral. We show that, because of their contrasting effects on different vital rates, these threats do not have the strong synergies or compensatory effects that might in theory be expected.

Focusing on the Mediterranean red coral, *Corallium rubrum*, which is a precious long-lived octocoral with an important structural role in Mediterranean hard-bottom communities, we first (1) quantify the effects of fishing (local stressor) and warming-driven mass mortality events (global stressor) to specific vital rates. Then, we (2) predict the long-term consequences of these two different threats. Finally, we (3) evaluate the interactive effects of global change and local protection in the fate of red coral populations. Our results reveal the detrimental effects of climate change on red coral dynamics, and also challenge previous assumptions of MPA capacity to buffer climatic impacts. We also provide insights into how local protection can shape the structural complexity and resilience patterns of temperate reefs. Our approach highlights how population models can be used to integrate individual-based demographic data on different impacts to predict the stochastic dynamics of populations threatened by multiple stressors, especially when data sets are incomplete.

METHODS

Study System

The Mediterranean red coral, *Corallium rubrum*, is an iconic and long-lived precious octocoral with an important structural role in Mediterranean hard-bottom communities (Ballesteros 2006, Garrabou et al. 2017). During the last several decades, there has been a growing concern about the conservation of Mediterranean red coral and other precious corals worldwide due to unsustainable fishing practices (Tsounis et al. 2010, Brukner 2013, Montero-Serra et al. 2015), and multiple mortality events associated to recent warming in the Mediterranean (Cerrano et al., 2000, Garrabou et al. 2001, 2009, Coma et al. 2009). As a result, this species has recently been listed as an endangered species in the IUCN Mediterranean Red List of Threatened Species due to the risks associated with overexploitation and climate change (Otero et al. 2017).

Study area and coral monitoring

Eight red coral populations located in different locations in the NW Mediterranean Sea at relatively shallow depths (15 to 25m), were monitored during periods ranging from 3 to 13 years (Table S1). Among the studied coral populations, five were located within MPAs and three were non-protected and subjected to several fishing events during the monitoring (Montero-Serra et al. 2015). One of the protected populations, located in the Réserve Natural de Scandola (Corsica, France), has been recurrently affected by positive thermal anomalies since 2003, which have triggered coral mass mortality events (Garrabou et al. 2009, Coma et al. 2009, for a detailed description of study sites see Table S1).

In each population from 2 to 4 replicate transects were marked using plastic screws attached to the substratum. Colonies were monitored once a year using photographic series, which allow the individual identification of colonies as well as an accurate assessment of life-history processes such as colony growth, partial mortality (e.g. shrinkage and necrosis), mortality and recruitment (for more details see Montero-Serra et al. 2017, Drap et al. 2017).

Demographic analyses

To estimate the spatial and temporal variability in demography for our study species, we fit a set of annual- and population-level models for size-specific vital rates. These vital rates models included colony size and year as fixed effects and were first fit separately for each population and vital rate: logistic GLMs described probabilities of annual survival and extreme shrinkage (described below) rates, a normally distributed GLM described normal growth data, and a Poisson GLM described fecundity.

As for many other clonal species, red coral can both grow and shrink over time. Height data from all annual photographs were not available, and growth is so slow in this species that even 7 to 8-year time periods only result in mean growth on the order of 10 to 40mm in maximum height (2.74 ± 0.19 $\text{mm}\cdot\text{yr}^{-1}$, Montero-Serra et al. 2017). Thus, growth data from two populations over variable length periods (7 and 8 years) were used to fit a single model characterizing mean annual growth rate depending on size. Shrinkage or negative growth is a common process in plants and sessile invertebrates that is usually accounted for by assuming normally distributed variation in size changes around a mean rate (e.g., Salguero-Gomez & Casper 2010). However, for many species assuming normally distributed growth variance is problematic, because a few individuals experience sporadic extreme shrinkage events and these results in a highly skewed distribution of growth rates (Shriver et al. 2012). We accounted for these two types of growth following the procedures proposed by Shriver and colleagues (2012), describing normal growth and extreme shrinkage as a two-part process (Montero-Serra et al. 2017). Size-dependent extreme shrinkage was fit as two parameters (annual probability of shrinking, and then mean and variance if it occurs). Unlike normal growth, extreme shrinkage probabilities were fit to each population and time-period.

To directly assess the mean effect of different disturbances on coral survival and extreme shrinkage rates, we also fit a set of Generalized Linear Mixed Models (GLMM) including colony size and disturbance level (protected, unprotected, warming) as fixed factors and population and year as random effects (Table S2 & S3).

Integral Projection Models

Based on the linear models characterizing each vital rate, we derived a set of annual size-structured integral projection models for each population (see Montero-Serra et al. 2017 for details on vital rates estimation and model construction). These sets of models were used to compute the long-term stochastic growth rate at each population, as well as growth rates assuming different combinations of local management and climate effects, as described below.

We computed long-term stochastic population growth rate (λs) for each red coral population, based on their observed variation in demography, by running 1000 Monte Carlo simulations over relevant time horizon of 100 years, choosing each of the 3 to 13 annual transition matrices estimated for each population with equal probability. This methodology is commonly used in population viability analysis (Genovart et al. 2017). In the simulations, we randomly drew each of the observed annual matrices with equal probability. Simulations were initiated with a population at the stable stage distribution of the mean matrix for the population. λs was estimated as:

$$= \frac{1}{1000} \; {}^{1000}_{=1} \quad \frac{\ln(\qquad {}_{,} = 100)) \quad \ln(\qquad (= 0))}{100}$$

Where $N_{total,t}$ is the summed population number across all sizes at time t.

Climate-induced mortality: demographic effects of extreme heat waves

The effects of heat waves were modeled under current conditions using 13yrs of demographic monitoring data in an affected red coral population located in the Scandola Natural Park (Corsica, France). This population has experienced several warming events that led to significant demographic effects. A total of 13 annual-level IPMs were derived from the demographic dataset and were used to forecast the long-term dynamics of this population under current trends. We compared the observed number of coral colonies from 2003 to 2016 to the projected trajectories by starting the simulations at 2003 with the observed initial abundance (n = 143 colonies) and size distribution. In addition, to estimate the effects of warming events on size-dependent survival rates (the main vital rate influenced by these events), we fit a logistic GLM to the survival data of 2016, when the highest intensity Mass Mortality Event was recorded.

Local protection effects on population size and colony-size structure dynamics

We tested the effect of local management on the dynamics of coral populations by simulating 1000 trajectories using 36 annual- and population-level IPMs derived from the demographic data on 4 protected red coral populations within MPAs (21 matrices) and 3 unprotected coral populations (15 matrices) (Table S1). As a starting population vector, we set 100 individuals at the stable stage distribution, which corresponded to the right eigenvector of a mean matrix that included both treatments. In each simulation, we randomly picked one annual transition matrix from the suite of matrices estimated across all years and populations for either protected or unprotected sites.

Structural complexity is an important indicator to assess the health status and functional role of key marine habitat-forming organisms such as corals and gorgonians. Thus, we quantified the proportion of large coral colonies (>100mm) as a proxy for population structural complexity (Linares et al. 2010, Montero-Serra et al. 2017).

Modeling the combined effect of fishing and warming-induced mass mortality events

To explore the interactive effects of local and global stressors (fishing and warming-driven mass mortality events) on the long-term stochastic growth rate and mean time to extinction of red coral populations, we simulated dynamics under 100 scenarios of fishing and warming impacts. To present stable mean results, in these simulations, we only included demographic variation due to local protection and warming events, but not population or annual variation in vital rates. Local management showed no significant effects on the survival rate of coral colonies but it revealed a strong impact on extreme shrinkage probability. Therefore, we used the predicted mean values from GLMMs for extreme shrinkage probability in protected vs. unprotected coral populations to explore the effects of MPAs. To provide a continuous gradient of local disturbances, we multiplied the effect size estimate of MPA effect by 10 levels (Table S3 and Figure S1). The maximum/high local disturbance intensity corresponds to shrinkage probability outside MPAs (where fishing is allowed), while the minimum/low probability corresponds to shrinkage rates observed in populations within MPAs (where fishing is completely forbidden). On the other hand, a gradient of 10 levels of probability of occurrence of high intensity MME (from 0.05 to 0.95) were set using mortality rates quantified during a high intensity mortality event occurred in 2016 in Palazzu (Fig. 4b), and background mortality rates quantified using data from all monitored populations (Table S1). These two gradients of local and global stressors resulted in 100 demographic combinations. We compared these different scenarios by computing the long-term stochastic population growth rate for 1000 simulations of the 100 demographic combinations using the same methodology described above. We also used stochastic projections to computed mean time to extinction for each combination of stressors by setting an initial population size of N_0 = 1000 individuals, and a quasi-extinction threshold of 10% that corresponded to 100 individuals.

RESULTS

Demographic consequences of fishing and no-take marine protected areas

All seven red coral populations not subject to mass mortality events had very low extinction risk, with long-term stochastic growth rates near at those for a stable population (X ± SE; $\log(\lambda_s) = 0.0108 \pm 0.0044$); and this was consistent across protected and unprotected populations

(ANOVA; F = 2.033; P = 0.2130; Fig. 2a). Size-dependent mortality rates also did not differ between unprotected sites and protected red coral populations (Logistic-GLMM; P = 0.6810; Fig. 2b, Table S2). Projected dynamics using IPMs fitted to data from protected and unprotected populations showed very similar patterns regardless of protection status, with no significant differences on the first 30 years of simulations (Fig. 2c).

In contrast, colony shrinkage rates depended strongly on local management status. The best fitted model for shrinkage probability included a significant interaction between coral colony size and protection status, with much higher shrinkage rates in large and unprotected coral colonies (Figure 2d, Logistic GLMM; P < 0.001; Table S3).

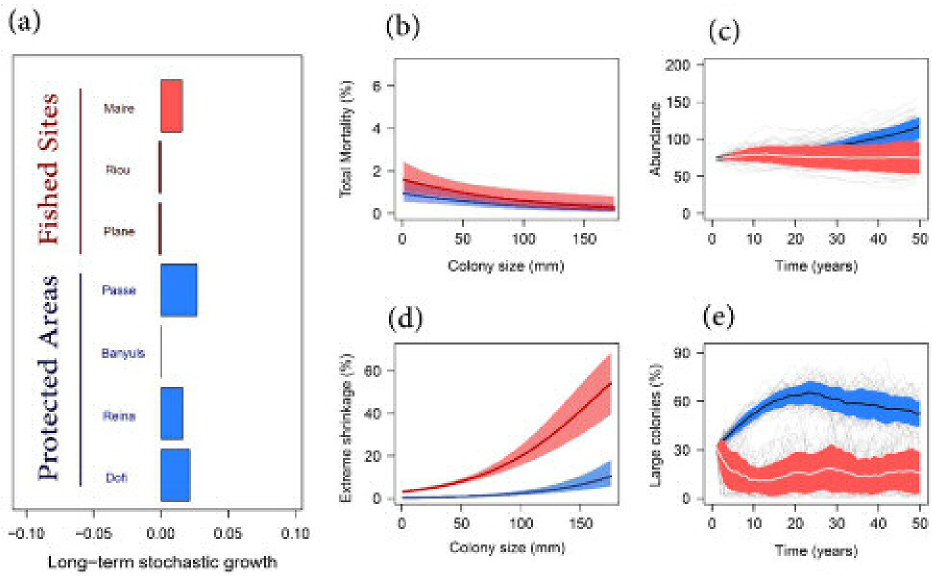


Figure 2. Local protection effects on coral population dynamics and structural complexity. Unprotected sites affected by recurrent fishing events (red) and protected protection within MPAs where fishing is not allowed (blue). (a) Long-term stochastic population growth rate at each site. (b, d) MPA effects in vital rates: (b) total mortality (% of annual dead colonies depending on maximum colony size) and (d) partial mortality (annual shrinkage probability depending on colony size). (c, e) Simulated stochastic dynamics in abundance (c) and structural complexity (e), represented as % of large colonies (>100mm).

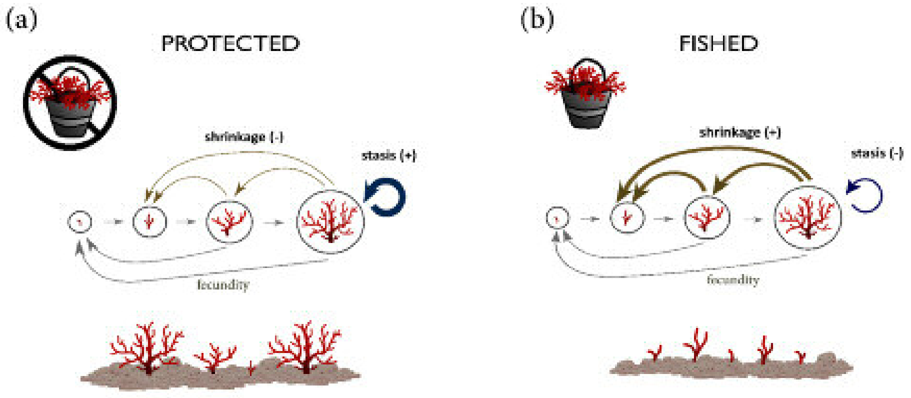


Figure 3. Effects of local protection and overfishing on demographic processes and structural complexity of red coral populations. The conceptual diagram shows how shrinkage rates and stasis of large colonies are shaped by local protection (a) and fishing (b). Protection from fishing results in more complex red coral populations with presence of large coral colonies, whereas recurrent fishing events outside MPAs cause a structural simplification of populations which are dominated by small to medium size coral colonies. (exact values are shown in Figure S2)

When considering the proportion of large colonies as proxy of population structural complexity, projected trajectories of coral populations within and outside MPAs showed divergent trajectories: starting at the stable-stage distribution, protected populations increased their structural complexity while unprotected populations showed a rapid and strong decrease in the presence of large coral colonies (Fig. 1e). This caused a change in the relative importance of life-history processes depending on local management schemes. In protected populations, stasis was the dominant life-history process, with large colonies remaining within the same state and resulting in high structural complexity. On the contrary, recurrent shrinkage events coupled to slow colony growth drive a structural simplification in unprotected populations, which are dominated by small and medium-size coral colonies (Fig. 3 & S2). Across colony sizes, stasis is the dominant demographic process in both protected and un protected sites. However, in large colonies, summed stasis probabilities shift from 0.991 in protected populations to 0.802 in unprotected ones (Figure S2).

Demographic consequences of warming-driven mass mortality events

Recurrent positive temperature anomalies caused several mass-mortality events in the red coral population at Palazzu (Corsica) during the 13 years of demographic monitoring (Fig. 4). These recurrent mass mortality events resulted in a negative long-term stochastic growth (λ_s = 0.98), and drove a steady decline that may result in the local extinction of the warming-affected population (Fig. 4a). The most severe event was observed during the summer of 2016, and caused whole-colony mortality rates of approximately 25% of the total coral colonies (Fig. 4b).

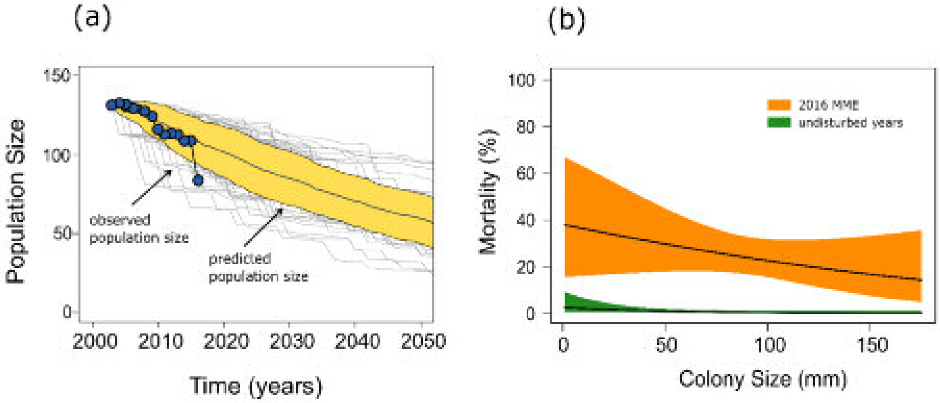


Figure 4. Demographics effects of warming-driven mass mortality events. (A) Long-term stochastic dynamics on a warming-affected red coral population. Dots show the observed abundance during the 13yrs of monitoring. Grey lines represent 100 stochastic projections using IPMs and yellow area represents the 95% CI around the predicted trajectories. (B) Logistic GLMMs describe undisturbed mortality rates across all populations and years (excluding MME) (green) and a GLM describe mortality rates during the high intensity MME recorded in 2016 at Palazzu population (orange).

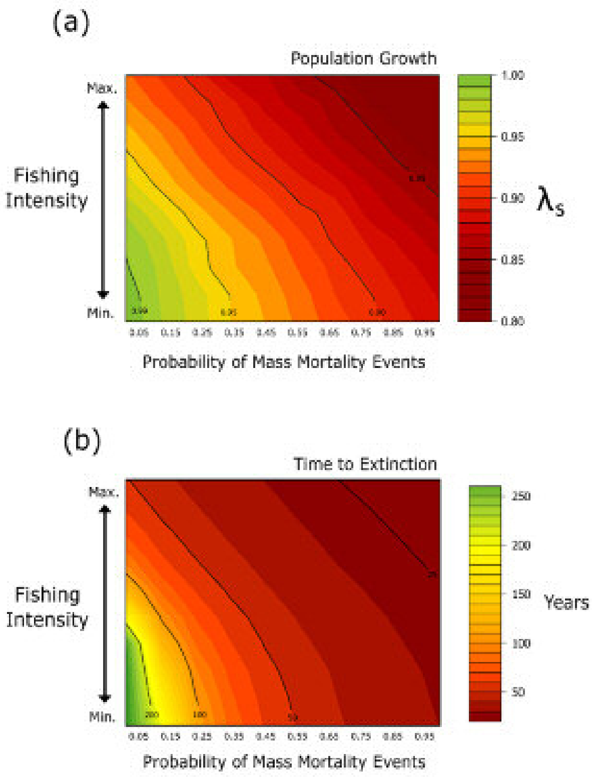


Figure 5. Interactive effects of local and global stressors on the stochastic population dynamics and extinction risk of Mediterranean red coral populations. (A) Long-term stochastic growth rate (λs) and (B) shows the mean time to extinction. Vertical axis represents ten levels of local disturbance intensity (see methods and figure S2) and horizontal axis represents ten levels of probability of mass mortality events.

Interactive effects of local and global stressors

Simulated trajectories under multiple scenarios of differing intensities of global warming and fishing revealed that red coral long-term stochastic population growth rate is highly sensitive to changes in frequency of climate-driven mass mortality events (MME) (Fig. 5 & 6). Local protection was an important factor enhancing population growth under low MME probability. However, its effects were negligible under hypothetical scenarios of increased frequency of mortality events. The interaction between these local and global scale stressors was mainly additive, with only very weak compensatory effects (Fig. 5 & 6).

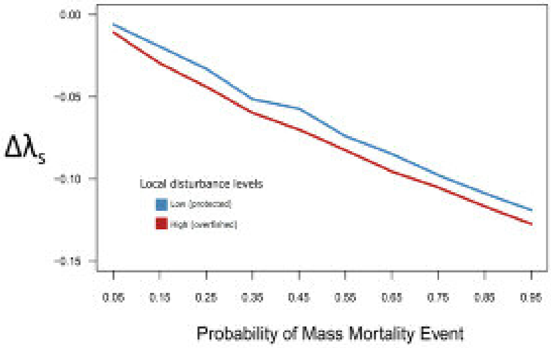


Figure 6. Interaction between local disturbances (fishing) and global warming (probability of Mass Mortality Event) on the long-term stochastic growth rate of Mediterranean red coral populations.

DISCUSSION

Predictions of future ecological change are currently challenged by a poor understanding of how multiple stressors interact to shape the dynamics and structure of populations and communities. Here, we show the strong but divergent demographic consequences of warming-induced mortality events and overfishing on a long-lived octocoral. Recurrent heat waves raise whole-colony mortality rates and compromise the long-term viability of coral populations. By contrast, banning fishing in MPAs did not affect coral mortality patterns but did reduce shrinkage rates, allowing colonies to attain large sizes and this strongly increased the structural complexity of populations. However, our results suggest that these local and global scale stressors are mostly additive, with MPAs having only a weak compensatory effect on the population-level effects of warming events.

Effects of global warming on red coral populations

In the Mediterranean, several mass mortality events have impacted multiple organisms, most of them slow-growing species, across vast regions (Cerrano et al. 2001, Garrabou et al. 2009). The immediate destructive effects of these widespread climate-driven mortality events in corals and other habitat-forming marine invertebrates are well known (Garrabou et al. 2009, Hughes et al. 2017). However, predictions of the long-term, population-level consequences of these events are still relatively scarce. In this study, stochastic projections based on individual-level demographic data over a 13-year period in a red coral population subjected to recurrent climatic disturbances revealed clear detrimental consequences for population viability (Fig. 4). Although there still is a large uncertainty around the expected future climatic impacts, current evidences suggest that the frequency and intensity of heat waves has already increased and is likely to continue follow this path during this century (Hughes et al. 2017b, 2018a). This is especially worrisome for the Mediterranean Sea, where warming is occurring at faster rates than in larger ocean basins (Vargas-Yanez et al. 2008, Macías et al. 2013). Under these trends, local extirpation of shallow red coral populations appears likely in a near future. The predicted declines can be even more adverse for long-lived species such as the red coral, in which rescue effects are very unlikely at ecological time-scales due to highly restricted larval dispersal (Ledoux et al. 2010a, b). For long-lived species with slow population dynamics, catastrophic consequences could go unnoticed by managers when looking at short-term trends (Hughes et al. 2013). Some authors have suggested that adaptive responses can lead to increased thermal resistance of red coral colonies to warming (Ledoux et al. 2015). However, observed increases on the severity of mortality events and their long-lasting consequences provide little empirical support to any adaptive process that could counterbalance these climate change impacts. Furthermore, long generation times for habitat-forming species such as the red coral make rapid genetic change unlikely. The largest survey of impacts of the mass bleaching event occurred in the Great Barrier Reef in 2016 also refutes any optimistic expectations that corals exposed to previous thermal stress may show increased resistance to future warming impacts (Ainsworth et al. 2016, Hughes et al. 2017).

Local stressors and the role of Marine Protected Areas

In the current context of rapid environmental change, understanding the effects of MPAs on population dynamics and extinction risk in marine sessile invertebrates is an essential but unresolved question. Our results show that local protection did not significantly alter red coral numbers or overall dynamics. Recurrently fished populations outside of MPAs displayed low extinction risk and their long-term stochastic growth was nearly at equilibrium (Figure 2a). This counterintuitive result could be explained by the clonal nature of the red coral and its capacity to survive and undergo re-growth of new branches after being partially harvested, which is common when fishers leave the colony bases attached to the substratum (Montero-Serra et al. 2015). It is important to note that highly destructive red coral fishing practices are still observed in some areas of the Mediterranean and they could lead to much worse ecological effects than those reported here (Cattaneo-Vietti et al. 2017). A slight increase in total mortality rates due to fishing would result in a dramatic increase on the population extinction risk outside MPAs and result on an enhanced role of local protection. Broad-scale quantification on the extent of these unsustainable practices is essential to improve current management strategies for the conservation of *Corallium rubrum* and other precious corals.

In contrast to the lack of effects on numbers, the absence of coral fishing in no-take areas had a strong positive effect on the structural complexity of coral populations by reducing the probability of colony breakage and allowing coral colonies to reach larger sizes (Figure 2d). Outside MPAs, structural simplification was observed with absence of large colonies, driven by both the natural slow colony growth of the species and recurrent colony breakage events due to fishing. Thus, local management can shape the relative importance of the demographic processes underlying red coral dynamics, enhancing the structural complexity and functionality of red coral populations (Fig. 3 & S2). These results are consistent with previous observations that found that populations within MPAs have larger biomass than unprotected sites, which can harbor more than 200-fold biomass as observed in a recently discovered pristine red coral population (Bavestrello et al. 2014, Garrabou et al. 2017). Here, we provide a mechanistic understanding on how differential shrinkage but similar whole colony mortality rates shape the consistent broad scale patterns observed in colony-size structures and population persistence of the red coral across the Mediterranean Sea (Linares et al. 2010, Garrabou et al. 2017, Fig. 2 & 3).

Interactive effect of local management and global warming on the viability of red coral populations

It remains unclear how effective local management tools such as Marine Protected Areas (MPAs) are in building resilience of benthic ecosystems to climate change. Local protection enhanced the size-structure of red coral populations and, since climate-driven whole colony mortality is size-dependent in the red coral (with smaller colonies being more susceptible, Fig. 4b), a compensatory effect of MPAs against climatic perturbations could be expected. However, our results show that MPAs provided only a very weak compensatory effect. This slows down the rate of population declines along a thermal stress gradient, but does so only under low to moderate frequencies of mass mortality events (MME) (Figure 5 & 6). When recurrent MME occurred at high frequencies, MPAs had a little buffering effect on the long-term persistence of coral populations. To date, only few studies provide data over relevant time-periods to assess the potential role of MPAs at buffering climatic impacts. Michelli and colleagues (2012) showed that, in a temperate abalone species, MPAs enhanced population resilience to climatic disturbances by increasing the presence of larger individuals that drove a major reproductive output as well as larvae export potential. Similarly, in tropical coral reefs, Mellin and colleagues (2016) reported a strong effect of MPAs at enhancing resilience of benthic communities to external perturbations, although the mechanisms underlying these patterns were not demonstrated.

In contrast, Graham and colleagues (2008) found that reefs under local protection had been more impacted by El Niño bleaching event in 1998. More recently, an unprecedented mass bleaching event occurred at the Great Barrier Reef, with more than 90% of the reefs affected irrespective of their level of local protection (Hughes et al., 2017). Our results add support to the latter findings in showing that local protection could be effective at lower levels of thermal stress, but have weak to nonexistent compensatory effects under potential future scenarios of increased ocean warming. Also, this study highlights the role of demographic approaches to provide a mechanistic understanding on how multiscale stressors interact to shape the dynamics of reef corals and other habitat-forming species, which is urgently needed to anticipate and manage threats driven by a rapid environmental change.

Conclusions

Long-term studies provide a unique window to understand and predict the responses of marine populations and communities to multiple stressors. This study demonstrates that MPAs are a good tool to enhance the structural dynamics of economically and ecologically important species such as the red coral. However, warming represents a new threat originated at global scale that can drive either subtle or more abrupt declines that will result in the "extinction debt" of these key habitat-forming species (Hughes et al. 2013). While the red coral and other long-lived habitat-forming species have persisted millennia of human pressures, novel climatic threats may lead to unanticipated and massive consequences for the integrity of temperate reefs. Unfortunately, local protection may not be enough to ensure the persistence of shallow populations under future scenarios of higher frequency and intensity of mass mortality events. A rapid and drastic reduction of greenhouse gas emissions seems the only effective way to prevent the widespread extinction of shallow red coral populations and other long-lived marine invertebrates. In the context of a variety of multi-scale stressors, any conservation action aimed to preserve the functional role and ensure the persistence of benthic communities will need to consider conservation actions at both local and global scales.

ACKNOWLEDGEMENTS

This study was partially funded by the Spanish Ministry of Economy and Innovation Biorock project (CTM2009-08045), Smart project (CGL2012-32194), TOTAL Foundation Perfect Project, Prince Albert II of Monaco Foundation MIMOSA project and the European Union's Horizon 2020 research and innovation programme under grant agreement No 689518 (MERCES). This output reflects only the author's view and the European Union cannot be held responsible for any use that may be made of the information contained therein. IMS was supported by a FPI grant (BES-2013-066150), CL by a Ramon y Cajal (RyC-2011-08134), and JBL by a Postdoctoral grant (SFRH/BPD/74400/2010) from the Portuguese Foundation for Science and Technology. Support for DFD came from National Science Foundation awards 1340024 and 1242355. IMS, CL, JBL and JG are part of the Marine Conservation research group (2017 SGR 1521) from the Generalitat de Catalunya.

CHAPTER IV

Accounting for life-history strategies and timescales in marine restoration

Ignasi Montero-Serra, Joaquim Garrabou, Daniel F. Doak, Laura Figuerola,
Bernat Hereu, Jean-Baptiste Ledoux and Cristina Linares

INTRODUCTION

Marine coastal ecosystems host high levels of biodiversity and provide goods and services to a large proportion of the world's human population (Palumbi et al. 2008). The cumulative effects of multiple stressors such as overfishing, habitat destruction, and pollution together with new global threats (i.e. climate change, biological invasions) have driven compositional changes, local extinctions, and wholesale destruction of many benthic communities (Jackson et al. 2001, Airoldi & Beck 2007). To face this challenge, actions at both global (i. e. reduction of greenhouse gas emissions) and local levels are urgently needed (Kennedy et al. 2013). At local scales, fishery regulations and marine protected areas can help to reduce or remove threats (Edgar et al. 2014). Even so, when the resilience of natural systems has been seriously diminished, active restoration may be necessary as a complementary tool to restore damaged populations and communities (Possingham et al. 2015).

Over the last few decades, the success of ecological restoration efforts in terrestrial landscapes has improved dramatically, with successful examples of enhancing ecosystem structure, function, and the provision of ecosystem services (Benayas et al. 2009, Perrings et al. 2015). In the marine realm, however, restoration approaches have generally been successful only at very small spatial scales and continue to present many challenges (Edwards & Gomez 2007). Strikingly, the degree of success in marine restoration actions is not generally related to the underlying costs of the project (Bayraktarov et al. 2016). This is partly due to the high methodological constraints, but also to relatively poor understanding of the drivers underlying successful actions.

Habitat-forming species such as corals and seagrasses have been the primary targets of marine restoration activities, and transplanting asexually produced units (i.e. coral fragments or seagrass shoots) has been proposed as the tool of choice for recovering habitats by bypassing sensitive early life stages (Edwards & Clark 1998). Recently, research has shown that corals display high survival rates after transplanting when compared to the dominant organisms found in seagrass beds, oyster reefs, or saltmarsh ecosystems (Bayraktarov et al. 2016). However, this generalization ignores the high diversity in life-history strategies of the dominant species in these benthic communities (Darling et al. 2012; Madin et al. 2014). Indeed, life-history tradeoffs between demographic rates have been observed in hard coral species, suggesting potential effects on short-term and long-term restoration success (Edwards & Clark 1998; Dizon & Yap 2006, Glassom & Chadwick 2006). Yet, quantitative evidence of how the life history of target species shapes restoration outcomes is lacking in the scientific literature. To advance the theoretical framework of marine restoration and provide tools to enhance the effectiveness of transplantation efforts, we need to go beyond habitat type towards a fuller quantitative analysis of how life-history strategies determine the best strategies or allow better prediction of the speed and eventual success of restoration efforts.

To date, most studies of transplant success in marine systems have focused on survival rates of transplanted individuals over relatively short monitoring periods (usually less than 2 years) (Bayraktarov et al. 2016). However, a broad goal of restoration efforts is to recover structural complexity that can provide ecosystem services at rates similar to natural ones. Thus, when planning restoration actions, managers should consider the factors affecting the time required from any transplantation action to reach the restoration goals for the target species and habitat. Long-term monitoring programs can provide suitable data to inform this issue, but funding often constrains the duration of monitoring after restoration actions and experiments (Lindenmayer & Likens 2009, Precht & Robbart 2006). Demographic modeling methods such as matrix and integral projection models (Morris & Doak 2002, Ellner & Rees 2006) can be used to synthesize individual data into predictions of the longer-term development of transplanted populations (Linares et al. 2008).

In the present study, we combined demographic monitoring of transplanted and natural of colonies of a temperate coral species, a comprehensive literature review of tradeoffs in the life histories of sessile marine species, and the use of population projection models to explore the dynamics of transplant efforts targeting species with different life-histories. Our results support the utility of explicitly linking life-history theory to marine restoration and provide an illustrative example of anticipating the expected dynamics and timescales of restored ecosystems.

METHODS

Study system

The precious red coral *Corallium rubrum* is a structural octocoral of a highly diverse coralligenous assemblage of the Mediterranean Sea and also possesses important cultural and economic value. Due to historical overexploitation, most shallow populations of *C. rubrum* can be considered functionally impaired and many are ecologically extinct (Bruckner 2009, Tsounis et al. 2010). To reverse this situation, an international agreement urged Mediterranean countries to strengthen their *C. rubrum* fishery regulations during the last decade (Cau 2013). Unfortunately, the lack of enforcement of regulations on coral harvesting along with poaching is widespread across the Mediterranean basin and represents a major problem for the management of the species, hindering the effectiveness of its conservation (Linares et al. 2012).

Study area and transplant experiment

In 2011, the Catalan authorities intercepted 14.5 kg of illegally harvested *C. rubrum* along the Montgrí Coast (Catalonia, Spain). About 300 red coral colonies, a small portion of the intercepted colonies, were selected for a transplant experiment. These colonies were initially kept at 16 ºC and fed in aquarium facilities at the Institute of Marine Sciences in Barcelona (Spain). After one week, the colonies were transported in coolers to the Parc Natural del Montgrí, Illes Medes i Baix Ter in the NW Mediterranean and transplanted onto a rocky wall ranging from 15 to 17m depth using a two-component epoxy putty as glue. The site was chosen because some sparse red colonies were found in the vicinity, indicating its suitability for the species (Fig. 1).

Demographic traits

Four transects were established within the transplanted population and surveyed through photographic sampling after transplantation, in May 2011, and again in May 2015 (Fig. 1). Survival rates of the transplanted colonies were quantified by individually

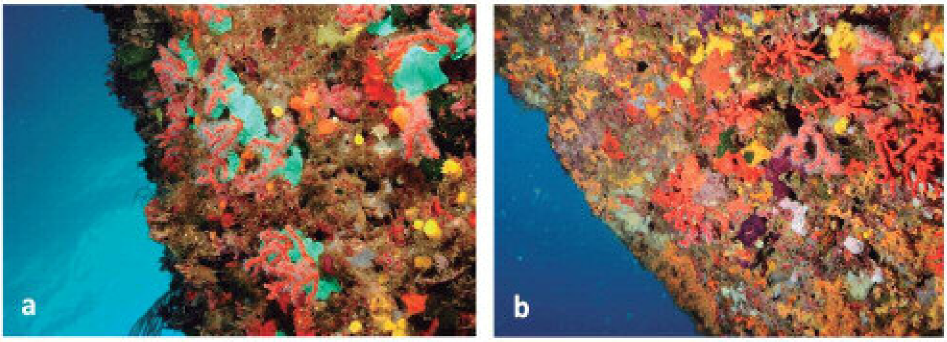


Figure 1. Restoration of *Corallium rubrum* populations. (a) A new population was transplanted in 2011; (b) most transplanted colonies survived in 2015, after four years of transplantation.

identifying coral colonies from the photographic series from 2011 and 2015. Natural survival rates of *C. rubrum* colonies were calculated from long-term data on 8 natural populations (see Supplementary Methods for a complete description of surveys). Reproductive potential of colonies was estimated for a sample of transplanted colonies (n = 35) outside the monitored transects and from a natural adjacent population (n = 35) in late June of 2015 by counting *C. rubrum* larvae found inside the polyps of the fertile female colonies (Tsounis *et al.* 2006). Samples were collected by SCUBA diving and fixed in 4% fromaldehyde. At the lab, 15 polyps per sample were dissected and larvae found inside the polyps were counted.

Literature review

We explored life history tradeoffs in marine restoration experiments following two steps. First, we systematically reviewed all transplantation experiments of marine sessile species we could identify in a search of the literature up to November 2015. Using *Google Scholar* we searched for a combination of the terms “restoration”, “transplantation”, or “rehabilitation” with a second term related to marine sessile taxa: “coral”, “gorgonian”, “sponge”, “macroalga” or “seagrass”. We then selected those studies that conducted experimental transplants as a restoration technique and reported survival rates during at least one year after transplanting.

We also compiled data on growth rates of sessile marine species since this vital, or demographic, rate is highly correlated to overall life history (Darling et al. 2012). We searched available studies reporting standard data on linear extension rates to approximate average species-specific growth rates for corals (Madin et al. 2016). In seagrasses, mean horizontal rhizome elongation rates were used as an indicator of the species growth rate (see Marbà & Duarte 1998), thus, seagrass and sessile invertebrates were analyzed separately.

Demographic projections

Red Coral. To synthesize data on growth, survival and reproduction into predictions of population growth and increasing sizes within populations, we used Integral Projection Models (IPMs) parameterized with long-term demographic data from several natural red coral populations (full description data analysis and model construction are in the Supplementary Material S1). Based on annual IPMs, we computed 1000 stochastic projections assuming that all annual models can occur with equal probability at each time-step. Maximum height of transplanted colonies was measured in 2015 using photogrammetric techniques (Drap et al. 2013) and the distribution of heights was used to establish the starting population vector for the projections.

Linares et al. (2010) argue that the structural complexity of *C. rubrum* populations can assessed by quantifying the proportion of large colonies (>100 mm), since these larger colonies provide structural complexity. Based on this parameter, we compared the outputs from our population projections to the proportion of large colonies in three relatively un-impacted *C. rubrum* populations that are located within old and well-enforced Mediterranean MPAs (Fig. 1 & S1, Linares et al. 2010).

Comparative Analyses. We also searched in the literature for published matrix population models of other marine sessile species. We then used these models to perform deterministic population projections of 100 individuals starting at the smaller size class and computing time periods until the population reached a proportion of large individuals (largest size class) equivalent to the 20% and 80% of the expected proportion when reaching the Stable Stage Distribution (SSD).

RESULTS

Demographic traits of *C. rubrum* transplanted colonies

After four years, 99.1% of transplanted *C. rubrum* colonies were still alive. Annual survival rates of transplanted colonies did not show significant differences from control populations (Fig. 2a). Transplanted colonies also had similar reproductive potential to colonies in natural populations, considering both the proportion of fertile colonies as well as the frequency of larvae per polyp (Fig. 2b, 2c).

Comparative survival and growth in transplant experiments/actions

We found 50 studies that allow calculation of mean annual survival rates after at least one year following transplanting for a total of 59 marine structural species (Fig. 3a). These included 40 species of hexacorals, which have a mean annual survival of 60.8% (range of 6.8 to 98.6%); 5 species of gorgonians, including the present study, with mean annual survival of 48.1 (range of 30.0 to 99.1%); 1 species of sponge, with mean annual survival of 85.7%; 11 species of seagrasses, with mean annual

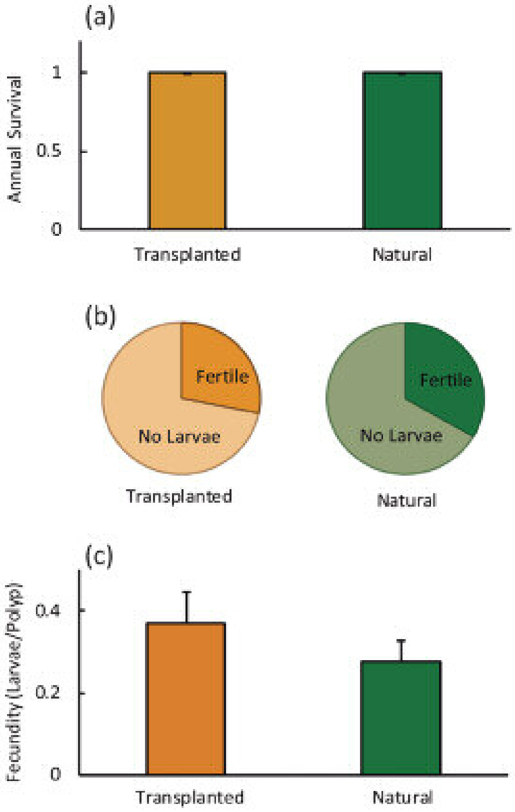


Figure 2. Demographic traits in transplanted and natural *C. rubrum* populations. (a) Mean annual survival rates; (b) Proportion of fertile colonies; (c) Mean polyp fecundity, calculated as the frequency of larvae found per polyp within fertile colonies.

survival of 42.5% (range of 28.9 to 69.2%) and 2 seaweeds, with mean annual survival of 43.1% (range of 25.1% to 80.0%). We observed a significant negative correlation between survival after transplantation and the species mean growth rates measured under natural conditions in marine sessile invertebrates (Fig. 3b; n = 35; Pearson's r = 0.47, P = 0.005; Spearman rho = 0.37, P = 0.046). Seagrass species revealed a parallel pattern (Fig. 3c; n = 8; Spearman

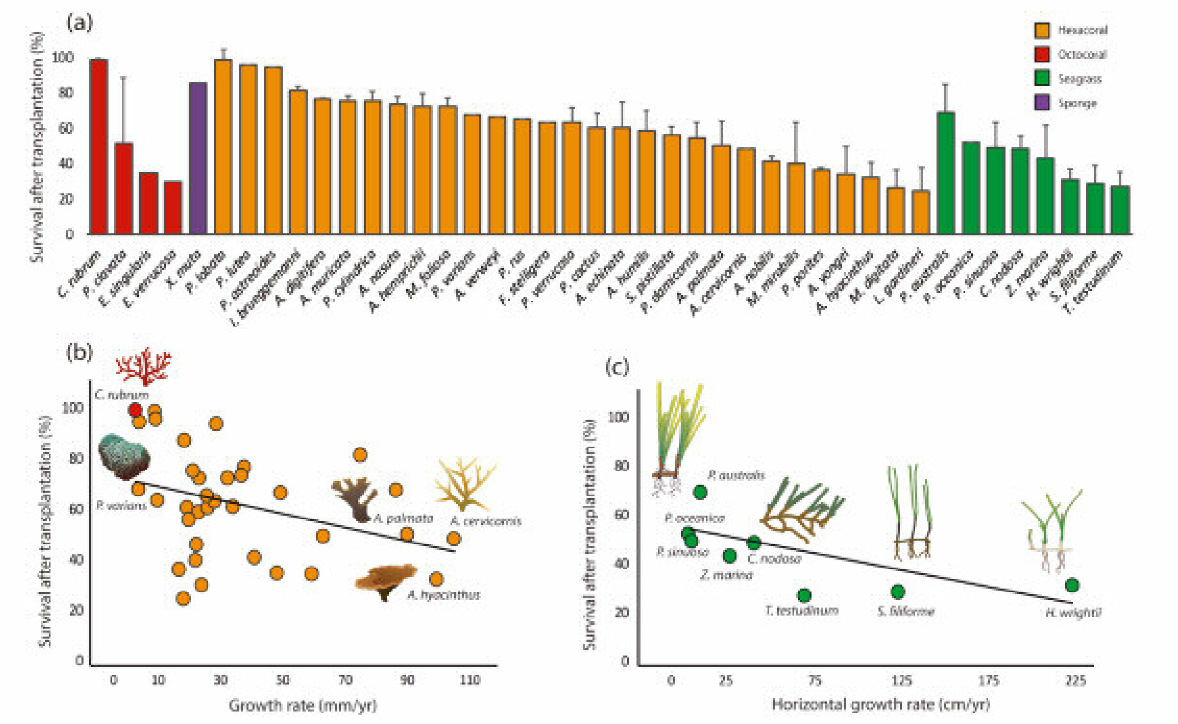


Figure 3. Survival rate of marine sessile species in transplant experiments. (a) Mean annual survival rates (Mean ± SE). (b) Life history tradeoff between survival after transplantation and growth rates in 35 marine sessile invertebrate species and (c) Life history tradeoff between survival after transplantation and growth rates in 8 seagrass species. Each dot represents a species for which mean annual survival after transplantation and mean growth rate could be calculated from a range of published studies (see Table S1). In seagrass species, growth represents mean horizontal rhizome elongation rate (see Marbà & Duarte 1998). Images: Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

rho = 0.81, P = 0.022), although the relationship was only marginally significant according to Pearson's correlation (Pearson's r = -0.69; P = 0.059). Growth data measured in natural and transplanted colonies for coral species were also highly correlated (Fig S3, n = 17; Pearson's r = 0.85; P < 0.001).

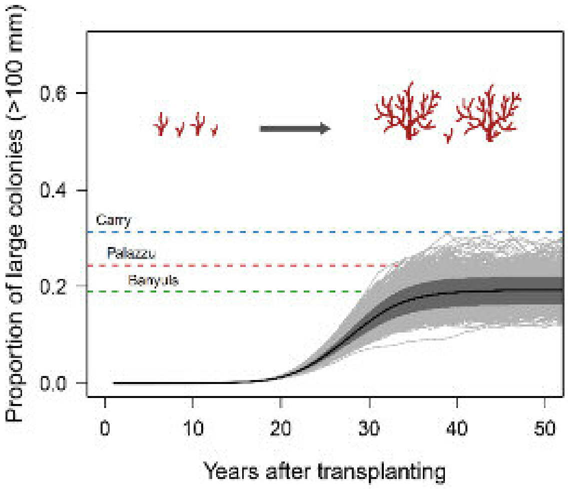


Figure 4. (a) Predicted temporal dynamics of the *C. rubrum* population size frequency distribution. Black line represents the mean and shaded area the confidence intervals of 1000 stochastic projections. The size frequency distribution of three natural and well protected *C. rubrum* populations (dotted lines) were used as an ecological baseline (Linares *et al.* 2010).

Demographic projections and recovery periods

Red coral. The transplanted population in 2015 was dominated by small individuals (most red coral colonies were < 35 mm in height, Fig. 1 & S1), while natural red coral colonies had extremely low growth rates (Fig. S2). The stochastic integral projection models incorporating these traits showed that a period ranging from 30 to 40 years after transplanting is needed for populations to have a proportion of large colonies comparable to that seen in the well-preserved *C. rubrum* populations used as an ecological reference (Fig 4).

Comparative analyses. The simulated recovery periods for 41 marine sessile species were highly variable in length, ranging from years to several decades (Fig 5, Table S3). The expected recovery length was strongly and positive associated with the species' mean survival rate regardless of the conservation goal (n = 41; 20% threshold: $R^2 = 0.419$; $P < 0.001$;

80% threshold: $R^2 = 0.495$; $P < 0.001$). After accounting for potential artifacts due to different matrix dimensions, mean survival rates were still a strong predictor of the expected recovery periods (Table S1).

DISCUSSION

Marine restoration is a relatively young discipline with most efforts only operating at very small spatial scales (Bayraktarov et al. 2016). Filling knowledge gaps on the processes underlying restoration success is therefore crucial to help further develop this field and ensure meaningful planning and success over larger spatial and temporal scales. In this study, we quantify the role of life history in shaping restoration outcomes and demonstrate a consistent tradeoff between survival and growth across different taxa with contrasting life-history and functional traits, which in turn drives a tradeoff between required minimal transplantation effort at the start of a project and the maximum possible speed of ecosystem recovery.

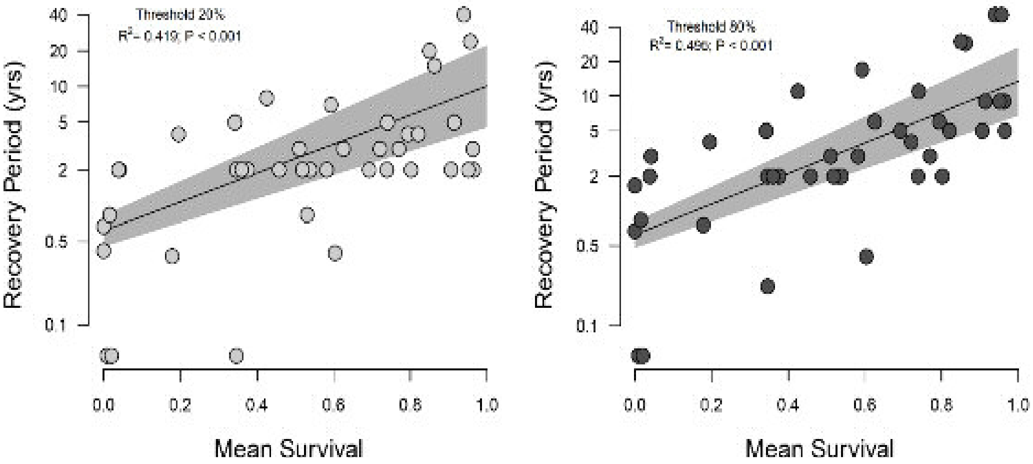


Figure 5. Projected recovery times for 41 marine sessile invertebrate species using published matrix populations models (Table S3) and setting a recovery threshold of (a) 20% and (b) 80% of the number of large colonies expected in a population at the Stable Stage Distribution. The black lines and the shaded areas correspond to the mean and standard errors of the linear models (Table S1).

Anticipating mortality patterns after transplantation is central to the design of any restoration action since it may determine the initial attaching effort required to achieve specific conservation goals. Here, a systematic review of transplantation experiments from tropical and temperate habitat-forming species revealed a negative tradeoff between growth and survival after transplantation that was supported despite differences in experimental techniques and physical properties of the environment that were not explored (Fig. 3b). Slow growing massive hard corals such as *Porites astreoides* and *P. lutea* and the sponge *X. muta* showed the highest survival after transplantation, with rates ranging from 86% to 98%. On the contrary, fast-growing corals such as *Acropora cervicornis*, *A. yongei* and *A. palmata* had survival rates that ranged from 35% to 44%. These results were consistent with previous transplant experiments in tropical coral species with contrasting life histories (Edward & Clark 1989, Dizon & Yap 2006). Similarly, among seagrasses, the three slow-growing *Posidonia* species showed higher shoot survival after transplantation (from 49% to 69%) compared to faster-growing *Syringodium filiforme* (29%) and *Halodule wrightii* (27%) (Fig. 3c). Our findings agree with allocation theory, which predicts that tradeoffs between vital rates such as growth, reproduction and survival may arise from energetic constraints acting at physiological levels (Stearns 1989). Further, branching morphologies associated to faster life histories may increase exposure to physical damage and result in higher mortality rates (Madin et al. 2014). There are also a number of external drivers that can strongly influence restoration success such as predation and herbivory, density of transplants, and catastrophic events (Shaish et al. 2010, Gomez et al. 2014). In spite of the clear importance of these effects, our results show that species' life histories can still provide strong predictive power concerning the outcome of transplantation projects.

Better understanding of both the intrinsic and extrinsic drivers of mortality patterns after transplantation would be ideal and could lead to the implementation of more successful restoration designs, since this combined approach can better define both anticipated time periods for restoration and also the relative benefits of direct transplantation effort.

There have been major calls worldwide to ban the international trade in precious coral and to implement management regulation aimed to ensure the conservation of these species (Bruckner 2014). Yet, the feasibility of restoration actions for these emblematic species has remained uncertain and this may hinder the potential for development of future restoration plans. In the present study, we observed that the colonies of the octocoral *Corallium rubrum* were extremely resistant to the stress of transplantation, displaying high survival rates similar to those in natural populations (Fig. 2a, Garrabou & Harmelin 2002). It is remarkable to observe this high survival rate in transplanted *C. rubrum* colonies that were subject to the stresses of being harvested, kept out of the water in the poachers' nets, transported, maintained in aquaria for one week, and then transplanted back into natural habitat. Yet these transplanted *C. rubrum* colonies had a similar proportion of fertile colonies and even higher frequency of larvae per polyp after 4 years than observed for colonies in natural populations (Fig. 2). Assessing reproductive potential is also critical when working with most marine sessile species which, like *C. rubrum*, show limited larval dispersal and high self-recruitment rates (Ledoux et al. 2010). Indeed, to effectively recuperate populations through a single transplantation effort, newly restored populations must also be viable in the long term, with reproduction reaching natural rates. Here, the high survival and reproductive potential displayed by transplanted *C. rubrum* confirmed the potential success of this restoration action and strongly support the feasibility of these techniques, at least at local spatial scales, with potential applications for other long-lived precious coral species.

As important as choosing a suitable species and restoration method is considering the appropriate time scale and ecological baselines over which to evaluate restoration outcomes or to expect the restoration of ecological functions (Bull et al. 2014). Stochastic projections developed revealed that periods ranging from 30 to 40 years may be necessary for newly established *C. rubrum* populations to show a colony size distribution comparable to those observed in well-preserved natural populations (Linares et al. 2010). These results suggest that, similar to relatively fast-growing terrestrial forest systems (Vesk et al. 2008), long-lived coral stands can take up to several decades to recover their functionality and to allow the development of associated organisms, such as fish and invertebrates, as may occur in tropical coral reefs (e.g., Cabaitan et al. 2008). More interestingly, we found that potential recovery periods can be accurately predicted by the specific mean survival, demonstrating the strong influence of the species' life histories on the temporal scales associated to restoration actions (Fig. 5).

Overall, this study demonstrates a tradeoff between initial transplantation effort needed to achieve a target density of individuals and the speed of recover that may be achieved in a restoration action. For instance, targeting fast-growing species such as *A. cervicornis or A. hyacinthus* (with survival rates ranging from 40 to 50%), will require a two-fold to three-fold initial amount of attached colonies to obtain the same density of survivors compared to actions targeting slow-growing resistant species such as the red coral *C. rubrum* or the massive coral *Porites lutea*. On the other hand, life histories of the target species will also have a strong effect on the expected recovery periods that may vary as much as 20 to 30 yrs (Fig. 5). Finally, because life-history and functional traits are highly correlated (Adler et al. 2014), favoring specific strategies can have long-term consequences for habitat complexity and ecosystem responses to global change (Ortiz et al. 2014).

ACKNOWLEDGEMENTS

The authors thank the Agents Rurals de Catalunya for their invaluable work against red coral poaching. We are indebted to A Lorente for his support. We thank E Aspillaga and L Navarro for field assistance. P Capdevila, A Gori, K Kaplan, A Medrano, and two anonymous reviewers provided valuable comments on the manuscript. Funding was provided by the Spanish MINECO (CTM2009-08045, CGL2012-32194), the Oak Foundation, the TOTAL Foundation Perfect Project and the European Union's Horizon 2020 research and innovation programme under grant agreement No 689518 (MERCES). This output reflects only the author's view and the European Union cannot be held responsible for any use that may be made of the information contained therein. IMS was supported by a FPI grant (BES-2013-066150), CL by a Ramon y Cajal (RyC-2011-08134), and JBL by a Postdoctoral grant (SFRH/BPD/74400/2010). Authors are part of the Medrecover group (2014SGR1297).

CHAPTER V

Predicting depth-mediated impacts of ocean warming at the end 21st century in Mediterranean coastal ecosystems

Ignasi Montero-Serra, Cristina Linares, Peter J. Mumby, Diego Macías,
Nathaniel Bensoussan and Joaquim Garrabou

INTRODUCTION

Anthropogenic global change threatens the structure, function and resilience of world's marine ecosystems (Hoegh-Guldberg & Bruno 2010, Ainsworth et al. 2016). Widespread changes in the distribution and population dynamics of marine organisms have been linked to recent warming (Perry et al. 2005, Pinsky et al. 2013), with negative consequences for both marine biodiversity and the provision of ecosystem services (Barange et al. 2014). In this context of rapid environmental change, understanding what shapes distribution ranges and, more importantly, how climate change will affect the biogeography and vertical range dynamics of structural marine species is central to designing sound adaptive conservation strategies.

Poleward distribution and elevation range shifts are well documented in terrestrial landscapes (Chen et al. 2011). In the marine realm, increasing evidences show how mobile organisms such as fish and invertebrates are tracking temperature trends over broad spatial scales (Pinsky et al. 2013, Montero-Serra et al. 2015). Importantly, strength and speed of responses to warming are mediated by functional traits (Sunday et al. 2015) and habitat requirements (Rutteford et al. 2015). Despite having a paramount role in coastal ecosystems, there still is a large uncertainty on whether structural marine species will track changing thermal habitats. Besides the lack of motility and long generation times, several environmental factors may constrain poleward movements for sessile species, including light limitation (Coma & Gili 2000, Muir et al. 2015), availability of suitable habitats (Rutteford et al. 2015), and large-scale geographic barriers (for example in enclosed seas such is the Mediterranean Sea). When environmental barriers prevent these poleward movements (Muir et al. 2015), widespread mortalities at shallow habitats may drive bathymetrical range contractions as a response to warming impacts

(Bridge et al. 2013, Linares et al. 2014, Muir et al. 2017).

Species distribution models (SDM) are a powerful tool to understand and predict the effects of global change on species geographic ranges (Pearson & Dawson 2003, Hijman et al. 2006, Rutteford et al. 2015). Yet, this field is still in its infancy for marine species, partly due to methodological constraints that lead to a relative scarcity of suitable data (Robinson et al. 2011). Oceans are inherently three-dimensional complex systems with strong environmental gradients at fine spatial scales. In spite of these features, a common assumption when modeling marine species distributions is that environmental parameters remain constant across depths (Sbrocco et al. 2013, Parravicini et al. 2015). Surface environmental conditions may be meaningful for shallow occurring species. However, they can be misleading when modeling potential warming impacts because they are often depth-dependent (Garrabou et al. 2001, Mumby et al. 2001, Bridge et. 2013, Muir et al. 2017). Exploring how depth mediates potential impacts of ongoing climate change in benthic ecosystems is thus a current challenge in conservation. The recent development of novel oceanographic models that include the third dimension (e. g. Macías et al. 2015), opens new opportunities to advance our predicting ability to explore potential warming impacts along depth gradients.

Temperate benthic ecosystems host great levels of marine biodiversity and provide goods and services to dense populated coastal communities. However, temperate regions are warming at faster rates than global averages and have been considered hotspots of present and future climate change (Oliver et al. 2018). The Mediterranean Sea is an example of such overlapping patterns: hosts high levels of biodiversity and provides ecosystem services to millions of people from 21 countries (Coll et al. 2010; NOAA 2015). Mediterranean coastal habitats have been historically damaged by multiple local and regional stressors such as overfishing, habitat destruction, pollution and invasive species (Lejeusne et al. 2010, Claudet & Fraschetti 2010). Recently, several heat waves linked to ongoing global change impacted benthic communities causing catastrophic mass mortalities over broad spatial scales (Cerrano et al. 2001, Coma et al. 2009, Garrabou et al. 2001, 2009). The frequency and intensity of these extreme climatic events is predicted to increase in the near future (Oliver et al. 2018). It is thus essential to fully understand and predict potential warming impacts on Mediterranean benthic communities to advance towards large-scale and cross-boundary sound adaptive conservation strategies (Game et al. 2008, Michelli et al. 2013, Mazor et al. 2015).

Here, we took advantage of a recently developed 3D hydrodynamic-biogeochemical coupled model of the entire Mediterranean Sea that provides predictions at different depth layers (Macías et al. 2015). We explored how present and future climate shapes the bathymetrical dynamics of two emblematic habitat-forming species across the Mediterranean Sea: the red gorgonian, *Paramuricea clavata*, and the red coral, *Corallium rubrum*. Firstly, we assessed the role of local thermal regimens and biogeochemical factors in shaping the upper range limits of gorgonian populations. Then, we applied logistic generalized additive models at different depths (from 5 to 55m) to predict present and future vertical patterns of habitat suitability. Our results revealed large-scale negative impacts of climate change and challenge current predictive modeling approaches based on surface temperature data by revealing complex patterns of differential warming impacts along depth gradients across the Mediterranean Sea.

METHODS

Model species

We focused on two dominant habitat-forming gorgonians of Mediterranean hard bottoms: the red gorgonian *Paramuricea clavata* and the precious red coral *Corallium rubrum*. They are slow-growing and long-lived suspension feeders with an important ecological role providing structural complexity in Mediterranean mesophotic reefs (Ponti et al. 2014). They display slow population dynamics driven by high adult survival and low reproduction success (Linares et al. 2007, Montero-Serra et al. 2018), which results in a high vulnerability to human-driven perturbation such as overfishing and climate change (Garrabou et al. 2009, Linares & Doak 2010). The precious *C. rubrum* is threatened by legal and illegal fisheries (Tsounis et al. 2010, Linares et al. 2012, Montero-Serra et al. 2015). During the past three decades, several mass-mortality events linked to climate change have impacted benthic communities over broad spatial scales (Cerrano et al. 2001, Garrabou et al. 2001, 2009). These events seem depth-dependent (Garrabou et al. 2001) and are putting at risk some shallow gorgonian populations (Linares & Doak 2010).

Modeling philosophy

Mediterranean gorgonians distribution and abundance are largely influenced by the availability of hard bottoms and other environmental conditions such as the irradiance levels, temperature, exposure to flow and food availability (Weinberg 1979, 1980, Zabala & Ballesteros 1989). Unfortunately, we still lack of comprehensive fine-scale cartography for Mediterranean seafloors features. Thus, exploring the biogeography of these species without considering the availability of rocky bottoms can seriously compromise the validity of predictions. Therefore, rather than predicting the distribution of our model species across geographic space, we restricted our predictive

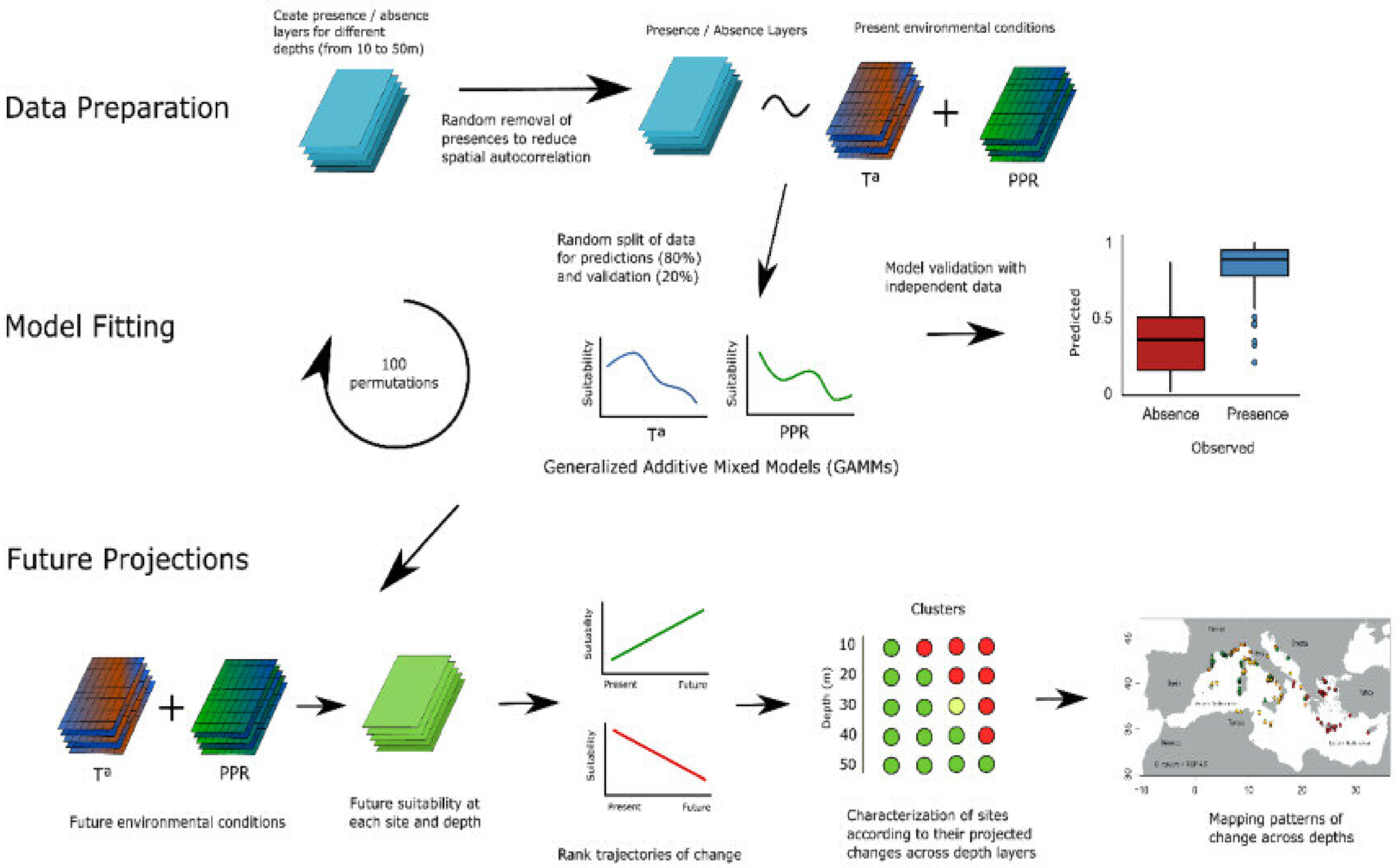


Figure 1. Modeling framework to predict the effects of climate change at different depths.

modeling approach to known locations. Based on a large dataset of reported occurrences and absences at different depth layers, from 5 to 55m, we fitted Generalized Additive Mixed Models (GAMMs) to link bathymetrical distribution of gorgonians to current environmental conditions (water temperature, organic and inorganic nutrients). We then used these trained models to forecast changes in habitat suitability conditions across depth layers within locations where gorgonians are present (Fig. 1). Additive models make no a priori assumptions about the nature of associations between predictors and response variables and have been used to assess the importance of different environmental drivers on patterns of distributions and relative abundance in marine ecosystems (Rutteford et al. 2015).

Biological data

Data on the horizontal and bathymetrical distribution of *Corallium rubrum* and *Paramuricea clavata* were obtained from surveys carried out by two citizen science programs: *SeaWatchers*, *ReefCheck Italy* and *Cigesmed*. Briefly, each survey included name and geographic coordinates, date and time, underwater visibility, survey depth range (min and max), and observation effort in terms of dedicated time. Additionally, a comprehensive literature review was conducted to compile all available occurrence data from published papers of *C. rubrum* and *P. clavata* (Table S1).

Ocean Model

A 3D General Estuarine Transport Model (GETM) was used to simulate the hydrodynamics in the Mediterranean Sea (Macías et al. 2015, Macías et al. 2018). A detailed description of the GETM equations could be found in Stips et al. (2004). The predictive ocean model has a horizontal resolution of 5’×5’ and includes 25 vertical layers. The bathymetric grid used was constructed based on topographic data from ETOPO1 (NOAA, www.ngdc.noaa.gov/mgg/global/). From this model, monthly temperatures, nutrient (phosphate and nitrate) concentrations and primary productivity were extracted. In the present study, we used two long-term model runs covering the periods 2000–2013 and 2085-2099 were used. Model runs were based on two different emissions scenarios according to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR5): the business as usual RCP8.5, in which CO_2 emissions will continue to grow at current rates, and the more optimistic RCP4.5, which includes a strong slow-down in the current CO_2 emissions' rate.

Data filtering and pre-analyses

Geographic distribution data was classified into three categories. We first removed duplicated data by randomly deleting all but one overlapping geographic data points. To account for data gaps on environmental parameters along the coastlines, we performed a spatial interpolation called "Inverse Distance Weighted (IDW)". The IDW technique computes an average value for unsampled locations using values from nearby weighted locations. The weights are proportional to the proximity of the sampled points to the unsampled location and can be specified by the IDW power coefficient (*idw()* function from the package "gstat" in R).

Exploring environmental drivers of upper bathymetrical limits

We subset the dataset to only include sites were the upper range limit of the population was known. Then, a set of linear models were fit to explore correlations with local environmental variables and upper range limits of both *C. rubrum* and *P. clavata*. Among the predictors, we included temperature and biogeochemical variables (phosphate, nitrate and primary productivity) at different depths (from 0 to 50m). Best fit models were selected using Akaike Information Criterion corrected for small sample sizes (AICc).

Modeling the relative probability of occurrence at different depth layers

A set of logistic generalized additive mixed effects models (GAMMs) were fitted to presence and absence data of *P. clavata* and *C. rubrum* populations at different depth layers from 5 to 55m deep (5-15m; 15-25m; 25-35m; 35-45m; 45-55m). These models included potential combinations of environmental predictors of both biotic and abiotic variables under current conditions (extracted from the ocean model during the period 1997 to 2012), topographic features and depth layer as fixed factor. In addition, site-specific coordinates were included in the models as a random effect in order to account for repeated measures within each site (non-independence of samples).

In a first exploratory analysis, we tested a set of potential environmental variables (temperature, nitrates, phosphates, primary productivity and topographic features) at driving the observed presences at each depth. To fit the models under present environmental conditions, we included the mean values of environmental predictors for the period from 1997 to 2012 at different temporal scales (annual mean, annual maximum, August maximum, September maximum). We also included topographic variables (slope, concavity, NS and EW aspect) extracted from MARSPEC (www.marspec.org) (Sbrocco & Barber 2013). Then, we kept only the most explanatory variables (annual mean temperature, August temperature, mean annual primary productivity, and slope) (Table S6).

We retained the best predictors (annual and august mean water temperatures and annual mean primary productivity) to fit GAMMs and predict the current and future occurrence of gorgonians at different depth layers. We performed 100 permutations as follows: first, to account for spatial autocorrelation we randomly selected only one data point for each cell in a pre-defined grid of 0.1º x 0.1º (Longitude / Latitude). Second, the dataset was further split into randomly selected 80% of data for model training and 20% for independent validations. Third, we fitted GAMMs using the training data and environmental variables under present conditions (see fitted GAMMs in Fig. 3), and we used these models to predict present and future probability of occurrence at each depth layer for 2100 according to two socio-economic scenarios (RCP4.5 and 8.5). Model outputs of the 100 permutations were averaged to obtain a single present and future suitability value for each site and depth. Finally, we used the remaining 20% of data for independent validations, comparing predicted occurrences at different depth layers to observed presences and absences (see schematic workflow in Fig. 1).

Classification of sites according their predicted trajectories of change

To summarizing the expected patterns of change across depths at each location, we ranked expected trajectories of change using a numerical index framework that indicates sign and strength of expected change across depths. Firstly, we categorized the present and future habitat suitability for each depth layer within locations in three levels: low (from 0% to 33%), medium (from 33% to 66%), or high (from 66% to 100%) (Fig. 4). Based on this classification, we then characterized the sign and strength of expected change from present to future conditions at each depth within sites. We rank suitability changes with numerical indexes from (-3) for large decreases to (+3) for large increases (Fig. 5). Briefly, sites that went from bad to good conditions received positive values from (+2 or +3); sites that went from good to bad conditions received negative values (-2 or -3), and sites that kept constant conditions received (+1) if they were good, (0) if they kept constantly medium, or (-1) if they showed constantly low probability of occurrence (see Fig. 5). Finally, a k-means cluster analysis was applied to the indexes of change for the 5 depth layers at all sites to identify the most common and informative patterns of change (Fig. 6).

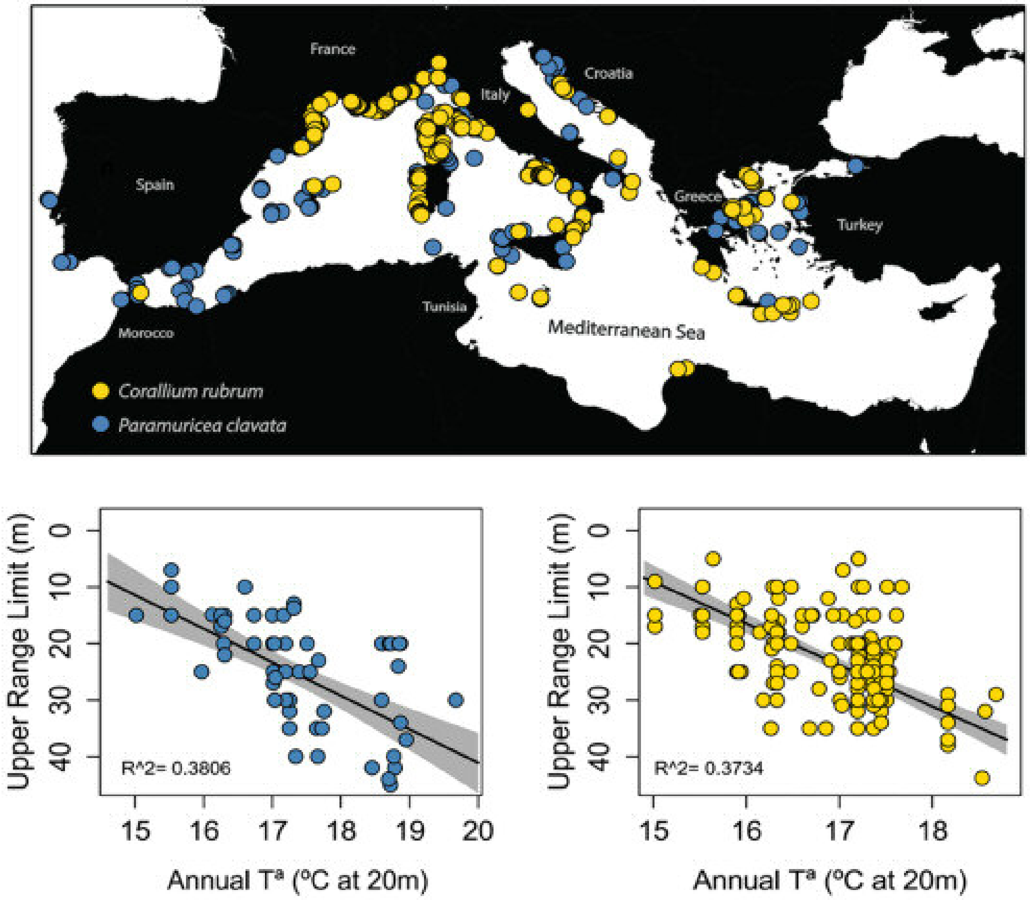


Figure 2. Study area and environmental drivers of the upper range dynamics for *P. clavata* and *C. rubrum*. (Top) Geographic distribution of *Paramuricea clavata* (blue) and *Corallium rubrum* (yellow). (Bottom) Relationship between upper range limits and local temperatures for *P. clavata* (left) and *C. rubrum* (right).

RESULTS

Current drivers of upper bathymetric limits

The red gorgonian *Paramuricea clavata* and precious red coral *Corallium rubrum* are extensively distributed across the entire Mediterranean Sea and adjacent Atlantic waters. More interestingly, upper range limit (i. e. shallowest occurrence) of both gorgonians were negatively correlated to local water temperature, showing a general pattern across the Mediterranean Sea, from frequent shallow presences in the generally cold-warm water NW Mediterranean Sea to deeper upper ranges in the warmer Eastern basin. A set of linear models including multiple potential environmental drivers (temperature and biogeochemical variables) revealed that mean annual temperature at 20m was the best predictor of the upper range limit for both *C. rubrum* and *P. clavata* (Fig. 2; Table 5). On the other hand, primary productivity also showed a significant positive correlation to upper range of both species (Table S5). Some exceptions were observed in the Western basin such as the warmer and more oligotrophic Balearic Islands, where gorgonian populations are only found from 35m or deeper waters. Overall, upper range limits of both species were strongly driven by local thermal regimes.

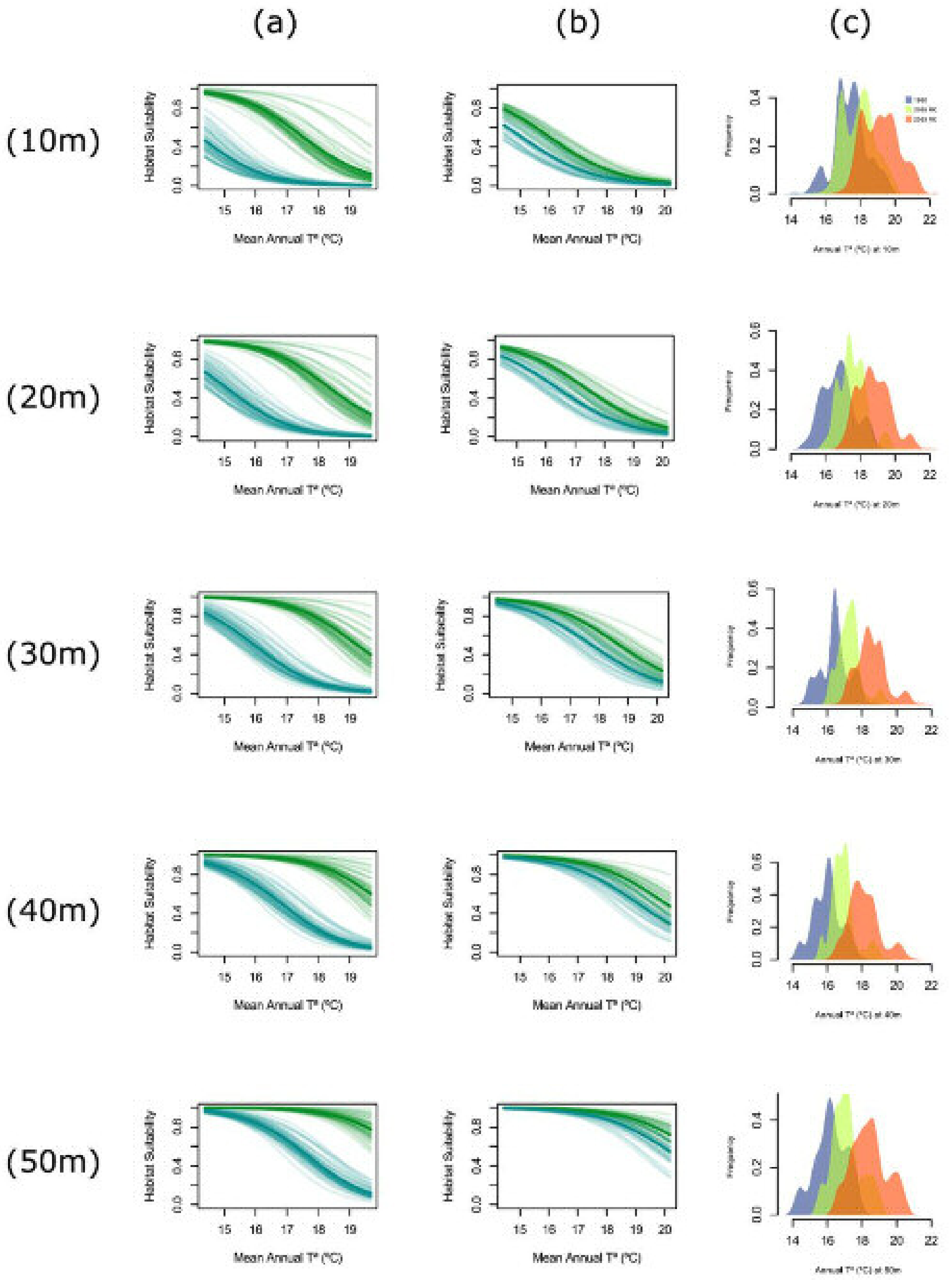


Figure 3. Logistic generalized additive mixed models (GAMMs) describing gorgonian's probability of occurrence at different depth layers depending on local mean annual temperature and primary productivity. Each row indicates a depth layer (from 5-15m, 15-25m; 25-35m; 35-45m; 45-55m). First and second columns show the modeled presence probability according to local temperature under high and low primary productivity conditions for *Corallium rubrum* (left) and *Paramuricea clavata* (center). The third column (right) show the density function of local temperature at the study sites under present conditions (blue), future optimistic RCP 4.5 scenario (green), and future business-as-usual RCP 8.5 scenario (red).

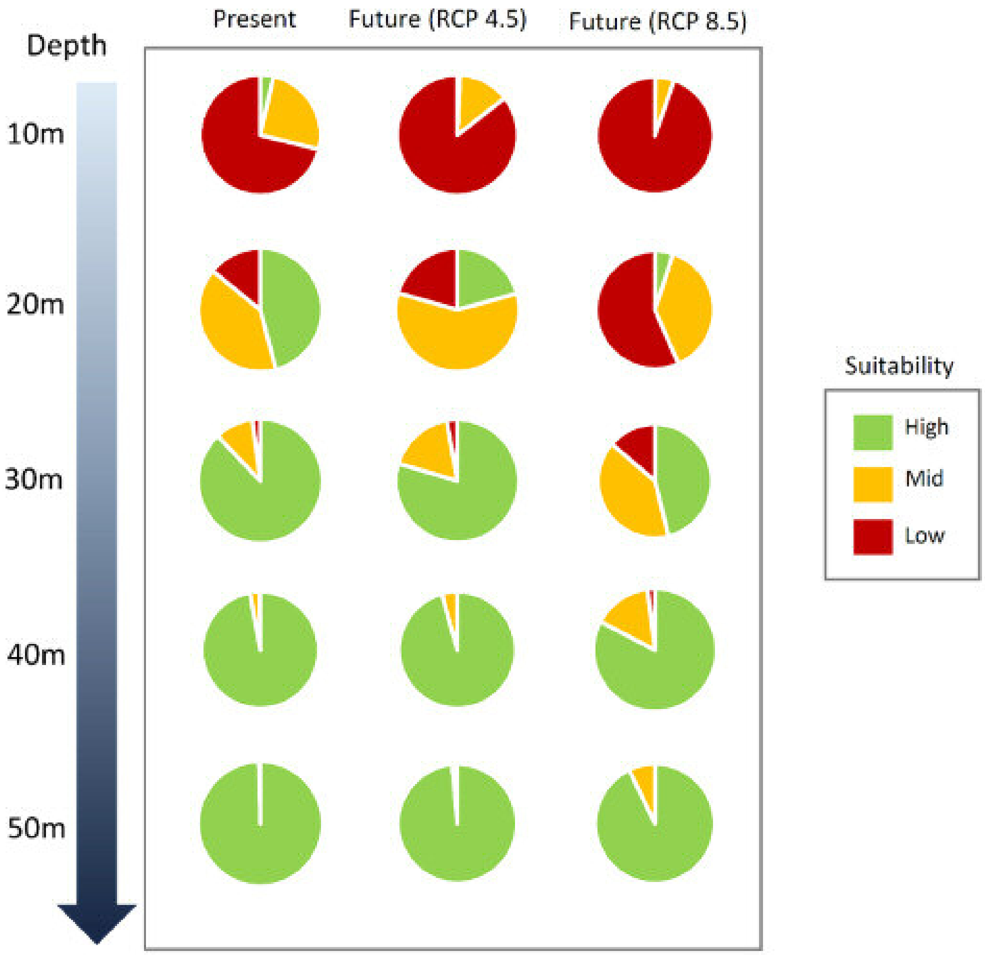


Figure 4. Present and future predicted probability of occurrence of gorgonians at the study sites across the Mediterranean Sea at different depths. Probability of occurrence was classified as low (from 0 to 33%), medium (from 33 to 66%), and high (from 66 to 100%).

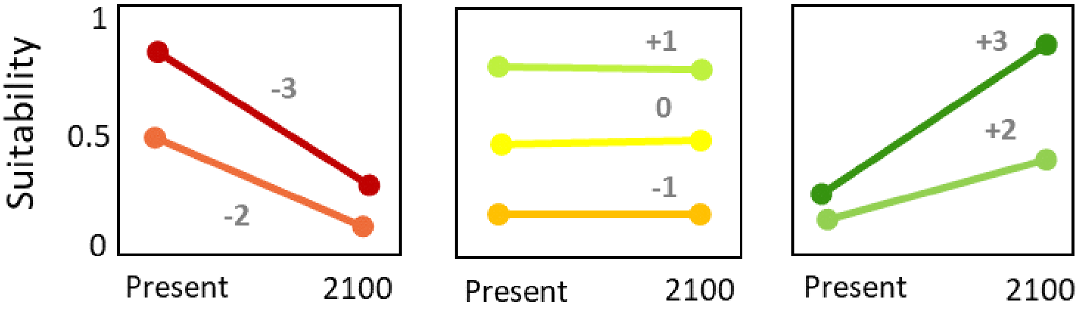


Figure 5. Potential trajectories of change according to present and future climate conditions. We classified each site and depth according to their expected rate of change. The first plot (left) shows positive trajectories; the second (center) show sites where no change is expected; the third plot (right) show sites that will experience negative changes (from good to medium or bad conditions).

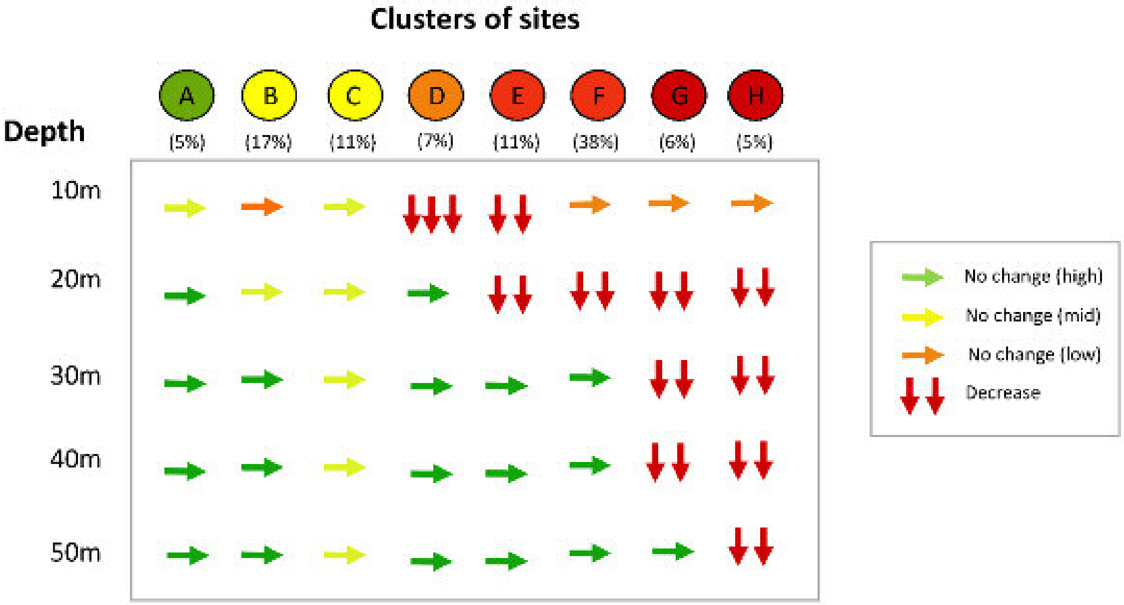


Figure 6. Patterns of expected warming impacts along a depth gradient. (A) K-means cluster analysis for sites according to their expected patterns of change across depth layers. Horizontal arrows indicate no change and down-pointing arrows indicate negative changes.

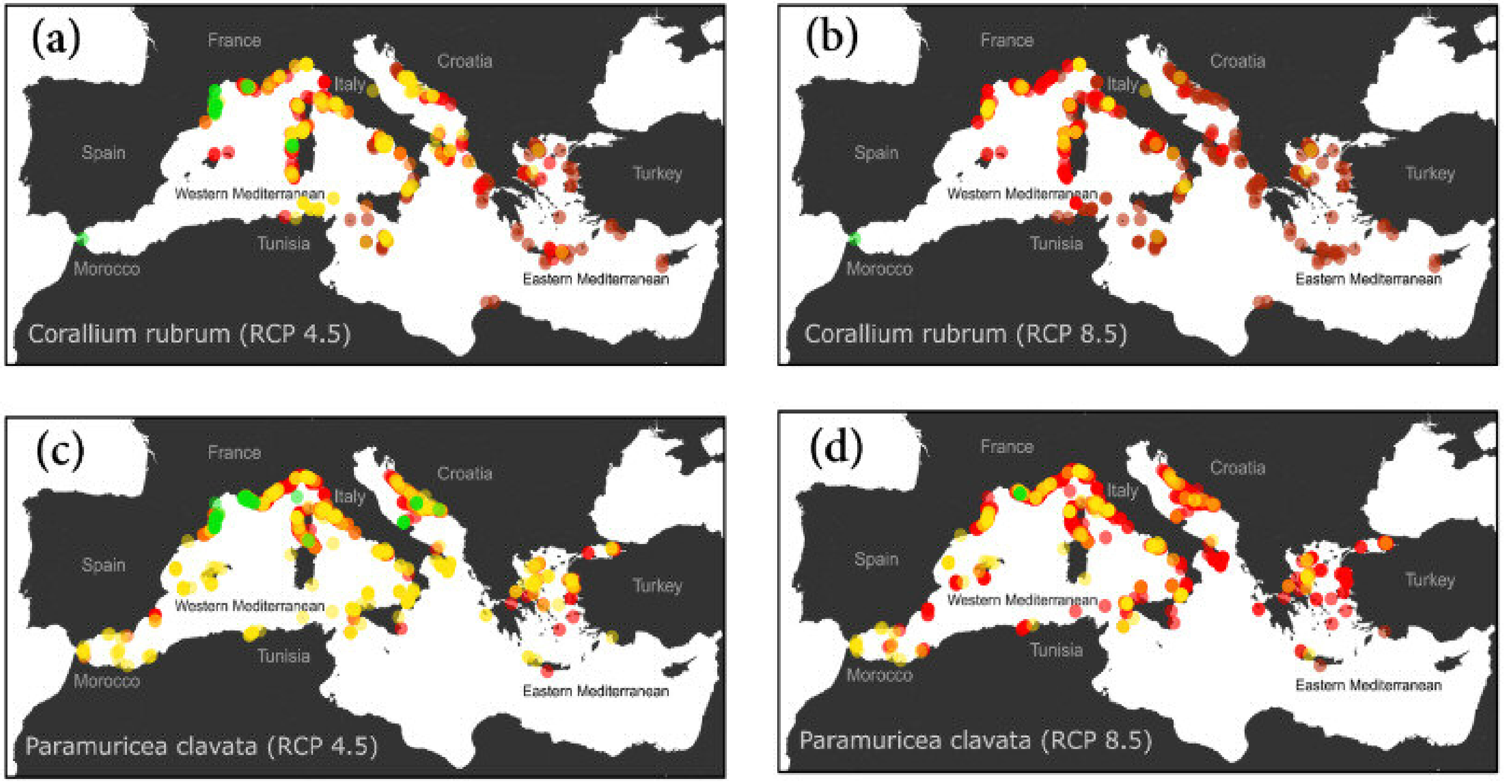


Figure 7. Geographic distribution of sites according to their expected patterns of change across depth layers. Colors correspond to clusters described in the top panel. Maps represent sites with known presence of *Corallium rubrum* (top) and *Paramuricea clavata* (bottom) under RCP4.5 (left) and RCP8.5 (right) emissions scenarios.

Projected impacts of climate change

Predictions for the end of the 21st century revealed extensive negative changes in probability of occurrence across the Mediterranean Sea. Overall, the frequency and intensity of changes appears strongly dependent on the CO_2 emission scenario and depth. Under the "business as usual" emission scenario (RCP8.5), almost all high suitability sites disappeared at shallow waters. Although less extensive, warming will cause impacts at deeper waters. We also observe broad regional differences: the proportion of sites that are predicted to become unsuitable at the end of the century was lower at deeper depths in the Western basin, but extensive in the Eastern Mediterranean Sea.

When looking at trajectories of change across sites, we found different patterns of change across depths (Fig. 6). Overall 33% of sites are expected to keep similar thermal conditions. From these, relatively few will keep high thermal suitability (Cluster A), and the frequency of these sites sharply decreases depending of emissions scenario (from 149 sites in RCP4.5 to only 5 sites in RCP8.5). Some sites that had already low suitability in shallow waters (up to 25m) under present conditions will kept consistent in the future (Cluster B and C). Other clusters included sites that experienced negative impacts of warming but differed among them on the bathymetrical extend of the expected impacts. Sites included in clusters D were strongly impacted only in very shallow waters (up to 15m). Clusters E and F included sites in which shallow waters were already non-suitable under present conditions but will experience further decreases in thermal suitability in deeper habitats up to 35m. Finally, clusters G and H are expected to experience the deepest impacts of climate change, including sites that had bad conditions at shallow waters under the present climate and will experience further negative changes in the thermal suitability up to 55m (Fig. 6 & Table S7).

When looking at the spatial arrangement of these clusters, we observe a gradient from frequent deep impacts at the Eastern Mediterranean Sea and heterogeneous patterns of warming impacts in the Western Mediterranean. There, future predictions reveal widespread decreases in habitat suitability due to warming, but these impacts will strongly depend on depth, basin (Western vs. Eastern), and IPCC emissions scenario. In the warmer Eastern Mediterranean basin, climatic impacts will generally reach deeper areas, while in the Western Mediterranean we expect highly heterogeneous patterns of changes across space and depth. Some areas that may experience negative changes at shallow depths, other will be affected up to 45m and 55m. On the other hand, there will be few climatic refugees, defined here by sites predicted to preserve high suitability at all depths. These sites are mainly found along in the NW Mediterranean along the coastline of Catalonia and France, in proximity of the generally cold-water masses of Gulf of Lions.

DISCUSSION

Understanding and predicting how warming impacts will spread across horizontal and vertical distributions of marine species is a major challenge in conservation yet partially unsolved. Here, using a novel three-dimension ocean model and extensive vertical distribution data of two dominant habitat-forming gorgonians across the Mediterranean Sea, we demonstrate a crucial role of considering depth when predicting future impacts of climate change in coastal marine ecosystems.

Current drivers of upper bathymetric limits

Our results demonstrate that upper bathymetric limits of *Paramuricea clavata* and *Corallium rubrum* are shaped by local environment across the Mediterranean Sea (Fig. 2). Upper edges were negatively correlated to local temperature and positively to primary productivity over broad spatial scales (Table S5). Previous physiological microcosm experiments provide mechanistic support of these results by showing that warm temperatures combined to shortages in food supply can be detrimental for the survival of both *P. clavata* and *C. rubrum* under controlled conditions (Torrents *et al.* 2005, Coma et al. 2009, Crisci et al. 2017). Therefore, populations may be strongly limited by warm and nutrient-depleted waters that remain stratified above the thermocline at the end of summer periods (Bensoussan et al. 2014). Indeed, several field studies have linked water temperatures above approximately 24-25ºC for a several days with catastrophic mass mortality events on both gorgonians up to certain depths (Cerrano et al. 2000, Garrabou et al. 2001, 2009; Linares et al. 2014). Despite having less explanatory power in our models, primary productivity was also positively correlated to the presence of shallow occurring populations (Table S5). Besides the role in food supply for the survival of these suspension feeders, primary productivity also controls light penetration across depth gradients, and this plays a key role in competition for substrate between benthic macroalgae and suspension feeders in Mediterranean rocky reefs (Zabala & Ballesteros 1989, Ballesteros 2006). Contrarily to what is generally observed in tropical coral reefs, temperate gorgonians commonly inhabit semi-dark habitats and their presence is enhanced when light availability is low due to higher primary productivity that reduces light penetration and allows outcompete macroalgae species that otherwise dominate benthic communities. Both parameters clearly play a role on the distribution of the bathymetrical dynamics of our model species. However, disentangling their relative contribution is challenging because of their high correlation across large spatial scales and will require further investigation through finer-scale analyses and manipulative experiments. Overall, these results provide new insights into environmental controls of the bathymetrical dynamics for two dominant habitat-forming species in temperate reefs with important implications for our general understanding of potential effects of rapid environmental changes.

Predicting potential deepening of gorgonian populations

In this study, we used a novel predictive framework to forecast how changing temperatures and primary productivity patterns will impact Mediterranean gorgonian populations across depth gradients. Our models predict extensive impacts of 21^{st} climate change that will strongly depend on emissions' scenario and depth. Under RCP8.5, most gorgonian populations are likely to experience shallow extinctions and bathymetrical range contractions (deepening of populations) (Fig. 4 & 7). The deepening of *P. clavata* population from 30 to 45m has been documented after recent warming events, suggesting that our predictions of potential extinction of shallow ranges may be already occurring (Linares et al. 2014). In addition, our predictions agree with more general observations on decreasing warming-driven mortality with depth in Mediterranean gorgonians as well as in tropical reef corals (Garrabou et al. 2001, Mumby et al. 2001, Bridge et al. 2013, Muir et al. 2017). A general deepening of shallow occurring gorgonians would be catastrophic for benthic ecosystems and coastal societies in the Mediterranean Sea. On one hand, gorgonians enhance biodiversity (Ponti et al 2014) and, although not yet fully understood, may provide thermal buffering effects to other benthic species (Jurgens & Gaylord 2018). But also, in cases in which shallow-water gorgonian forests deepen their distribution beyond the recreational scuba diving limits (~40m), small local economies dependent on tourism can be negatively affected. Scuba diving and related tourism activities represent a growing economic sector in the Mediterranean Sea and worldwide and have a key role in marine conservation by promoting the enthusiasm and support of great part of coastal societies that benefit either directly or indirectly from tourism (Badalamenti et al. 2000, Sorice et al. 2007).

Climatic refugees and complex depth-mediated impacts of warming

Identifying warming hotspots and potential climatic refugees is a challenging endeavor but essential to incorporate the global change dimension into spatial conservation planning. Here, we provide strong evidences that warming can differentially impact marine biodiversity at different depths, and these potential depth-mediated impacts should be considered when adapting the configuration of MPA networks to a warming ocean. There have been recent calls to include depth-related biodiversity gradients into large-scale spatial priorizations (Levin et al. 2017, Venegas-Li et al. 2018). While ecologists often use surface temperatures for predicting the negative consequences of future climate change, our results call for a carefully reconsideration of the vertical dynamics of habitat-forming species as well as the importance of three-dimension patterns of warming, since they may not be homogenous across large geographical areas (Levin et al. 2017). This shifting paradigm is essential anticipation of these complex patterns of warming will have major implications for the conservation of mesophotic reefs and may lead some important socio-economic negative consequences for coastal areas that depend upon the tourism industry.

Finally, major differences in extend and severity of warming impacts were predicted depending on the CO_2 emission scenario (Fig. 4 and 7). For instance, the observed climatic refugees in the NW Mediterranean Sea became drastically reduced under RCP8.5. these results highlight the importance of global political actions to drastically reduce emissions to ensure the conservation of benthic marine ecosystems. While the role of local actions to increase the resilience of marine communities to global change is still unclear, our results clear demonstrate a strong role of global emissions trends on the conservation of Mediterranean gorgonian forests.

Limitations

This study represents a crucial step forward in the way we conceive predictions of climate change impacts for coastal marine ecosystems. However, there still are important limitations of our modeling framework that must be acknowledged. First, we believe that the spatial resolution of the model (5 arc-minutes), despite being much finer than most of the environmental data currently used in predictive spatial models (Nadeu et al. 2017), is still too coarse to accurately reproduce the micro-climatic conditions experienced by individual gorgonian corals. Finer-scale predictive models validated and corrected by local temperature records are needed to improve our predictive capacity. Indeed, the best fitted GAMMs for both species included annual mean temperatures. While annual averages are suitable for representing broad trends and highly correlate to frequency and severity of marine heat waves (Oliver et al. 2018), they could underestimate short-term high intense warming events. On the other hand, envelope models are a powerful tool to understand and project realized niches from a holistic perspective, but they fail to link environmental drivers to demographic mechanisms and interspecific interactions that drive the distributions of marine organisms, and this can potentially lead to misleading correlations between environmental predictors and the presence of the species (Fordham et al. 2018). These limitations can be addressed by a deep understanding of the species biology and natural history and a critical evaluation of environmental predictors used and their relationship to geographic data. Coupling correlative approaches to mechanistic modeling frameworks that can explicitly link patterns to underlying processes would also aid improving model accuracy. For instance, hybrid models combining envelop models and thermal physiological thresholds from controlled experiments would represent a step forward to obtain more robust estimates and increase our predictive capacity of marine benthic dynamics in a changing world (Talluto et al. 2016). Despite these limitations, our models showed a relatively high predictive capacity in validations against independent. Overall, the projections presented here are unique in three aspects: (I) they have higher spatial resolution of the climate projections (5 arc min is a 20 times higher spatial resolution than most of previous works that commonly use 1x1º (van Hooidonk et al. 2013, Couce et al. 2013). (II) The inclusion of the third dimension, which is inherent to marine ecosystems, provides a much more accurate and detailed picture of the ongoing and future warming-driven impacts to marine biota, and this is relevant to most coastal marine ecosystems. (III) A novel use of multiple abiotic and biotic environmental variables, including primary productivity, which is very relevant for heterotrophic octocorals, and may play a crucial role in predictions of future global change scenarios for other dominant habitat-forming species such as seagrass meadows or kelp forests.

Conclusions

Our study predicts large-scale negative impacts of climate change and challenge current modeling approaches based on surface temperature data by revealing complex patterns of differential warming impacts depending on depth. These results should have important implications for the design of adaptive management strategies in the Mediterranean Sea. The dramatic change in the expected impacts depending on different socio-economic scenarios highlights the importance of global political decisions on the conservation of Mediterranean gorgonian populations and hence, all the associated biodiversity. Finally, this study provides a novel approximation to better understand the consequences of warming along depth gradients with potential applications to other costal marine ecosystems worldwide.

AKNOWLEDGEMENTS

We thank the citizen science programs Reef Check Italy, SeaWatchers, and CIGESEMED for providing valuable geographic data. Comments by YM Bozek, JC Ortiz, N. Kruek, and K. Kaplan helped improving this manuscript. Funding was provided by the European Commission (MERCES), the Prince Alberto II Foundation (MIMOSA) and the Spanish Minister of Innovation (SMART).

General discussion

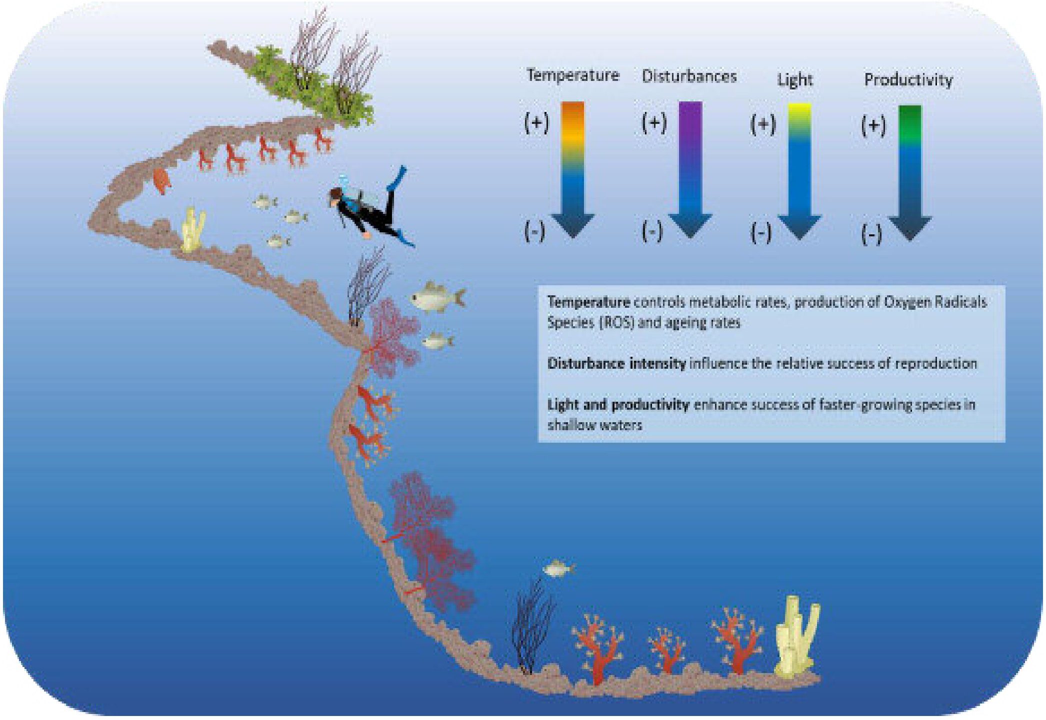
A current challenge for policymakers, managers and society is to counterbalance multiple threats to marine ecosystems and ensure the preservation of biodiversity and ecosystem functions for next generations. Habitat-forming species play a crucial role in benthic communities; unfortunately, they are experiencing large declines all over the world. Understanding how multiple stressors impair their resilience requires field monitoring efforts over large temporal and spatial scales, but gathering long-term data in marine ecosystems is challenging and often needs to involve large collaborative networks of scientists that can persist beyond the typical short time windows of most PhDs and funded research projects. Consequently, we generally lack high quality field data on benthic species at relevant scales, and this can hinder decision-making and the implementation of effective management strategies. This is especially valid for the management of long-lived species, such as our model species, where the scale of the studies is far to be representative of their long lifespans. In the present thesis, we benefit from unique long-term demographic and geographic distribution datasets which we combined with innovative approaches using quantitative tools, principles of life-history theory, and meta-analyses to advance in the field of marine conservation in a context of rapid environmental change.

Through this thesis, we used the red coral, *Corallium rubrum,* as a study case to explore resilience patterns and drivers for long-lived octocorals, with the final goal of guiding conservation strategies for Mediterranean benthic habitats. We documented the dramatic impacts of fishing and climate change on different demographic processes and predicted their long-term consequences, estimated periods required to recover functional complexity of coral populations, and revealed potential benefits as well as limitations of local conservation tools such as marine protected areas (MPAs) and active restorations actions. More generally, I provided novel applications of population and spatial modeling for conservation and climate change research and used meta-analyses to go beyond the model species to show general drivers and consequences of high longevity in marine benthic ecosystems.

Life-history theory: from evolutionary ecology to conservation

Life-history evolution

The role of the environment in shaping the evolution of life histories is a long-standing question in ecology and evolution that remains partially unresolved. In Chapter 1, we explored longevity patterns of marine habitat-forming species, asking how predictable longevity is across depths and whether there are consistent consequences of individual longevity for population dynamics. We found strong positive relationships between depth and maximum lifespan across multiple sessile marine taxa, including corals, bivalves, sponges and macroalgae. Depth-related environmental gradients may exert an external forcing to the evolution of sessile life histories, which lead to highly predictable general distribution patterns. These findings have implications for our general understanding on drivers of life-history evolution in the marine realm but also provide some important insights into potential vulnerability of less known deep-sea benthic communities.



Temperature controls metabolic rates, production of Oxygen Radicals Species (ROS) and ageing rates

Disturbance intensity influence the relative success of reproduction

Light and productivity enhance success of faster-growing species in shallow waters

Figure 1. Conceptual diagram showing environmental drivers generally shaped by depth that may play a role in the dominance of long-lived species in deeper benthic habitats.

On one hand, our results suggest that local environmental variables that generally decrease along depth gradients - including temperature (both mean and variance), light penetration, physical disturbances (i. e. storms) and primary productivity - shapes evolutionary success of sessile species (Fig.1). Among several metrics commonly used in comparative demography, longevity is one of the most powerful descriptors of life-history strategies: it positively correlates to survival and negatively to growth and reproductive rates (Salguero-Gomez et al. 2016, Fig. 2). A successful life-history strategy of long-lived species inhabiting deeper benthic habitats (which tend to be colder, less exposed to physical disturbances, and less productive) may thus be based on a disproportional allocation of

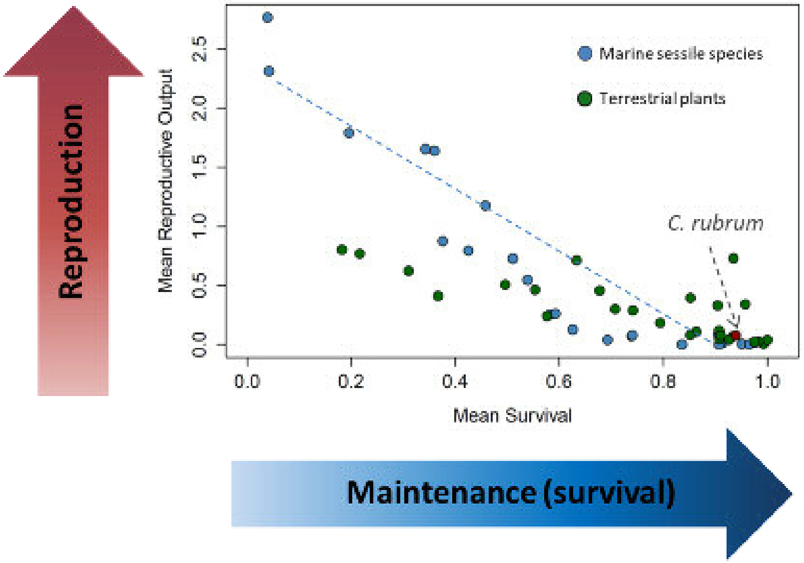


Figure 2. Life-history tradeoff between mean survival over an individual lifetime and mean reproductive output. Data were computed using matrix models from published demographic studies of a range of marine sessile species and terrestrial plants (see Table S10 in Chapter 1).

resources to physiological maintenance of cells and tissues, favoring individual survival over growth or reproduction. It is important to consider some important limitations of our global but basic comparison. Firstly, we used maximum depth occurrence as a metric to assess the overall bathymetrical range of the species, but it could be inaccurate for some species, especially for those dwelling in deep sea habitats. Secondly, intra-specific longevities can vary across latitudes as well as depth ranges. For instance, Pratched et al. (2015) showed that reef building corals grow slower at deeper sites, but he also found strong correlations between coral growth and latitude. Thirdly, some notable exceptions must to be noted to this general pattern of longevity and depth and they may provide interesting questions for further consideration. For instance, some highly longevous organisms such as seagrasses (p. e. *Posidonia oceanica*), inhabit shallow waters. Disproportionally large body-sizes and a great capacity to modify local habitats may aid these organisms to scape environmental pressures that generally favor short-lived species.

Finally, while this study represents an important step forward in comparative demography, our correlative approach does not allow for a mechanistic understanding of the observed patterns nor assessing the relative role and potential interactive effects of different environmental features at enhancing longevity of benthic species. These important questions should be addressed in detail by conducting finer-scale comparative studies or manipulative experiments that allow separating the effects of the different potential drivers.

Life-history theory and conservation

In Chapter 1, we also demonstrate that high longevity drives high demographic stability across a range of marine sessile species and terrestrial plants. The underlying mechanism of this pattern is likely to be the general tradeoff between survival (which positive correlates to longevity) and reproductive success (Fig. 2).

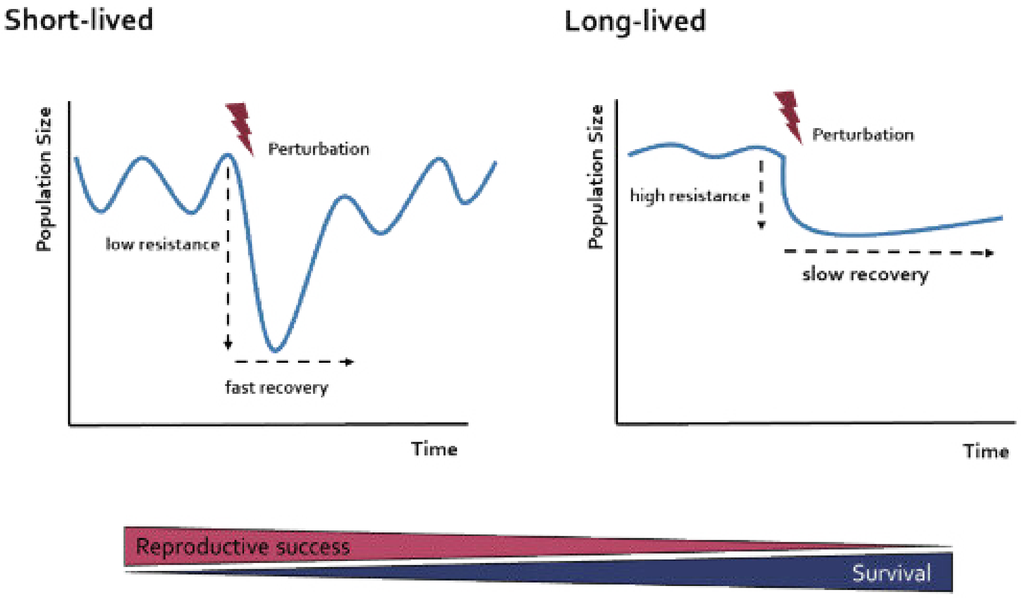


Figure 3. Conceptual model showing potential effects of life-history tradeoffs in two components of resilience at the population-level: resistance and recovery.

Life-history tradeoffs can play an important role underpinning resilience of populations and communities to recurrent high intensity disturbances. Resilience is a popular concept in natural and social sciences defined as the capacity of a system to withstand recurrent disturbances by resisting (avoiding change) or recovering (Côté & Darling 2010, Bernhardt & Leslie 2013, Darling & Cotte 2018). Theoretically, longer-lived species should show higher resistance to external perturbations and lower recovery capability due to a more limited reproductive success compared to shorter-lived species (Fig. 3). Our comparative analysis revealed low temporal demographic variability and low reproductive success in long-lived species, suggesting a relatively high resistance but low recovery potential due to limited recruitment. Overall, long-lived sessile species will tend to be low resilient to any external perturbation that causes high mortality events. However, resilience includes ecological processes at different levels of biological organization, from populations and communities to ecosystems. In the present thesis, we narrowed this definition and focused on population-level resilience for long-lived species with highly restricted dispersal, in which recovery depends on local reproductive success (also called self-recruitment). For systems with higher dispersal potential, connectivity patterns and potential rescue effects will be crucial processes to consider when exploring resilience (Mumby & Hasting 2008).

From an applied perspective, our results predict a high vulnerability of long-lived species, which tend to be dominant in deep benthic communities, to external stressors that increase mortality such as direct and indirect human impacts of bottom fishing, deep-sea mining, oil spills, etc. (Van Dover et al. 2017, Danovaro et al. 2017). A recent study exploring recovery of deep-sea gorgonians after the Oil Spill of the Gulf of Mexico, supports these conclusions by showing that long-lived gorgonians are highly vulnerable and their recovery can take hundreds of years (Girard et al. 2018). Their vulnerability arises from a naturally low resilience of these demographic stable communities. Therefore, evaluations of potential impacts of human activities that can damage deep-sea habitats should always include the precautionary principle, even in cases in which the affected benthic communities are not fully known (Danovaro et al. 2017).

On the other hand, in Chapter 4, we revealed that the tradeoffs among vital rates predicted by life-history theory are reflected in ecological restoration actions for habitat-forming species. A global meta-analysis demonstrated that slow-growing species tend to show higher survival after transplantation compared to fast-growing species. Thus, targeting faster-growing species may take larger transplantation efforts due to higher mortality of the manipulated individuals. On the other hand, using population models, we showed that long-lived species with higher survival rates after transplantation may need much longer recovery periods to form fully functional populations. These results highlight the crucial role of life-history tradeoffs on the response of benthic species to transplantation and have implications for better designing and enhancing the overall effectiveness of ecological restoration efforts for marine benthic communities.

These examples add compiling evidence supporting the important role of life-history classifications to understand and predict the response of benthic communities to multiple stressors and conservation actions (Darling et al. 2012).

Quantitative tools in marine conservation: opportunities and limitations

Through the work presented in this thesis, we combined life-history classifications and quantitative tools to address conservation issues: anticipating expected recovery times (see Chapter 1) and the overall timescales that can be expected after restoration actions for species with contrasted life-histories (Chapter 4), or exploring potential impacts of fishing and climate change at different temporal and spatial scales. Novel applications of quantitative tools such as integral projection models (IPMs) and general additive mixed models (GAMMs, for spatial analyses) have been successfully applied yielding new insights into the conservation of Mediterranean gorgonians such as assessing the role of MPAs and climate change in shaping population dynamics or predicting geographic and bathymetrical patterns of future climate change impacts. However, there are several limitations that must be considered when using modeling tools. In Table 1, we highlighted relevant benefits as well as limitations of the quantitative tools included in the present thesis: population models, spatial models and meta-analyses. One of the most important aspects to consider when using quantitative tools is the inherent tradeoff that exists between model complexity and transferability (Johnson & Lidström 2018). Under some circumstances, basic models can represent a powerful tool to find generalities for a broad range of systems and provide important advances for the field. Simple models and processes can also be easier to communicate to a broader audience of non-specialists, including policymakers and society. However, it is essential to recognize that simplifying study systems comes to a cost of ignoring ecological complexity that exist in the real world. Indeed, in some cases, avoiding complexity could prevent to unravel the underlying drivers of observed patterns. For instance, in this dissertation, we used data from eight populations over relatively long-term periods to explore general drivers and resilience patterns for the red coral as a species. We tried to find broad generalities that can inform large-scale conservation initiatives, but it is important to keep in mind that these findings are somehow a simplification of real dynamics. The red coral is widely distributed along the Mediterranean Sea and living from shallow to deep habitats, likely to experience slightly different environmental conditions than the populations studied here. In addition, our longest demographic dataset comprises 13 years of individual-level data. Although only rarely we find temporal scales in current marine ecological studies, it represents a tiny time window for a long-lived species such as the red coral that can live several hundreds of years. This means that, while the present work represents an important advance into sound principles for the conservation of this species, we must be cautious and recognize that there still some knowledge gaps and processes that may vary between and even within red coral populations. For instance, the responses to global warming can be shaped by adaptive processes that occur at the population-level (Ledoux et al. 2015) and may result in different sensitivity levels across geographic scales and depths (Torrents et al. 2005). Expanding demographic studies to cover broader spatial scales, including deeper habitats, is crucial to assess conservation status and trends of the red coral and over its entire bathymetric range. Importantly, according to our findings, deeper dwelling red coral populations may be even more vulnerable to external stressors. The fast development of Remotely Operated Underwater Vehicles (ROVs) provides new opportunities to investigate deeper habitats (Rossi et al. 2008). Unfortunately, using these technologies is still very expensive and they rarely allow gathering high-quality individual-level demographic data (but see Girard et al. 2018 for an illustrative example of a fine demographic analysis on gorgonian populations dwelling at more than 1000m depth). Account for indirect or delayed effects of warming using more complex models is another aspect that should be addressed to advance our predictive capacity in the context of global change. For instance, when analyzing the recurrent impacts of climate change on coral populations, for simplicity, ecologists often consider only immediate whole-colony mortality rates due to acute thermal stress, ignoring any potential delayed effect of these events. However, in the case of the red coral, we observed that warming also leads to increased mortality probability of affected colonies some years after the event. Thus, more accurate demographic analysis should model not only the immediate mortality due to warming but also any potential delayed effect on mortality of colonies that were partially affected. Increased complexity in demographic models may allow addressing novel questions but it can also make studies overly data-demanding or hinder their general transferability. Balancing these two aspects is a critical decision that must be thoughtfully taken considering all potential implications (logistics and data availability, temporal and spatial variance in measured traits and specific ecological questions).

Table 1. Benefits and limitations of quantitative tools used in the present thesis.

Quantitative Tool	Benefits	Limitations
Population Models	Projections beyond the temporal scales covered by the field period to unravel subtle trends and to estimate extinction risk. Quantify relative contribution of each vital rate to the population growth, which informs about evolutionary drivers and conservation priorities. Explore responses of populations under different management scenarios and hypothetical changes in exposure to stressors. Estimate recovery periods after management interventions such as MPAs designation, fishing closures or restoration actions. Integrate field data into a standardized model that allows deriving life-history descriptors and systematic demographic comparisons.	Assume that field data is representative of current temporal and spatial variability. This is challenging for long-lived species. Assumes environmental conditions to remain constant in the future. Unlike under the present context of climate change. Ignores potential inter- and intra-population variability in life-history traits and vulnerability Accurately quantifying key processes such as larvae production, settlement and recruitment is challenging in marine ecosystems. In high dispersal species, modeling recruitment is more challenging and may require increased complexity and more assumptions.
Spatial Models	Explore species distribution ranges and realized niches. Identify environmental parameters that control species distribution boundaries. Forecast current and future habitat suitability according to different climatic scenarios.	Lack of fine-scale topographic and climatic data that can accurately reproduce micro-habitat features experienced by individuals. Potential biases in data collection and lack of systematic surveys. Correlative approaches may not capture real drivers such as interspecific interactions.
Meta-analyses	Compare species-specific responses of species with divergent life-histories to management interventions to find generalities and advance in our predictive power. Describe life-history changes along ecological gradients to infer potential evolutionary drivers. Assess global patterns in conservation issues.	Data quality can be variable and difficult to assess. Potential biases in reporting results can lead to misleading conclusions. Phylogenies and non-independent sampling issues when comparing species.

Box 1 Global perspectives on MPAs and habitat-forming species

In this thesis, I assessed the role of local protection and climate change for an emblematic and overexploited coral in the Mediterranean Sea. MPAs can be effective at enhancing the functionality of red coral populations but our models suggest a limited role in buffering climatic impacts. Nonetheless, from a broader perspective, some crucial questions remain unresolved. Can we anticipate when and how MPAs will be most effective at protecting benthic habitats and enhancing their resilience to climate change? This crucial topic for marine conservation still generates intense debates in peer-reviewed journals, scientific conferences, and even in social media. In an exercise to synthetize current scientific evidences of MPA effects on habitat-forming marine species, I did a systematic review on Web of Knowledge using the keywords ("Marine Protected Areas" or "Marine Reserves" or "Local Protection" and "Corals" or "Benthic" or "Gorgonians" or Macroalgae" or "Seagrass") and a deep search on GoogleScholar selecting the first 100 references. I found 78 relevant studies and classified them according to their observed effects (positive, null or negative) on different ecological parameters (benthic cover, density, size-structure, and species richness) to assess conservation status of habitat-forming species.

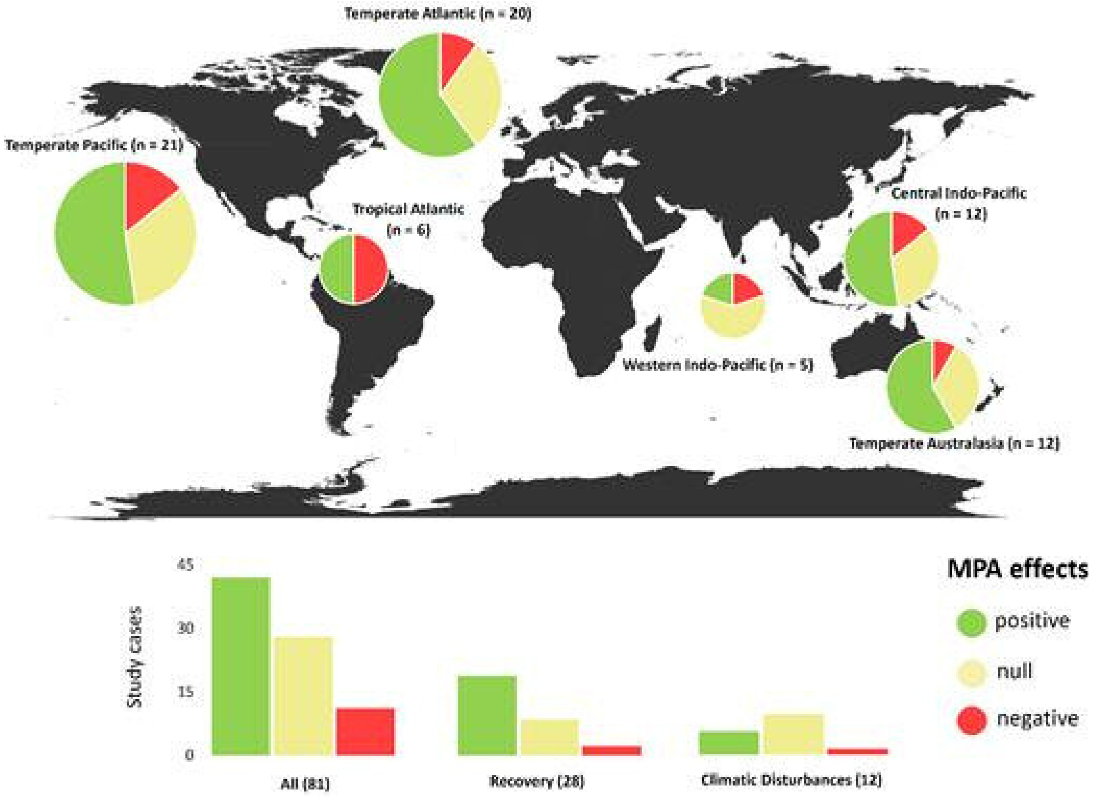


Figure 4. Global empirical evidences of marine protected areas effects on habitat-forming benthic species. A. Effects represented by global ecoregion according to classification by Spalding et al. (2007). B – D Show proportion of positive, null and negative effects in: all cases (B), only studies that look at recovery patterns (C), and only studies that assessed responses to climatic perturbations (D).

Overall, in approximately half of the relevant studies, MPAs provided positive effects on benthic communities, and these broad patterns were consistent across different ecoregions (Fig. 4). Interestingly, when looking only at studies that assessed recovery processes, the proportion of positive effects becomes much higher. In contrast, when looking at studies that have assessed responses to climatic perturbations, positive effects are less frequent (Fig. 4). This shows that MPAs will not always benefit habitat-forming species and suggest that benthic community responses to local protection can be much more complex than what it is often assumed. They are likely to depend on the species-specific processes that are affected by local protection and complex inter-specific interactions (Fig. 5). For instance, while evidences for enhanced resistance in protected sites against climatic perturbations appears not well supported (Hughes et al. 2017a); a key process in ecosystem resilience such as recovery seems much more sensitive to MPA implementation (Mumby et al. 2007, Micheli et al. 2010). For this reason, when studying effectiveness of MPAs for habitat-forming species, we need to clearly define priory expectations and metrics of conservation success, linking them to specific ecological process that can be affected by protection. Although this is a basic preliminary exploration that will require finer analyses to account for potential confounding factors, it provides a novel overview of a highly relevant topic and opens new questions on the overall role of local protection at enhancing different processes involved in benthic ecosystems resilience.

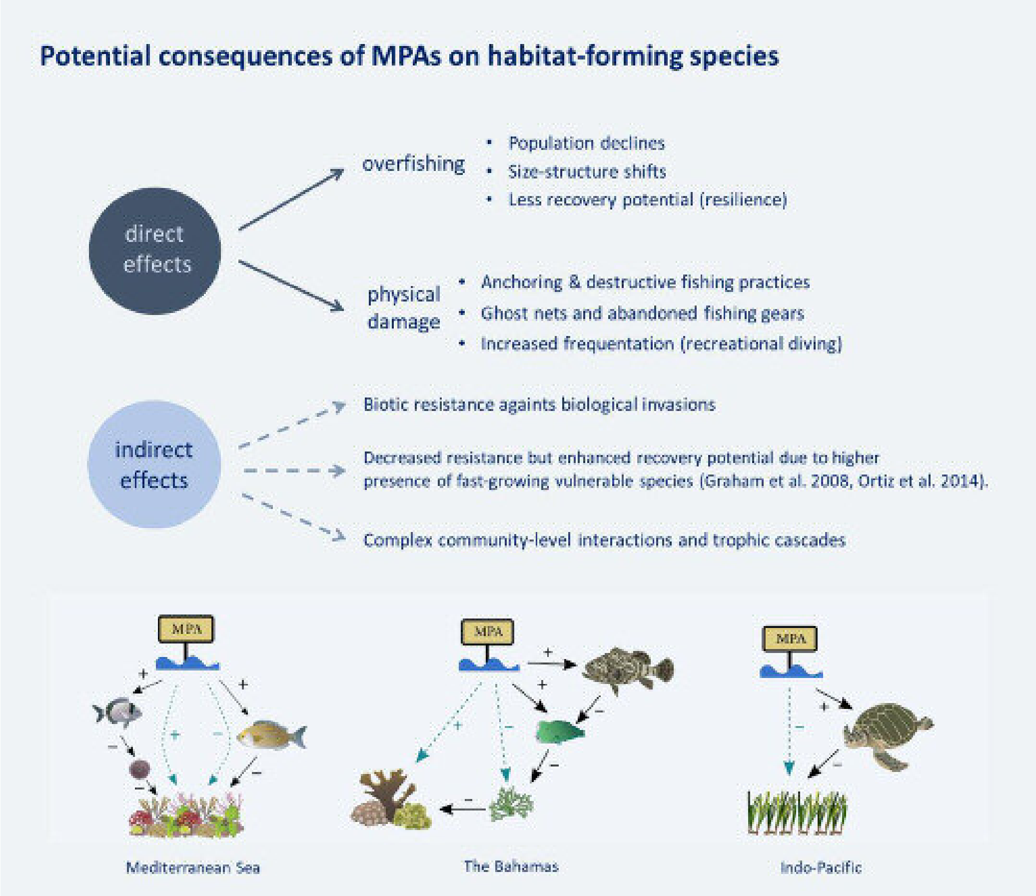


Figure 5. Processes involved in potential direct and indirect effects of marine protected areas (MPAs) on habitat-forming species.

Study case: Resilience of Mediterranean red coral populations to fishing and climate change

Precious corals are found in several seas across the world and have been collected for thousands of years for use as jewelry, homeopathic medicines, and cultural artifacts. They are vulnerable to depletion because of their slow life history, small and patchy populations, and have been subjected to “boom and bust” fishing strategies with a variety of fishing gears (Bruckner 2016). Today, there is a growing concern on their conservation due to historical unsustainable fisheries and novel threats associated global change (Bruckner 2013; Garrabou et al. 2009). In the Mediterranean, the red coral *Corallium rubrum* has been recently enlisted as Endangered in the Mediterranean Red List of the International Union for the Conservation of Nature (IUCN), and several European countries are increasing their commitment and efforts to ensure the persistence of this charismatic species (Otero et al. 2017; Cau et al. 2013). In Chapter 2, we explored the short and long-term consequences of fishing based on data in two affected populations on the coast of Marseille (France). Our results reveal dramatic reductions of coral biomass and minimal recovery after 7yrs. We then predicted that full recovery would take several decades. Interestingly, we unraveled an important recovery mechanism for this species: when fishers remove coral branches but leave the colony basis attached to the substratum, most colonies can survive and regrow new branches through asexual reproduction. This recovery mechanism had not been quantified before and may explain the paradoxal persistence of this extremely slow-growing species that has been intensive overexploited since ancient times. These results highlight that not only minimum colony-size or harvesting quotes are important to enhance the sustainability of red coral fisheries, but also regulating fishing methods can aid enhancing population recovery. We must also note that, although in our studied populations open to fishing we observed relatively low impact practices, highly destructive fishing gears are still used in Mediterranean waters (Cattaneo-Vietti et al. 2017), and historical records and local ecological knowledge clearly indicate that several red coral populations have gone locally extinct due to overfishing or remain functionally impaired (Garrabou et al. 2017b, Linares et al. 2017).

Based on the findings presented here and evidences from several scientists across the Mediterranean (Garrabou et al. 2017b), minimum requirements for improving the sustainability of red coral fisheries may include: (1) banning on all red coral fishing for a long recovery period of at least two decades until populations can recover its structural role and detailed management plants can be developed; (2) gathering enough information on the distribution, genetic pool and size-distribution of potentially target populations to evaluate vulnerability levels and assess feasible quotes; (3) a long-term rotatory harvesting scheme coupled to restrictions on minimum sizes and the obligation of leaving all colony bases attached to the substratum. These would be minimum regulations needed to ensure a more sustainable fishery. However, considering that red coral products are a non-locally marketed and only provide few jobs, while causing disproportional damage to benthic ecosystems and long-lasting ecological effects, we advocate for a fully protecting of the red coral as a cultural and ecologically important species, abandoning any type of extractive practice, and develop a re-insertion plan for artisanal red coral fishers into education tasks or alternative community services. In this sense, a recent new legislation approved by the Government of Catalonia in 2018, which will totally ban red coral extractions for a period of ten years, provides a glimpse of hope for this species and the overall conservation of coralligenous habitats. Besides the case of the Mediterranean red coral, our findings can inform fishery management on other precious coral species that share similar life-history traits such as the Japanese red coral *Paracorallium japonicum* or pink coral *Corallium elatius*, in which the sustainability of current practices is also at concern (Bruckner 2013, 2016).

Red coral poaching is still widespread across European and African Mediterranean coasts. Thus, if not properly enforced, new and more restrictive fishery regulations can be *dead papers* and remain ineffective at meeting conservation goals. In an increasingly globalized world, growing Asian demands for goods are putting at risk several vulnerable species, including precious corals (Bruckner et al. 2016). Banning external trade for endangered species such as the red coral will therefore be an essential step to prevent illegal fishing.

The Mediterranean Sea is a socially complex multi-state ecosystem that currently faces great politically challenges, including large income inequality among different regions and high immigration pressure of refugees escaping from wars and hanger. Reversing historical depletion of coastal habitats and buffering novel global threats will be especially challenging in this context. The European Union is embracing several conservation initiatives that aim to protect and restorevulnerable species and habitats in EU coastal waters. However, the success of any large-scale conservation plan will require cooperation between non-EU Mediterranean states and those along Nord-African coasts as well as global agreements to regulate trade of endangered species.

Marine Protected Areas

An alternative conservation tool to recover fish stocks and enhance the conservation of benthic habitats is the implementation of spatially-explicit fishery closures or Marine Protected Areas (MPAs). Previous studies demonstrated that MPAs can recover size-structure of red coral populations after several decades of proper enforcement (Linares et al. 2010, 2012, Bavestrello et al. 2015). Whether MPAs also shape their resilience in the context of climate change is an important further question yet to be addressed. In Chapter 3, we used Integral Projection Models (IPMs) to explore the demographic consequences of MPAs and climate change. Contrary to priory expectations, our results showed that there was no high extinction risk for fished red coral populations, nor significant differences in long-term growth between fished and protected populations. These observed patterns could be explained by similar survival rates of fished colonies due to low impact fishing practices in the studied populations (see Chapter 2 for a detailed analysis). However, colony shrinkage rates were strongly shaped by local protection: much higher in unprotected than protected populations. This drives a pattern of similar population size dynamics regardless of protection status but strongly divergent dynamics in structural complexity, with unprotected populations remaining highly simplified and dominated by small colonies. This allows for a mechanistic understanding of the broad-scale patterns that have been reported for Mediterranean waters, which showed unprotected populations to be heavily depleted in terms structural complexity but found no consistent patterns in population densities (Garrabou et al. 2017a, 2017b) and highlight the role of MPAs at enhancing the functionality of benthic habitats. More broadly, these results call for a reconsideration of traditional measures of extinction-risk that have been largely based on population sizes or densities. For clonal marine habitat forming-species, we need to move towards a more holistic characterization of conservation status for benthic populations and communities that includes trends in population sizes but also take into account their structural complexity and functional role.

Climate Change

Ongoing climate change is a novel threat to the conservation of most habitat-forming species inhabiting shallow waters. In the NW Mediterranean, red coral populations have been impacted by several heat waves during past decades, and there is compiling evidence from field studies and aquaria experiments that warm temperatures can cause their partial and whole-colony mortality (Garrabou et al. 2001, 2009, Torrents et al. 2008). Here, by integrating observed warming-driven mortality rates into demographic models, we show the detrimental population-level consequences of climate change in the long-term. While *C. rubrum* has persisted after historical overexploitation due to a high resistance, several shallow populations may be now at risk due to recurrent warming events that sharply decrease survival rates of coral colonies. Even if declines seem subtle in the short-term, and may go unnoticed for managers, our demographic projections reveal consistent declines and potential local extinctions in the long-term with low uncertainty (Hughes et al. 2013).

To predict potential consequences of future increases of thermal stress in coral populations, we used demographic and spatial models. On one hand, in Chapter 3, we tested whether MPAs enhance resilience of coral population to current and future warming scenarios. Because our demographic data series did not include the interaction between fishing and warming (we did not have unprotected sites open to fishing also affected by warming), we used IPMs to simulate their stochastic dynamics into different levels of local impacts (fishing) and warming-driven mortality frequencies. Our simulations reveal that MPAs may provide a slight buffering effect under low to moderate warming scenarios, but their effect become much weaker and almost negligible at higher frequencies of warming. These results agree with recent large-scale surveys in tropical coral reefs, which demonstrated that local protection had no influence on coral resistance to high intensity heat waves (Hughes et al. 2017).

On the other hand, in Chapter 5, we used spatial models to explore geographic and depth-related patterns of expected impacts of climate change for 2100 under two emissions scenarios (RCP4.5 and RCP8.5). Our models predict broad-scale decreases in the probability of occurrence for *C. rubrum* as well as for another long-lived gorgonian, *Paramuricea clavata*. This modeling exercise revealed a crucial role of depth in shaping the extent and severity of thermal impacts across the Mediterranean Sea. Shallow populations (up to 25m depth) may experience extensive thermal stress across the Mediterranean Sea, suggesting the warming is likely to drive a regional-scale deepening of gorgonian populations. At deeper sites, however, we expect heterogeneous spatial patterns with some regions highly affected up to 45 and 55m depth.

Earth's oceans are inherently three-dimensional. Many environmental and biotic processes vary widely across depths. However, most current predictive modeling approaches and management decisions and policies do not incorporate the 3D patterns of expected impacts into consideration. Our results provide a characterization of potential impacts of climate change across depth layers and call for considering this third dimension when analyzing broad scale conservation area priorities (Levin et al. 2017, Venegas-Li et al. 2018). Although they represent an important step forward in our understanding of the geographic and bathymetric dynamics of future climate, we are aware of some potential limitations of the climatic data, distribution data and the correlational nature of our modeling framework (see Quantitative Approaches section for a detailed discussion).

Future directions

Coping with damage to marine ecosystems from multiple interacting stressors will require major efforts from managers, policymakers, and society. Science should also play a crucial role in this endeavor by providing effective tools and evidence-based frameworks for optimal decision-making in conservation. I strongly believe that new scientific paradigms and large steps forwards can only be accomplished if we broaden our perspectives on how natural systems work. It is critically to advance our current understanding on how benthic systems will respond to changing environments and, more importantly, when and how can we use local management to enhance ecosystem resilience to global change.

To address this important question, we need to work towards to a more inclusive and interdisciplinary science, enlarge collaborative networks, and bridge traditionally isolated disciplines. For instance, since marine reserves manage people and the uses they make of the ocean, we cannot keep isolating marine ecosystems from human dynamics when projecting trends and responses to multiple drivers. Thus, one of my future goals is to include the social dimensions into ecological models to provide more realistic projections of social-ecological change.

My personal experience tells me that combining fieldwork and quantitative tools is a powerful approach to explore patterns and unravel mechanisms driving the dynamics of ecosystems and I would like this to keep playing a major role in my future career. However, exploring alternative perspectives using theoretical models could guide novel research lines and feed parallel empirical studies. Theoretical ecology forces an in-deep evaluation of how natural systems work, allowing to test a wider range of hypotheses and evaluate the sensitivity of the overall system to different components. I believe a hybrid approach using fieldwork and theoretical models could provide new insights into expected responses of vulnerable ecosystems to global change. Also, by comparing theoretical predictions against empirical observations, we may be able to identify crucial knowledge gaps, misperceptions, and challenge current paradigms.

Finally, I would like to explicitly bridge molecular and population ecology to assess the relevance of potential adaptive responses of corals to climate change. Recent studies suggest a potential critical role of adaptive responses such as evolutionary genetic adaptation and acclimatization in the future persistence of coral reefs. Most of these studies, however, have looked at molecular responses at the individual level. In would like to use novel statistical approaches and complex ecosystem models as a platform to scale-up from the observed adaptive responses of individuals to explore the broad implications of adaptation and acclimatization for the resilience of coral populations under present and future climatic scenarios.

General conclusions

Chapter I

There are strong positive relationships between depth and longevity across multiple sessile marine taxa.

Extreme longevity leads to stable population dynamics.

The red coral *Corallium rubrum* is an extreme long-lived species with low reproduction success, stable population dynamics, and high vulnerability to increased mortality sources.

Chapter II

Red coral fishing causes large decreases in biomass and strong size-class distribution shifts towards populations dominated by small colonies.

Recovery after fishing is a very slow process that can take decades and relies on regrowth of new branches of colonies that survive.

High survival and regrowth capacity explain the persistence of this species after overexploitation during millennia.

Chapter III

Climate change has dramatic population consequences for the red coral in the long-term.

MPAs are an effective local conservation tool to enhance the structural complexity of red coral populations.

However, MPAs may not be enough to ensure their persistence under future scenarios of increased thermal stress.

Chapter IV

Life-history strategies affect the outcomes and timescales of active restoration actions.

Transplantation of slow-growing species will tend to require lower initial effort due to higher survival after transplanting, but the period required to fully recover habitat complexity will tend be far longer.

Chapter V

Temperature and primary productivity shape the upper bathymetric range of *Corallium rubrum* and *Paramuricea clavata*.

At the end of the present century, climate change will strongly impact gorgonian populations across the Mediterranean Sea.

The severity of warming impacts will be strongly mediated by depth and global greenhouse gas emissions.

References

1. Abbiati M, Buffoni G, Caforio G, Di Cola G, Santangelo G (1992) Harvesting, predation and competition effects on a red coral population. Netherlands Journal of Sea Research 30: 219-228
2. Adler PB, Salguero-Gómez R, Compagnoni A et al. (2014) Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences of the United States of America, 111(2), 740-745
3. Ainsworth TD, Heron, SF, Ortiz JC, Mumby PJ, Grech A, Ogawa D & Leggat W (2016) Climate change disables coral bleaching protection on the Great Barrier Reef. Science, 352(6283), 338-342
4. Airoldi L & Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. Oceanogry and Marine Biology: An Annual Review, 45, 345–405
5. Angiolillo M, di Lorenzo B, Farcomeni A, Bo M, Bavestrello G, Santangelo G & Canese S (2015) Distribution and assessment of marine debris in the deep Tyrrhenian Sea (NW Mediterranean Sea, Italy). Marine Pollution Bulletin, 92(1-2), 149-159
6. Anthony K, Marshall PA, Abdulla A, Beeden R, Bergh C, Black R, & Green A (2015) Operationalizing resilience for adaptive coral reef management under global environmental change. Global Change Biology, 21(1), 48-61
7. Arnaud-Haond S, Duarte CM, Diaz-Almela E et al. (2012) Implications of extreme life span in clonal organisms: millenary clones in meadows of the threatened seagrass *Posidonia oceanica*.. PLoS ONE 7, e30454
8. Auer SK, Dick CA, Metcalfe NB & Reznick DN (2018) Metabolic rate evolves rapidly and in parallel with the pace of life history. Nature Communications, 9(1), 14
9. Badalamenti F, Ramos AA, Voultsiadou E, Lizaso JS, Anna G, Pipitone C & Riggio S (2000) Cultural and socio-economic impacts of Mediterranean marine protected areas. Environmental Conservation, 27(2), 110-125
10. Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanogry and Marine Biology: An Annual Review, 123–195
11. Barange M, Merino, G, Blanchard JL, Scholtens J, Harle J, Allison EH & Jennings S (2014) Impacts of climate change on marine ecosystem production in societies dependent on fisheries. Nature Climate Change, 4(3), 211-216
12. Barker NH & Roberts CM (2004) Scuba diver behaviour and the management of diving impacts on coral reefs. Biological Conservation, 120(4), 481-489
13. Barnes RSK & Hughes RN (1999) An introduction to marine ecology. John Wiley & Sons
14. Baudisch A, Salguero-Gómez R, Jones OR, Wrycza T, Mbeau-Ache C, Franco M et al. (2013) The pace and shape of senescence in angiosperms. Journal of Ecology, 101:596-606

15. Bavestrello G, Bo M, Bertolino M, Betti F, Cattaneo-Vietti R (2015) Long-term comparison of structure and dynamics of the red coral metapopulaion of the Portofino Promontory (Ligurian Sea): a case study for a Marine Protected Area in the Mediterranean Sea. Marine Ecology 36(4):1354-63.
16. Bayraktarov E, Saunders MI, Abdullah S et al. (2016) The cost and feasibility of marine coastal restoration. Ecological Applications, 26(4), 1055-1074
17. Benayas JMR, Newton AC, Diaz A & Bullock JM (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science, 325(5944), 1121-1124
18. Bensoussan N, Romano JC, Harmelin JG, Garrabou J (2010) High resolution characterization of northwest Mediterranean coastal waters thermal regimes: to better understand responses of benthic communities to climate change Estuarine. Coastal and Shelf Science, 87:431-441
19. Bentlage B, Peterson AT, Barve N & Cartwright, P (2013) Plumbing the depths: extending ecological niche modelling and species distribution modelling in three dimensions. Global Ecology and Biogeography, 22(8), 952-961
20. Bernhardt JR & Leslie HM (2013) Resilience to climate change in coastal marine ecosystems. Annual Review of Marine Sciences, 2013 5:371–92
21. Bielby J, Mace GM, Bininda-Emonds OR, Cardillo M, Gittleman JL, Jones KE & Purvis A (2007) The fast-slow continuum in mammalian life history: an empirical reevaluation. The American Naturalist, 169(6), 748-757
22. Bo M, Bava S, Canese S, Angiolillo M, Cattaneo-Vietti R & Bavestrello G (2014) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biological Conservation, 171, 167-176
23. Bozec YM, Alvarez-Filip L, & Mumby PJ (2015) The dynamics of architectural complexity on coral reefs under climate change. Global Change Biology, 21(1), 223-235
24. Bramanti L, Magagnini G, De Maio L & Santangelo G (2005) Recruitment, early survival and growth of the Mediterranean red coral *Corallium rubrum* (L 1758), a 4-year study. Journal of Experimental Marine Biology and Ecology, 314: 69 – 78
25. Bramanti L, Movilla J, Guron M, Calvo E, Gori A, et al. (2013) Detrimental effects of ocean acidification on the economically important Mediterranean red coral (*Corallium rubrum*). Global Change Biology, 19(6): 1987-1908
26. Bridge TC, Hoey AS, Campbell SJ, Muttaqin E, Rudi E, Fadli N et al. (2013) Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. F1000Res, 2
27. Bruckner AW (2009) Rate and extent of decline in *Corallium* (pink and red coral) populations: existing data meet the requirements for a CITES Appendix II listing. Marine Ecology Progress Series, 397:319–332

28. Bruckner AW (2010) Quantifying the decline in *Corallium rubrum* populations: Reply to Santangelo & Bramanti (2010) Marine Ecology Progress Series, 418: 299-303
29. Bruckner AW (2014) Advances in management of precious corals in the family Corallidae: are new measures adequate? Current Opinion in Environmental Sustainability, 7: 1-8
30. Bruno JF & Valdivia A (2016) Coral reef degradation is not correlated with local human population density. Scientific Reports, 6, 29778
31. Buffenstein R (2005) The naked mole-rat? A new long-living model for human aging research. The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 60, 1369-1377
32. Bull, J W, Gordon, A, Law, E A et al (2014) Importance of Baseline Specification in Evaluating Conservation Interventions and Achieving No Net Loss of Biodiversity. Conservation Biology 28: 799–809
33. Cabaitan, P C, Gomez, E D, & Aliño, P M (2008) Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. Journal of Experimental Marine Biology and Ecology, 357(1), 85-98
34. Cailliet GM, Andrews AH, Burton EJ, Watters DL, Kline DE, & Ferry-Graham LA 2001 Age determination and validation studies of marine fishes: do deep-dwellers live longer? Experimental Gerontology, 36(4), 739-764
35. Cardinale BJ et al. (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67, and erratum (2012) 489:326
36. Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A & Edgar GJ (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science, 321(5888), 560-563
37. Casas-Güell E, Cebrian E, Garrabou J, Ledoux JB, Linares C & Teixidó N (2016) Structure and biodiversity of coralligenous assemblages dominated by the precious red coral *Corallium rubrum* over broad spatial scales. Scientific Reports, 6, 36535
38. Caswell H (2001) Matrix Population Models: Construction, Analysis, and Interpretation 2nd edition Sinauer Associates, Sunderland MA
39. Cattaneo-Vietti R, Bavestrello G, Bo M, Canese S, Vigo A & Andaloro F (2017) Illegal ingegno fishery and conservation of deep red coral banks in the Sicily Channel (Mediterranean Sea). Aquatic Conservation: Marine and Freshwater Ecosystems, 27(3), 604-616
40. Cau A, Cannas R, Sacco F & Follesa MC (2013) Adaptive management plan for red coral (*Corallium rubrum*) in the GFCM competence area. FAO, Rome
41. Cebrian E, Linares C, Marschal C & Garrabou J (2012) Exploring the effects of invasive algae on the persistence of gorgonian populations. Biological Invasions, 14(12), 2647-2656
42. Cerrano C, Bavestrello G, Bianchi C N, Cattaneo Vietti R, Bava S, Morganti C & Siccardi A (2000) A catastrophic mass

mortality episode of gorgonians and other organisms in the Ligurian Sea (North western Mediterranean), summer 1999. Ecology Letters, 3(4), 284-293

43. Cerrano C, Cardini U, Bianchelli S, Corinaldesi C, Pusceddu A & Danovaro R (2013) Red coral extinction risk enhanced by ocean acidification. Scientific Reports, 3, 1457
44. Charnov EL (1993) Life history invariants: some explorations of symmetry in evolutionary ecology. (Vol 6) Oxford University Press, USA
45. Chen IC, Hill JK, Ohlemüller R, Roy DB & Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming Science, 333(6045), 1024-1026
46. Christianen MJ, Herman PM, Bouma TJ, Lamers LP, van Katwijk MM, van der Heide T & Kiswara W (2014) Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. Proceedings of the Royal Society of London B: Biological Sciences, 281(1777), 20132890
47. Claudet J & Fraschetti S (2010) Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. Biological Conservation, 143(9), 2195-2206
48. Clutton-Brock T & Sheldon BC (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution, 25(10), 562-573
49. Colchero F, Rau R, Jones OR, Barthold JA, Conde DA, Lenart A et al. (2016) The emergence of longevous populations. Proceedings of the National Academy of Sciences of the United States of America, 113, E7681-E7690
50. Coll M, Piroddi C, Steenbeek J, Kaschner K, Lasram FBR, Aguzzi J, & Danovaro R (2010) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PloS ONE, 5(8), e11842
51. Coma R, Ribes M, Serrano E, Jiménez E, Salat J & Pascual J (2009) Global warming-enhanced stratification and mass mortality events in the Mediterranean. Proceedings of the National Academy of Sciences of the United States of America, 106(15), 6176-6181
52. Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science, 199, 1302-1310
53. Costantini F, Fauvelot C & Abbiati M (2007) Fine-scale genetic structuring in *Corallium rubrum* (l): evidences of inbreeding and limited effective larval dispersal. Marine Ecology Progress Series, 340: 109-119
54. Costello MJ, May RM & Stork NE (2013) Can we name Earth's species before they go extinct? Science, 339(6118), 413-416
55. Côté IM, Darling ES & Brown CJ (2016) Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B, 283 (1824): 20152592
56. Côté IM, Darling ES (2010) Rethinking Ecosystem Resilience in the Face of

Climate Change. PLoS Biology, 8(7): e1000438

57. Couce E, Ridgwell A & Hendy EJ (2013) Future habitat suitability for coral reef ecosystems under global warming and ocean acidification. Global Change Biology 19, 3592-3606
58. Cox C, Valdivia A McField M, Castillo K & Bruno JF (2017) Establishment of marine protected areas alone does not restore coral reef communities in Belize. Marine Ecology Progress Series, 563, 65-79
59. Crain CM, Kroeker K & Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters, 11(12), 1304-1315
60. Crisci C, Ledoux JB, Mokhtar-Jamaï K et al. (2017) Regional and local environmental conditions do not shape the response to warming of a marine habitat-forming species. Scientific Reports, 7(1), 5069
61. Crouse DT, Crowder LB & Caswell H (1987) A stage based population model for loggerhead sea turtles and implications for conservation. Ecology, 68(5), 1412-1423
62. Crowder LB, Crouse DT, Heppell SS, & Martin TH (1994) Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications, 4: 437 - 445
63. Danovaro R, Aguzzi J, Fanelli E, Billett D, Gjerde K, Jamieson A et al. (2017) An ecosystem-based deep-ocean strategy. Science 355, 452-454
64. Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR & Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecology Letters, 15(12), 1378-1386
65. Darling ES & Côté IM (2008) Quantifying the evidence for ecological synergies. Ecology Letters, 11(12), 1278-1286
66. Darling ES & Côté IM (2018) Seeking resilience in marine ecosystems. Science, 3596379: 986-987
67. Darling ES, McClanahan TR & Côté IM (2010) Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. Conservation Letters, 3(2), 122-130
68. De'ath, G & Fabricius K (2010) Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecological Applications, 20, 840–850
69. Delgado O, Ruiz J, Pérez M, Romero J & Ballesteros E (1999) Effects of fish farming on seagrass (*Posidonia oceanica*) in a Mediterranean bay: seagrass decline after organic loading cessation. Oceanologica Acta, 22(1), 109-117
70. Diffenbaugh NS, Pal JS, Giorgi F & Gao X (2007) Heat stress intensification in the Mediterranean climate change hotspot. Geophysical Research Letters, 34, L11706
71. Dizon R & Yap H (2006) Effects of coral transplantation in sites of varying distances and environmental conditions. Marine Biology, 148, 933-943
72. Drap P, Merad D, Mahiddine A, et al. (2013) Automating the measurement of red coral in situ using underwater

photogrammetry and coded targets. XXIV International CIPA Symposium, Strasbourg, France XL-5/W2, pp231–236

73. Drap P, Royer JP, Nawaf MM, Saccone M, Merad D, López-Sanz À, & Garrabou J (2017) Underwater photogrammetry, coded target and plenoptic technology: a set of tools for monitoring red coral in mediterranean sea in the framework of the" Perfect" project. The International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences, 42, 275
74. Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA & Edgar GJ (2016) Biodiversity enhances reef fish biomass and resistance to climate change. Proceedings of the National Academy of Sciences of the USA, 113(22), 6230-6235
75. Easterling MR, Ellner SP & Dixon PM (2000) Size-specific sensitivity: applying a new structured population model. Ecology, 81:694-708
76. Edgar GJ, Stuart-Smith RD, Willis TJ et al. (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature, 506(7487), 216-220
77. Edwards AJ & Clark S (1998) Coral Transplantation: A Useful Management Tool or Misguided Meddling? Marine Pollution Bulletin, 37, 474-48
78. Edwards AJ & Gomez ED (2007) Reef Restoration Concepts and Guidelines: making sensible management choices in the face of uncertainty. Coral Reef Targeted Research & Capacity Building for Management Programme: St Lucia, Australia 38 pp
79. Ellner SP & Rees M (2006) Integral projection models for species with complex demography. The American Naturalist, 167(3), 410 – 428
80. Estes JA & Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs, 65(1), 75-100
81. FAO 2014 The State of World Fisheries and Aquaculture 2014. Rome, 223 pp
82. Ferrigno F, Appolloni L, Russo GF & Sandulli R (2017) Impact of fishing activities on different coralligenous assemblages of Gulf of Naples (Italy). Journal of the Marine Biological Association of the United Kingdom, 1-10
83. Forbis TA & Doak DF (2004) Seedling establishment and life history trade-offs in alpine plants. American Journal of Botany, 91, 1147-1153
84. Fordham DA, Bertelsmeier C, Brook BW, Early R, Neto D, Brown SC & Araújo MB (2018) How complex should models be? Comparing correlative and mechanistic range dynamics models. Global Change Biology, 24(3), 1357-1370
85. Fourqurean JW, Duarte CM, Kennedy H, Marbà N, Holmer M, Mateo MA & Serrano O (2012) Seagrass ecosystems as a globally significant carbon stock. Nature Geoscience, 5(7), 505
86. Franco M & Silvertown J (1996) Life history variation in plants: an exploration of the fast-slow continuum hypothesis. Philosophical Transactions of the Royal

Society of London B, 351(1345), 1341-1348

87. Francour P, Ganteaume A & Poulain, M (1999) Effects of boat anchoring in Posidonia oceanica seagrass beds in the Port-Cros National Park(north-western Mediterranean Sea). Aquatic Conservation: Marine and Freshwater Ecosystems, 9(4), 391-400
88. Frölicher TL & Laufkötter C (2018) Emerging risks from marine heat waves. Nature Communications
89. Gaillard JM, Lemaître JF, Berger V, Bonenfant C Devillard F et al. (2016) Life history axes of variation In: Encyclopedia of Evolutionary Biology, ed: Kliman RM Academic Press, Oxford, UK, 312-323
90. Gallmetzer I, Haselmair A, Velimirov B (2010) Slow growth and early sexual maturity: Bane and boom for the red coral *Corallium rubrum*. Estuarine, Coastal and Shelf Science 90: 1-10
91. Game ET, Watts ME, Wooldridge S & Possingham HP (2008) Planning for persistence in marine reserves: a question of catastrophic importance. .Ecological Applications, 18(3), 670-680
92. Garcia MB, Dahlgren JP & Ehrlén J (2011) No evidence of senescence in a 300 year old mountain herb. Journal of Ecology, 99, 1424-1430
93. García MB, Pico FX & Ehrlén J (2008) Lifespan correlates with population dynamics in perennial herbaceous plants. American Journal of Botany, 95, 258-262
94. García-Rodriguez M & Massò C (1986) Estudio biomètrico de poblaciones del coral rojo (*Corallium rubrum* L) del litoral de Gerona (NE de Espana). Bolletin del Instuto Español de Oceanografía, 3: 61-64
95. Garrabou J, Ballesteros E & Zabala M (2002) Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient Coast Shelf Sci 55, 493-508
96. Garrabou J & Harmelin JG (2002) A 20 year study on life history traits of a harvested long lived temperate coral in the NW Mediterranean: insights into conservation and management needs. Journal of Animal Ecology, 71(6), 966-978
97. Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P, Cigliano M & Ledoux JB (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Global Change Biology, 15(5), 1090-1103
98. Garrabou J, Linares C, Montero-Serra I, Ledoux JB, Lopez Sanz À, Olvera À & Domínguez-Carrió, C (2017b) Informe sobre l'estat de les poblacions de corall vermell (*Corallium rubrum*) a les aigües de Catalunya.
99. Garrabou, J, Perez, T, Sartoretto, S, & Harmelin, J G (2001) Mass mortality event in red coral *Corallium rubrum* populations in the Provence region (France, NW Mediterranean). Marine Ecology Progress Series, 217, 263-272
100. Garrabou J, Sala E, Arcas A & Zabala M (1998) The impact of diving on rocky sublittoral communities: a case study of a bryozoan population. Conservation Biology, 12(2), 302-312

101. Garrabou J, Sala E, Linares C, Ledoux JB, Montero-Serra I, Dominici JM, & Harmelin JG (2017a) Re-shifting the ecological baseline for the overexploited Mediterranean red coral. Scientific Reports, 7, 42404
102. Genovart M, Doak DF, Igual JM, Sponza S, Kralj J & Oro D (2017) Varying demographic impacts of different fisheries on three Mediterranean seabird species. Global Change Biology, 23(8), 3012-3029
103. Gili JM & Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends in Ecology and Evolution, 13: 316–321
104. Gill DA, Mascia MB, Ahmadia GN et al. (2017) Capacity shortfalls hinder the performance of marine protected areas globally. Nature, 543(7647), 665-669
105. Giorgi F & Lionello P (2008) Climate change projections for the Mediterranean region. Global Planetary Change, 63, 90–104
106. Girard F, Shea K & Fisher CR (2018) Projecting the recovery of a long-lived deep-sea coral species after the Deepwater Horizon oil spill using state-structured models. Journal of Applied Ecology
107. Glassom, D & Chadwick NE (2006) Recruitment, growth and mortality of juvenile corals at Eilat, northern Red Sea. Marine Ecology Progress Series, 318, 111-122
108. Gomez ED, Cabaitan PC Yap HT & Dizon RM (2014) Can coral cover be restored in the absence of natural recruitment and reef recovery? Restoration Ecology, 22(2), 142-150,
109. Graham NA, McClanahan TR, MacNeil MA et al. (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS ONE, 3(8), e3039
110. Griffith AB (2017) Perturbation approaches for integral projection models Oikos, 126(12), 1675-1686
111. Griffith AB, Salguero Gómez R, Merow C & McMahon S (2016) Demography beyond the population. Journal of Ecology, 104(2), 271-280
112. Grigg RW (2008) Resource Management of Precious Corals: A Review and Application to Shallow Water Reef Building Corals. Marine Ecology 5(1), 57-74
113. Grigg RW (1988) Recruitment limitation of a deep benthic hard-bottom octocoral population in the Hawaiian Islands. Marine Ecology Progress Series, 45, 121-126
114. Gunderson DR (1980) Using rK selection theory to predict natural mortality. Canadian Journal of Fisheries and Aquatic Sciences, 37(12), 2266-2271
115. Hall VR & Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef building corals Ecology, 77(3), 950-963
116. Halpern BS (2003) The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications, S117-S137
117. Halpern BS, Frazier M, Potapenko J et al. (2015) Spatial and temporal changes in cumulative human impacts on the world/'s ocean. Nature Communications, 6

118. Halpern BS, Walbridge S, Selkoe KA et al. (2008) A global map of human impact on marine ecosystems. Science, 319(5865), 948-952
119. Harris DL, Rovere A, Casella E et al. (2018) Coral reef structural complexity provides important coastal protection from waves under rising sea levels. Science Advances, 4(2), eaao4350
120. Healy K, Guillerme T, Finlay S, Kane A & Kelly SB (2014) Ecology and mode-of-life explain lifespan variation in birds and mammals. Proceedings of the Royal Society of London B: Biological Sciences, 281(1784), 20140298
121. Heppell SS, Caswell H & Crowder LB (2000) Life histories and elasticities patterns: perturbation analysis for species with minimal demographic data. Ecology 81: 654–665
122. Hereu B, Linares C & Zabala M (1999) Avaluació de l'impacte de l'episodi de corall vermell (*Corallium rubrum*) de la zona protegida de les Illes Medes detectat durant l'hivern del 2000 In: Seguiment temporal de les Illes Medes (1999) Informe técnic per al Departament de Medi Ambient, Generalitat de Catalunya
123. Hiddink JG, Jennings S, Sciberras M et al. (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proceedings of the National Academy of Sciences USA, 114(31):8301-6.
124. Hijmans RJ & Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology, 12(12), 2272-2281
125. Hoegh-Guldberg O & Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science, 328(5985), 1523-1528
126. Hoegh-Guldberg O, Beal D, Chaudhry T et al. (2015) Reviving the Ocean Economy: the case for action – 2015 WWF International, Gland, Switzerland, Geneva, pp 60
127. Hoegh-Guldberg O, Mumby PJ, Hooten AJ et al. (2007) Coral reefs under rapid climate change and ocean acidification. Science, 318(5857), 1737-1742
128. Hughes TP & Tanner JE (2000) Recruitment failure, life histories, and long term decline of Caribbean corals. Ecology, 81, 2250-2263
129. Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef Science 265: 1547-1551
130. Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR & et al. (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301, 929-933
131. Hughes TP (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. The American Naturalist, 123(6), 778-795
132. Hughes TP & Jackson JBC (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. Science, 209(4457), 713-715

133. Hughes TP & Tanner JE (2000) Recruitment failure, life histories, and long term decline of Caribbean corals. Ecology, 81(8), 2250-2263
134. Hughes TP, Anderson KD, Connolly et al. (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science, 359(6371), 80-83
135. Hughes TP, Barnes ML, Bellwood DR et al. (2017b) Coral reefs in the Anthropocene. Nature, 546(7656), 82
136. Hughes, T P, Graham, N A, Jackson, J B et al (2010) Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution, 25(11), 633-642
137. Hughes, T P, Kerry, J T, Álvarez-Noriega, M et al. (2017a) Global warming and recurrent mass bleaching of corals Nature, 543(7645), 373-377
138. Hughes, T P, Linares, C, Dakos, V et al (2013) Living dangerously on borrowed time during slow, unrecognized regime shifts Trends in Ecology & Evolution, 28(3), 149-155
139. Hughes TP, Kerry JT et al. (2018b) Global warming transforms coral reef assemblages. Nature 1
140. Husebø A, Nøttestad L, Fosså JH, Furevik DM, Jørgensen SB (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471: 91–99
141. IUCN (2014) IUCN Red list of threatened species Version 20132 http://wwwiucnredlistorg/Accessed February 2014
142. Jackson, JBC, Kirby, MX, Beger, WH et al (2001) Historical Overfishing and the recent collapse of coastal ecosystems. Science, 293, 629–637
143. Jiguet, F, Gadot, A S, Julliard, R, Newson, S E & Couvet, D (2007) Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biology, 13(8), 1672-1684
144. Jochum KP, Wang X, Vennemann TW, Sinha B & Müller WE (2012) Siliceous deep-sea sponge Monorhaphis chuni: A potential paleoclimate archive in ancient animals. Chemical Geology, 300, 143-151
145. Johnson AF & Lidström S (2018) The balance between concepts and complexity in ecology. Nature Ecology & Evolution, 2(4), 585
146. Jones CG, Lawton JH & Shachak M (1994) Organisms as ecosystem engineers. Oikos 69: 373–386
147. Jones OR, Scheuerlein A, Salguero-Gómez R et al. (2014) Diversity of ageing across the tree of life Nature 505, 169-173
148. Jurgens LJ & Gaylord B (2018) Physical effects of habitat forming species override latitudinal trends in temperature. Ecology Letters, 21(2), 190-196
149. Kaiser MJ, Hormbrey S, Booth JR, Hinz H & Hiddink, JG (2018) Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear. Journal of Applied Ecology
150. Kennedy EV, Perry CT, Halloran PR et al. (2013) Avoiding coral reef functional collapse requires local and global action. Current Biology, 23(10), 912-918
151. Kerr NZ, Baxter PW, Salguero Gómez R, Wardle GM & Buckley YM (2016) Prioritizing management actions for

invasive populations using cost, efficacy, demography and expert opinion for 14 plant species world wide. Journal of Applied Ecology, 53(2), 305-316

152. Kersting DK, Ballesteros E, De Caralt S & Linares C (2014) Invasive macrophytes in a marine reserve (Columbretes Islands, NW Mediterranean): spread dynamics and interactions with the endemic scleractinian coral Cladocora caespitosa. Biological Invasions, 16(8), 1599-1610
153. Kersting DK, Cebrian E, Casado C, Teixidó N, Garrabou J & Linares C (2015) Experimental evidence of the synergistic effects of warming and invasive algae on a temperate reef-builder coral. Scientific Reports, 5, 18635
154. Kersting DK, Teixidó N & Linares C (2014) Recruitment and mortality of the temperate coral Cladocora caespitosa: implications for the recovery of endangered populations. Coral Reefs, 33(2), 403-407
155. Knittweis L, Aguilar R, Álvarez H et al. (2016) New depth record of the precious red coral *Corallium rubrum* for the Mediterranean. Rapp Comm Int Mer Médit, 41
156. Kortsch S, Primicerio R, Fossheim M, Dolgov AV & Aschan M (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc R Soc B, 282(1814), 20151546
157. Kroodsma DA, Mayorga J, Hochberg T et al. (2018) Tracking the global footprint of fisheries. Science, 359(6378), 904-908
158. Larson DW (2001) The paradox of great longevity in a short-lived tree species. Experimental Gerontology, 36, 651-673
159. Lasker HR (2013) Recruitment and Resilience of a Harvested Caribbean Octocoral. PLoS ONE 8(9): e74587
160. Ledoux JB, Aurelle D, Bensoussan N, Marschal C, Féral JP & Garrabou J (2015) Potential for adaptive evolution at species range margins: contrasting interactions between red coral populations and their environment in a changing ocean. Ecology and Evolution, 5(6), 1178-1192
161. Ledoux JB, Mokhtar Jamaï K, Roby C et al. (2010a) Genetic survey of shallow populations of the Mediterranean red coral [*Corallium rubrum* (Linnaeus, 1758)]: new insights into evolutionary processes shaping nuclear diversity and implications for conservation. Molecular Ecology, 19(4), 675-690
162. Ledoux JB, Garrabou J, Bianchimani, O et al. (2010b) Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, *Corallium rubrum*. Molecular Ecology, 19, 4204–4216
163. Lejeusne C, Chevaldonne P, Pergent-Martini C, Boudouresque CF & Perez T (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends in Ecology & Evolution, 25(4), 250-260
164. Levin N, Kark S & Danovaro R (2017) Adding the third dimension to marine conservation. Conservation Letters
165. Linares C, Arizmendi-Mejía R, Ballesteros E et al. (2014) Response of coralligenous

to global change: evidences from field and experimental studies in gorgonian forests Proceedings of the 2nd Mediterranean Symposium on the conservation of coralligenous and other calcareous bio-concretions

166. Linares C & Doak DF (2010) Forecasting the combined effects of disparate disturbances on the persistence of long-lived gorgonians: a case study of *Paramuricea clavata*. Marine Ecology Progress Series, 402, 59-68
167. Linares C, Bianchimani O, Torrents O et al. (2010) Marine Protected Areas and the conservation of long-lived marine invertebrates: the Mediterranean red coral. Marine Ecology Progress Series, 402, 69-79
168. Linares C, Coma R, Diaz D et al. (2005) Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean Sea. Marine Ecology Progress Series, 305, 127-137
169. Linares C, Coma R, Garrabou J, Díaz D & Zabala M (2008) Size distribution, density and disturbance in two Mediterranean gorgonians: *Paramuricea clavata* and *Eunicella singularis*. Journal of Applied Ecology, 45(2), 688-699
170. Linares C, Coma R & Zabala M (2008) Restoration of threatened red gorgonian populations: an experimental and modelling approach. Biological Conservation, 141: 427-437
171. Linares C, Doak DF, Coma R, Diaz, D & Zabala, M (2007) Life history and viability of a long lived marine invertebrate: the octocoral *Paramuricea clavata*. Ecology, 88(4), 918-928
172. Linares, C, Garrabou, J, Hereu, B, Diaz, D, Marschal, C, Sala, E, & Zabala, M (2012) Assessing the effectiveness of marine reserves on unsustainably harvested long lived sessile invertebrates. Conservation Biology, 26(1), 88-96
173. Lindenmayer, DB & Likens GE (2009) Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends in Ecology & Evolution, 2, 482-486,
174. Ling SD, Scheibling RE, Rassweiler, A et al. (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. Phil Trans R Soc B, 370(1659), 20130269
175. Lotze HK, Coll M, Margera AM, Ward-Paige C & Airoldi L (2011) Recovery of marine animal populations and ecosystems. Trends in Ecology and Evolution 26(11): 595-605
176. Macias DM, Garcia-Gorriz E & Stips A (2015) Productivity changes in the Mediterranean Sea for the twenty-first century in response to changes in the regional atmospheric forcing. Frontiers in Marine Science, 2:79
177. Macias D, Garcia Gorriz E & Stips A (2018) Major fertilization sources and mechanisms for Mediterranean Sea coastal ecosystems. Limnology and Oceanography, 63(2), 897-914
178. Madin JS, Anderson KD, Andreasen MH et al (2016) The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Scientific Data, 3

179. Madin JS, Baird AH, Dornelas N et al (2014) Mechanical vulnerability explains size dependent mortality of reef corals. Ecology Letters, 17, 1008–1015
180. Marbà N & Duarte C (1998) Rhizome elongation and seagrass clonal growth. Marine Ecology Progress Series, 174, 269-280
181. Marschal C, Garrabou J, Harmelin JG, & Pichon M (2004) A new method for measuring growth and age in the precious red coral *Corallium rubrum* (L). Coral Reefs, 23, 423-432
182. Martin CS, Giannoulaki M, De Leo F et al. (2014) Coralligenous and maërl habitats: predictive modelling to identify their spatial distributions across the Mediterranean Sea. Scientific Reports, 4, 5073
183. McClanahan TR (2008) Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. Oecologia, 155(1), 169-177
184. McDonald JL, Franco M, Townley S, Ezard TH, Jelbert K & Hodgson DJ (2017) Divergent demographic strategies of plants in variable environments. Nature Ecology & Evolution, 1, 0029
185. McIntyre S, Lavorel S & Tremont RM (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. Journal of Ecology 31-44
186. Mellin C, Aaron MacNeil M, Cheal A J et al. (2016) Marine protected areas increase resilience among coral reef communities. Ecology Letters, 19(6), 629-637
187. Merow C, Dahlgren JP, Metcalf CJE et al. (2014) Advancing population ecology with integral projection models: a practical guide. Methods in Ecology and Evolution, 5(2), 99-110
188. Micheli F, Halpern BS, Walbridge S, Ciriaco S, Ferretti F, Fraschetti S, et al (2013) Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. PLoS ONE 8(12): e79889
189. Micheli F, Levin N, Giakoumi S, Katsanevakis S, Abdulla A, Coll M & Maiorano L (2013) Setting priorities for regional conservation planning in the Mediterranean Sea PLoS ONE, 8(4), e59038
190. Micheli F, Saenz-Arroyo A, Greenley A et al. (2012) Evidence that marine reserves enhance resilience to climatic impacts. PloS ONE, 7(7), e40832
191. Miller RJ, Lafferty KD, Lamy T et al. (2018) Giant kelp, Macrocystis pyrifera, increases faunal diversity through physical engineering. Proc R Soc B, 285(1874), 20172571
192. Moles AT, Ackerly DD, Tweddle JC et al. (2007) Global patterns in seed size. Global Ecology Biogeography, 16, 109-116
193. Montefalcone M, Chiantore M, Lanzone A et al. (2008) BACI design reveals the decline of the seagrass Posidonia oceanica induced by anchoring. Marine Pollution Bulletin, 56(9), 1637-1645
194. Montero Serra I, Edwards M & Genner MJ (2015) Warming shelf seas drive the

subtropicalization of European pelagic fish communities. Global Change Biology, 21(1), 144-153

195. Montero-Serra I, Garrabou J, Doak DF et al. (2018) Accounting for life-history strategies and timescales in marine restoration. Conservation Letters, 11(1), e12341
196. Montero-Serra I, Linares C, García M et al. (2015) Harvesting effects, recovery mechanisms, and management strategies for a long-lived and structural precious coral. PloS ONE, 10(2), e0117250
197. Montero-Serra I, Linares C, Doak DF, Ledoux JB & Garrabou J (2018) Strong linkages between depth, longevity and demographic stability across marine sessile species. Proc. R. Soc. B., 285(1873):20172688.
198. Mora C, Aburto-Oropeza O, Ayala Bocos A et al. (2011) Global Human Footprint on the Linkage between Biodiversity and Ecosystem Functioning in Reef Fishes. PLoS Biology, 9(4): e1000606
199. Morris WF, Pfister CA, Tuljapurkar S et al. (2008) Longevity can buffer plant and animal populations against changing climatic variability. Ecology 89, 19-25
200. Morris WF & Doak DF (2002) Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis Sinauer Associates, Inc Publishers; Sunderland, Massachusetts USA
201. Morrison C & Hero JM (2003) Geographic variation in life history characteristics of amphibians: a review. Journal of Animal Ecology, 72, 270-279
202. Muir PR, Marshall PA, Abdulla A & Aguirre JD (2017) Species identity and depth predict bleaching severity in reef-building corals: shall the deep inherit the reef? Proc R Soc B, 284(1864), 20171551
203. Muir PR, Wallace CC, Done T & Aguirre JD (2015) Limited scope for latitudinal extension of reef corals. Science, 348(6239), 1135-1138
204. Mumby PJ & Harborne AR (2010) Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS ONE, 5, e8657
205. Mumby PJ, Dahlgren CP, Harborne AR et al. (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. Science, 311(5757), 98-101
206. Mumby PJ, Edwards AJ, Arias-González J E et al. (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature, 427(6974), 533
207. Mumby PJ, Harborne AR, Williams J et al. (2007) Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences USA, 104(20), 8362-8367
208. Mumby P, Chisholm J, Edwards A et al. (2001) Unprecedented bleaching-induced mortality in Porites spp at Rangiroa Atoll, French Polynesia. Marine Biology, 139(1), 183-189
209. Mumby PJ & Hastings A (2008) The impact of ecosystem connectivity on coral reef resilience. Journal of Applied Ecology, 453: 854-862
210. Munch SB & Salinas S (2009) Latitudinal variation in lifespan within species is explained by the metabolic theory of

ecology. Proc Natl Acad Sci USA, 106, 13 860–13 864

211. Nadeau CP, Urban MC & Bridle JR (2017) Coarse climate change projections for species living in a fine scaled world. Global Change Biology, 23(1), 12-24
212. Neumann B, Vafeidis AT, Zimmermann J & Nicholls RJ (2015) Future coastal population growth and exposure to sea-level rise and coastal flooding - a global assessment. PLoS ONE 10(3): e0118571
213. Nielsen J, Hedeholm RB, Heinemeier J et al. (2016) Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*). Science 353, 702-704
214. NOAA, National Oceanic and Atmospheric Administration (2009) Large marine ecosystems Web page: http://wwwlmenoaagov/ The Mediterranean LME Accessed December, 2009
215. Olds AD, Pitt KA, Maxwell PS et al. (2014) Marine reserves help coastal ecosystems cope with extreme weather. Global Change Biology, 20(10), 3050-3058
216. Oliver EC, Benthuysen JA, Bindoff NL et al. (2017) The unprecedented 2015/16 Tasman Sea marine heatwave. Nature Communications, 8, 16101
217. Oliver EC, Donat, MG, Burrows MT et al. (2018) Longer and more frequent marine heatwaves over the past century. Nature Communications, 9(1), 1324
218. Ortiz JC, Bozec YM, Wolff NH et al. (2014) Global disparity in the ecological benefits of reducing carbon emissions for coral reefs. Nature Climate Change, 4(12), 1090-1094
219. Otero MM, Numa C, Bo M et al, (2017) Overview of the conservation status of Mediterranean anthozoans. IUCN, Malaga, Spain 73 pp
220. Palumbi SR, Sandifer PA, Allan JD, et al (2008) Managing for ocean biodiversity to sustain marine ecosystem services. Front Ecol Environ, 7, 204–211
221. Parravicini, V, Azzurro, E, Kulbicki, M, & Belmaker, J (2015) Niche shift can impair the ability to predict invasion risk in the marine realm: an illustration using Mediterranean fish invaders. Ecology Letters, 18(3), 246-253
222. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1988) Fishing down marine food webs. Science, 279: 860-863
223. Pauly, D & Zeller, D (2016) Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. Nature Communications, 7:10244
224. Pauly, D, Watson, R & Alder, J (2005) Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical Transactions of the Royal Society B: Biological Sciences, 360(1453), 5-12
225. Pearson, RG & Dawson, TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12(5), 361-371
226. Perrings, MP, Sandish, RJ, Price, JN et al (2015) Advances in restoration ecology:

rising to the challenges of the coming decades. Ecosphere, 6(8), 1–25

227. Perry, AL, Low, PJ, Ellis, JR & Reynolds, JD (2005) Climate change and distribution shifts in marine fishes. Science, 308(5730), 1912-1915
228. Pinsky, M L, Worm, B, Fogarty, M J, Sarmiento, J L, & Levin, S A (2013) Marine taxa track local climate velocities. Science, 341(6151), 1239-1242
229. Ponti, M, Grech, D, Mori, M, Perlini, R A, Ventra, V, Panzalis, PA & Cerrano, C (2016) The role of gorgonians on the diversity of vagile benthic fauna in Mediterranean rocky habitats. Marine Biology, 163(5), 120
230. Ponti, M, Perlini, RA, Ventra, V, Grech, D, Abbiati, M & Cerrano, C (2014) Ecological shifts in Mediterranean coralligenous assemblages related to gorgonian forest loss. PloS ONE, 9(7), e102782
231. Possingham, HP, Bode, M, Klein, CJ (2015) Optimal conservation outcomes require both restoration and protection. PLoS Biology, 13(1): e1002052
232. Reznick D, Nunney L & Tessier A (2000) Big houses, big cars, superfleas and the costs of reproduction. Trends Ecol Evol 15, 421-425
233. Riedl R (1984) Fauna und Flora des Mittelmeers Paul Parey, Hamburg
234. Rinkevich, B (2015) Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? Curr Opin Environ Sustain, 7, 28–36
235. Rivetti, I, Fraschetti, S, Lionello, P, Zambianchi, E & Boero, F (2014) Global warming and mass mortalities of benthic invertebrates in the Mediterranean Sea. PLoS ONE, 9(12), e115655
236. Roark EB, Guilderson TP, Dunbar RB, Fallon SJ & Mucciarone DA (2009) Extreme longevity in proteinaceous deep-sea corals. Proc Natl Acad Sci USA 106, 5204-5208
237. Roberts CM, O'Leary BC, McCauley DJ et al (2017) Marine reserves can mitigate and promote adaptation to climate change. Proceedings of the National Academy of Sciences USA, 114(24), 6167-6175
238. Robinson LM, Elith J, Hobday AJ et al. (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. Global Ecology and Biogeography, 20(6), 789-802
239. Rutterford LA, Simpson SD, Jennings S et al. (2015) Future fish distributions constrained by depth in warming seas. Nature Climate Change, 5(6), 569
240. Sæther BE, Coulson T, Grøtan V et al. (2013) How life history influences population dynamics in fluctuating environments. The American Naturalist, 182(6), 743-759
241. Sala E, Ballesteros E, Dendrinos P et al. (2012) The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. PLoS ONE, 7(2), e32742
242. Sala, E, Garrabou, J & Zabala, M (1996) Effects of diver frequentation on Mediterranean sublittoral populations of

the bryozoan Pentapora fascialis. Marine Biology, 126(3), 451-459

243. Sala E et al. (2018) Assessing real progress towards effective ocean protection Marine Policy 911 (2018): 11-13
244. Salguero-Gómez R, Jones OR, Jongejans E et al. (2016) Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. Proc Natl Acad Sci USA, 113, 230-235
245. Salguero-Gómez, R, & Casper, B B (2010) Keeping plant shrinkage in the demographic loop. Journal of Ecology, 98(2), 312-323
246. Salguero-Gómez, R, Siewert, W, Casper, BB & Tielbörger, K (2012) A demographic approach to study effects of climate change in desert plants. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 367(1606), 3100-3114
247. Santangelo G, Abbiati M, Giannini F, Cicogna F (1993) Red coral fishing trends in the western Mediterranean Sea. Scientia Marina 57: 139–143
248. Santangelo G & Bramanti L (2010) Quantifying the decline in Corallium rubrum populations. Marine Ecology Progress Series, 418: 295-297
249. Santangelo G, Bramanti L, Rossi S et al. (2012) Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral *Corallium rubrum*. J Exp Mar Bio Ecol, 411, 7-13
250. Santangelo G, Carletti E, Maggi E, Bramanti L (2003) Reproduction and population sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. Marine Ecology Progress Series, 248: 99–108
251. Sbrocco EJ & Barber PH (2013) MARSPEC: ocean climate layers for marine spatial ecology. Ecology, 94(4), 979-979
252. Scheffers BR, De Meester L, Bridge TC et al. (2016) The broad footprint of climate change from genes to biomes to people. Science, 354(6313), aaf7671
253. Selig ER & Bruno JF (2010) A global analysis of the effectiveness of marine protected areas in preventing coral loss. PLoS ONE 5(2): e9278
254. Serrano, O, Serrano, E, Inostroza, K et al. (2017) Seagrass meadows provide 3D habitat for reef fish. Frontiers in Marine Science, 4, 54
255. Shaish, L, Levy, G, Katzir, G & Rinkevich, B (2010) Employing a highly fragmented, weedy coral species in reef restoration. Ecol Eng, 36(10), 1424-1432
256. Short FT, Polidoro B, Livingstone SR et al. (2011) Extinction risk assessment of the world’s seagrass species. Biological Conservation, 144(7), 1961-1971
257. Shriver, RK, Cutler, K & Doak, DF (2012) Comparative demography of an epiphytic lichen: support for general life history patterns and solutions to common problems in demographic parameter estimation. Oecologia, 170(1), 137-146
258. Smith KF & Brown JH (2002) Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. Glob Ecol Biogeo, 11(4), 313-322

259. Sorice MG, Oh CO & Ditton RB (2007) Managing scuba divers to meet ecological goals for coral reef conservation AMBIO: A Journal of the Human Environment, 36(4), 316-322
260. Squires DF (1959) Results of the puritan-American museum of natural history expedition to western Mexico. Bulletin of the American Museum of Natural History, New York, USA 118, 371-431
261. Stearns SC (1977) The evolution of life history traits: a critique of the theory and a review of the data. Annu Rev Ecol Evol Syst 8, 145-171
262. Stearns SC (1983) The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos, 173-187
263. Stearns SC (1989) Trade-offs in life-history evolution. Functional Ecology, 3(3), 259-268
264. Sunday JM, Pecl GT, Frusher S et al. (2015) Species traits and climate velocity explain geographic range shifts in an ocean warming hotspot. Ecology Letters, 18(9), 944-953
265. Talluto MV, Boulangeat I, Ameztegui A et al. (2016) Cross-scale integration of knowledge for predicting species ranges: a metamodelling framework. Global Ecology and Biogeography, 25(2), 238-249
266. Tanner JE (2001) The influence of clonality on demography: patterns in expected longevity and survivorship. Ecology 82, 1971-1981
267. Teixidó N, Garrabou J & Harmelin JG (2011) Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. PLoS ONE 6, e23744
268. Tilman D, Reich PB, Knops J et al. (2001) Diversity and productivity in a long-term grassland experiment. Science, 294(5543), 843-845
269. Tilman, D, Wedin, D & Knops, J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature, 379(6567), 718
270. Tittensor DP, Mora C, Jetz W et al. (2010) Global patterns and predictors of marine biodiversity across taxa. Nature, 466(7310), 1098-1101
271. Torrents O (2007) Biologie des populations du corail rouge *Corallium rubrum* (L 1758) de Méditerranée nord–occidentale. PhD Thesis Université de la Méditerraneé Aix-Marseille II
272. Torrents O, Tambutte E, Caminiti N, Garrabou J (2008) Upper thermal thresholds of shallow vs deep populations of the precious Mediterranean red coral *Corallium rubrum* (L): assessing the potential effects of warming in the NW Mediterranean. Journal of Experimental Marine Biology and Ecology, 357: 7–19
273. Torrents O, Garrabou J, Marschal C & Harmelin JG (2005) Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L) in the Marseilles area (France, NW Mediterranean). Biological Conservation, 121(3), 391-397
274. Toth LT, Van Woesik R, Murdoch TJT et al. (2014) Do no-take reserves benefit Florida's corals? 14 years of change and

stasis in the Florida Keys National Marine Sanctuary. Coral Reefs, 33(3), 565-577

275. Tsounis G, Rossi S, Bramanti L & Santangelo G (2013) Management hurdles for sustainable harvesting of *Corallium rubrum*. Marine Policy 39: 361–364
276. Tsounis G, Rossi S, Gili JM & Arntz WE (2007) Red coral fishery at the Costa Brava (NW Mediterranean): Case study of an overharvested precious coral. Ecosystems 10: 975-986
277. Tsounis G, Rossi S, Aranguren M, Gili JM & Arntz, W (2006) Effects of spatial variability and colony size on the reproductive output and gonadal development cycle of the Mediterranean red coral (*Corallium rubrum* L). Marine Biology, 148(3), 513-527
278. Tsounis G, Rossi S, Grigg R, Santangelo G, Bramanti, L & Gili JM (2010) The exploitation and conservation of precious corals. Oceanography and Marine Biology: An Annual Review 48, 161-212
279. Van Hooidonk R, Maynard JA and Planes S (2013) Temporary refugia for coral reefs in a warming world. Nature Climate Change
280. Vargas-Yanez, M, García, M J, Salat, J, García-Martínez, M C, Pascual, J, and Moya, F (2008) Warming trends and decadal variability in the Western Mediterranean shelf. Glob Planet Chang 63, 177–184
281. Vasek FC (1980) Creosote bush: long-lived clones in the Mojave Desert. Am J Botany, 246-255
282. Venegas-Li, R, Levin, N, Possingham, H & Kark, S (2017) 3D spatial conservation prioritisation: Accounting for depth in marine environments. Methods in Ecology and Evolution.
283. Vermeij MJA & Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population ecology. Ecology 89(7): 1994–2004
284. Vesk AP, Nolan R, Thomson JR et al (2008) Time lags in provision of habitat resources through revegetation. Biol Cons, 141(1):174-186
285. Villellas J, Doak DF, García MB & Morris WF (2015) Demographic compensation among populations: what is it, how does it arise and what are its implications? Ecology Letters 18, 1139-1152
286. Wernberg T, Bennett S, Babcock RC et al. (2016) Climate-driven regime shift of a temperate marine ecosystem. Science, 353(6295), 169-172
287. Wolff NH, Mumby PJ, Devlin M & Anthony KRN (2018) Vulnerability of the Great Barrier Reef to climate chnage and local pressures. Global Change Biology, 1-14
288. Worm B, Barbier EB, Beaumont N et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. Sicence, 314(5800), 787-790
289. Zabala M & Ballesteros E (1989) Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean. Scientia Marina, 53(1), 3-17

Annexes

Supplementary Materials Chapter I

Figure S1. Long-term population trends at nine red coral populations in the NW Mediterranean.

Figure S2. *Corallium rubrum* mean and maximum longevity estimates depending on matrix dimensions**.**

Figure S3. *Corallium rubrum* normalized age-dependent vital rates and size-dependent elasticity patterns.

Table S1. Red coral populations in the NW Mediterranean Sea studied in this work.

Table S2. Correlation coefficients between maximum depth and maximum lifespan in marine sessile species.

Table S3. Best fit models for different longevity estimates based on matrix models of octocorals, hexacorals and sponges.

Table S4. Summary statistics of best supported multiple linear regression model between maximum depth occurrence and maximum lifespan marine sessile species

Table S5. Summary statistics of best-supported multiple linear models for the effect of maximum depth occurrence on maximum lifespan of marine sessile species, including the potential effects of different ageing methods (annual ring counts, radiocarbon dating, demographic simulations and growth curves) and taxonomic levels (Phylum, Class, Order). Model support was based on Akaike Information Criteria corrected for small sample sizes (AICc).

Table S6. Summary statistics of quantile linear regression models between maximum depth occurrence and maximum lifespan across all marine sessile species (n = 223).

Table S7. Multiple linear regression models used to assess the effects of maximum longevity on temporal variance in population size in terrestrial plant species (n=25) and marine sessile invertebrates (n=9).

Table S8. Mean fecundity values of marine sessile species (n = 28). Fecundity values correspond to the mean annual recruitment rate per adult and were computed based on the F values of each size-class of the population matrix (first row), weigthed by the proportion of each class at the Stable Stage Distribution. We only included species in which the first stage corresponded to recruits.

Table S9. Source studies of longevity estimates and maximum occurrence depth for marine sessile species included in the comparative analysis.

Table S10. Source studies of long-term demographic variability estimates included in the comparative analysis.

Supplementary Methods (I): Model Construction

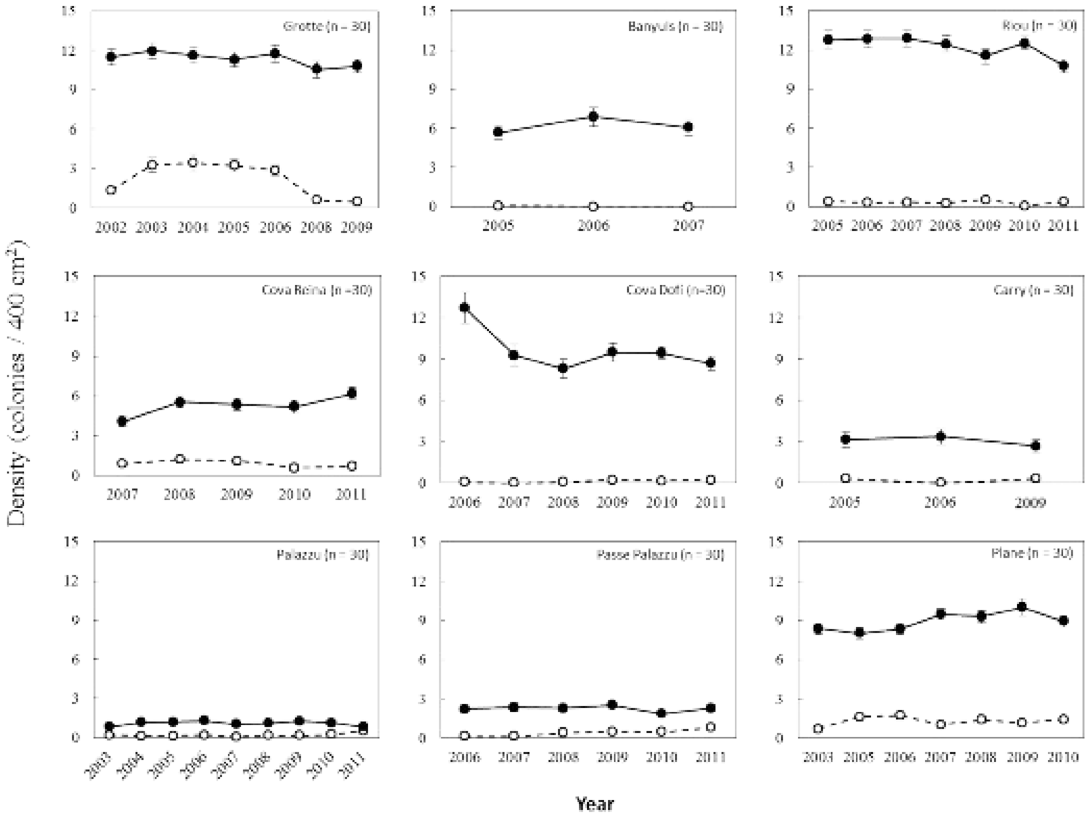


Figure S1. Long-term population trends at nine red coral populations in the NW Mediterranean. Black dots indicate adult and white dots recruit densities.

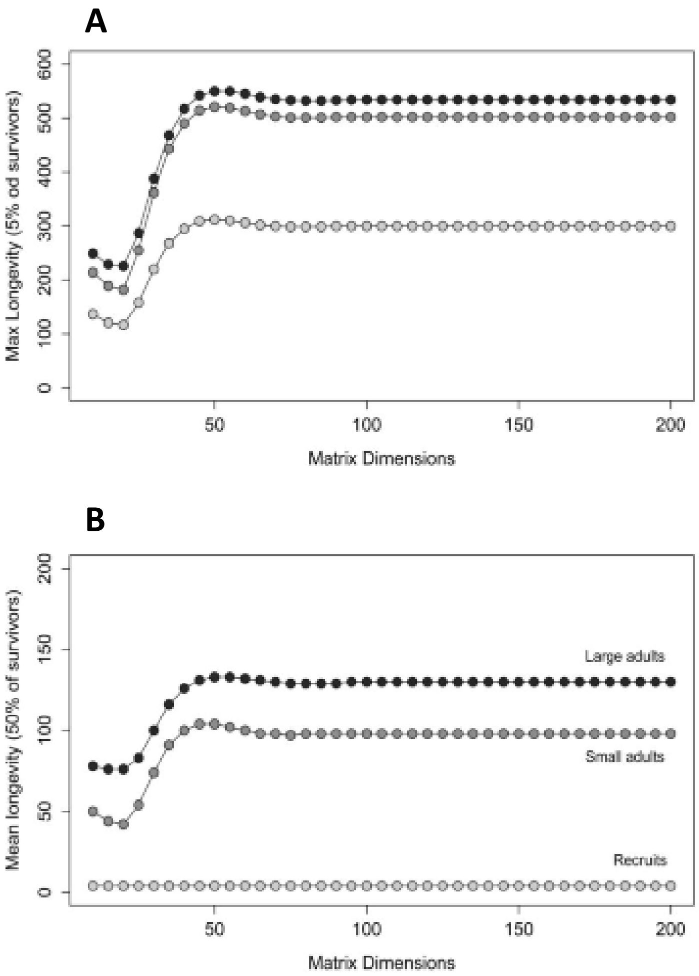
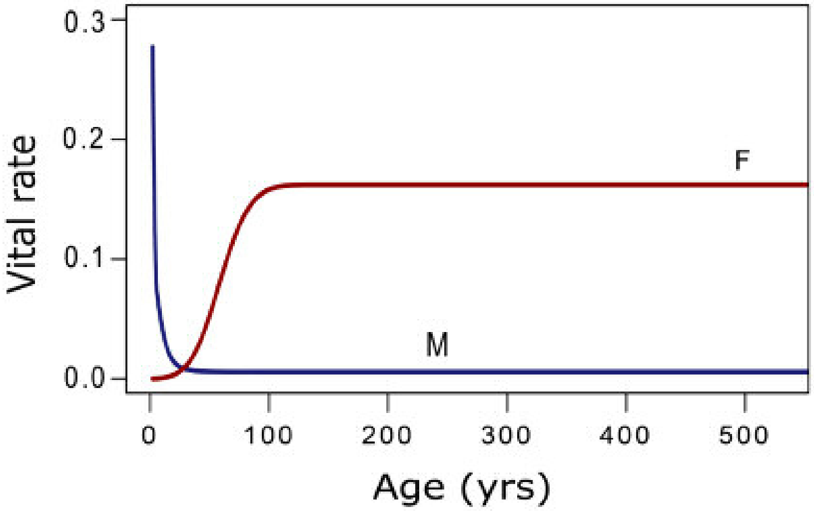


Figure S2. *Corallium rubrum* mean and maximum longevity estimates depending on matrix dimensions**.** A. Shows maximum potential lifespan, the number of years until 5% of the initial population remains alive. B. Shows the mean lifespan, the number of years until the 50% of the initial population remains alive. Simulations were performed based on 100 individuals starting as recruits (light grey), adults of the smallest size class (grey), and adults of the largest size class (black).



S3. *Corallium rubrum* Normalized age-dependent vital rates: mortality (M) and fecundity (F).

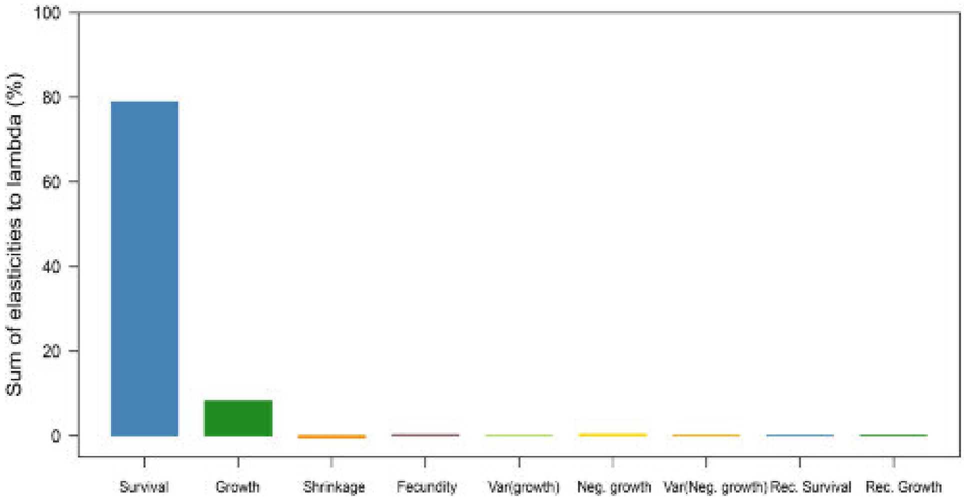


Figure S4. Patterns of sum of elasticity values to the asymptotic population growth rates of different vital rates in the red coral *Corallium rubrum*. From left to right: survival of adult colonies, mean normal growth of adult colonies, probability of extreme shrinkage, fecundity, variance in normal growth of adult colonies, mean negative growth, variance in mean negative growth, recruits survival, and recruits growth.

Table S1. Red coral (*Corallium rubrum*) populations in the NW Mediterranean Sea used in this study.

Name	**Longitude**	**Latitude**	**Depth (m)**	**Area**	**Protection Level**	**N**	**Years Surveyed**
Dofi	3° 13' 44" E	42° 2' 29" N	17 - 22	Catalan Sea	Partial Protection	148	2006 to 2011
Reina	3° 13' 34" E	42° 2' 49" N	17 - 24	Catalan Sea	Partial Protection	140	2007 to 2011
Banyuls	3°7'50" E	42°28' 60" N	23 - 25	Catalan Sea	Integral Protection	108	2005 to 2007
Maire	5°20'14" E	43°12'32" N	15 - 18	Marseille	Unprotected	140	2002 to 2009
Riou	5° 14' 3" E	43° 6' 13" N	17 - 24	Marseille	Unprotected	204	2005 to 2009
Plane	5° 14' 3" E	43° 11' 54" N	17 - 24	Marseille	Unprotected	154	2003 to 2010
Passe	8° 33' 27" E	42°21' 35" N	24 - 27	Corsica	Integral Protection	145	2006 to 2011
Palazzu	8° 33' 27" E	42° 21' 35" N	19 - 22	Corsica	Integral Protection	137	2003 to 2011

Table S2. Correlation coefficients between maximum depth and maximum lifespan in marine sessile species. The category "All Marine Sessile" includes data on species in five most-represented taxa plus those fromother taxa, including bryozoan, hydrozoan, polychaeta, cirripeds and one tunicate species. Statistics shown are: n = number of species included in the analysis, rho = Spearman's correlation coefficient; P = Pearson's correlation coefficient.

Spearmank' Rank correlation

Taxa	Maximum Lifespan vs. Maximum Depth Occurrence			Maximum Lifespan vs. Depth at the Study Site		
	n	**rho**	**P value**	**n**	**rho**	**P value**
Octocorals	35	0.673	P < 0.001	34	0.546	P = 0.008
Hexacorals	40	0.592	P < 0.001	34	0.704	P < 0.001
Sponges	17	0.647	P < 0.001	16	0.729	P = 0.001
Bivalves	93	0.358	P < 0.001	34	0.700	P < 0.001
Macroalgae	14	0.600	P = 0.023	9	0.597	P = 0.089
All Marine Sessile	223	0.503	P < 0.001	138	0.695	P < 0.001

Pearson's R correlation

Taxa	Maximum Lifespan vs. Maximum Depth Occurrence			Maximum Lifespan vs. Depth at the Study Site		
	n	**R**	**P value**	**n**	**R**	**P value**
Octocorals	35	0.714	P < 0.001	34	0.594	P = 0.0002
Hexacorals	40	0.650	P < 0.001	34	0.790	P < 0.001
Sponges	17	0.739	P < 0.001	16	0.727	P = 0.0014
Bivalves	93	0.456	P < 0.001	34	0.679	P < 0.001
Macroalgae	14	0.620	P = 0.018	9	0.674	P = 0.046
All Marine Sessile	223	0.547	P < 0.001	138	0.674	P < 0.001

Table S3. Sumary of the four best supported models predicting longevity estimates based on matrix models of octocorals, hexacorals and sponges.

Model	Predictors / Levels	Estimate	Std. Error	P value	AICc	delta AIC
Maximum Longevity Adults ~ Depth + Dimensions	Intercept	0.849207	0.278340	0.0072	67.219	0
	Maximum Depth	0.020635	0.008199	0.0222		
	Dimensions	-0.157308	0.082079	0.0723		
	Overal Model: $R^2 = 0.4298$; F = 8.161; df = 17; P = 0.0033					
Maximum Longevity Adults ~ Depth	Intercept	0.956596	0.292187	0.0042	67.965	0.746
	Maximum Depth	0.005170	0.001558	0.0038		
	Overal Model: $R^2 = 0.\ 3796$; F = 11.01; df = 18; P = 0.0038					
Mean Longevity Recruits ~ Depth + Dimensions + Depth*Dimensions	Intercept	2.0324517	1.0345084	0.067	68.833	1.613
	Maximum Depth	0.0143110	0.0088083	0.124		
	Dimensions	-0.6189497	0.2300075	0.016		
	Maximum Depth*Dimensions	0.0006347	0.0002998	2.117		
	Overal Model: $R^2 = 0.\ 5463$; F = 8.625; df = 18; P = 0.001232					
Mean Longevity Adults ~ Depth + Dimensions + Depth*Dimensions	Intercept	1.9999077	1.0460125	0.074	69.275	2.056
	Maximum Depth	0.0164804	0.0089062	0.083		
	Dimensions	-0.4057816	0.2325653	0.100		
	Maximum Depth*Dimensions	0.0003458	0.0003032	0.271		
	Overal Model: $R^2 = 0.\ 4397$; F = 5.97; df = 16; P = 0.00624					

Table S4. Summary statistics of best supported multiple linear regression model between maximum depth occurrence and maximum lifespan for all marine sessile species (n = 223). Model support was based on Akaike Information Criteria corrected for small sample sizes (AICc). The second-best model had deltaAICc of 3.568. Data were log-transformed.

Best Fit Model	Predictors / Levels	Estimate	Std. Error	t value	P value
Longevity ~ Depth + Taxa + Method + Depth*Taxa	Intercept	0.67424	0.14385	4.687	< 0.001
	Maximum Depth	0.29642	0.07414	3.998	< 0.001
	Taxa (Hexacoral)	-0.01922	0.34657	-0.055	0.9558
	Taxa (Macroalgae)	-0.43510	0.33371	-1.304	0.1939
	Taxa (Octocoral)	0.62504	0.36226	1.725	0.0861
	Taxa (Sponge)	-0.71140	0.56550	-1.258	0.2100
	Method (Matrix/Survival)	-0.17426	0.09751	-1.787	0.0756
	Method (Oxygen)	0.33719	0.09751	0.883	0.3785
	Method (Radiometric Age)	0.39427	0.38196	2.492	0.0136
	Maximum Depth * Taxa (Hexacoral)	0.21700	0.15820	1.223	0.2228
	Maximum Depth * Taxa (Macroalgae)	0.59011	0.17740	2.176	0.0308
	Maximum Depth * Taxa (Octocoral)	-0.05002	0.27123	-0.294	0.7689
	Maximum Depth * Taxa (Sponge)	0.74739	0.29825	2.506	0.0131
	Overall model statistics: $R^2 = 0.5105$; F = 18.12; df = 185; $P < 0.0001$				

Table S5. Summary statistics of best supported multiple linear regression models between maximum depth occurrence and maximum lifespan in marine sessile species, including the potential effects of different ageing methods (annual ring counts, radiocarbon dating, demographic simulations and growth curves) and taxonomic levels (Phylum, Class, Order). Model support was based on Akaike Information Criteria corrected for small sample sizes (AICc).

Formula	**Intercept**	**Depth slope (P value)**	**df**	**AICc**	**Delta AICc**
Longevity ~ Depth + Class + Method	1.0129	0.3633 (>0.0001)	15	315.0721	0
Longevity ~ Depth + Class + Method + Depth*Class	0.8859	0.4299 (0.00101)	21	316.2796	1.2075
Longevity ~ Depth + Phylum + Depth*Phylum	-2.0621	1.4262 (0.2853)	15	316.8752	1.803146
Longevity ~ Depth + Method + Phylum	-2.8295	1.8155 (0.175)	12	319.1589	4.086796
Longevity ~ Depth + Class + Depth*Class	0.4153	0.6715 (>0.0001)	18	322.0485	4.0868

Table S6. Summary statistics of quantile linear regression models between maximum depth occurrence and maximum lifespan across all marine sessile species (n = 223)
.

Quantile	Intercept (IC 95%)	Slope (IC 95%)
10%	-0.0682 (-0.516 – 0.083)	0.441 (0.361 – 0.677)
20%	0.0691 (-0.174, 0.173)	0.486 (0.427 – 0.593)
80%	0.811 (0.547 – 0972)	0.628 (0.570 – 0.791)
90%	0.9031 (0.691 – 1.071)	0.715 (0.550 – 0.918)

Table S7. Multiple linear regression models used to assess the effects of maximum longevity on temporal variance in population growth (realized log-lambda values) in terrestrial plant species (n=25) and marine sessile invertebrates (n=9).

Model	R^2	AICc	Delta	Weight
log(Variance) ~ log(Longevity) + Habitat	0.543	125.4652	0	0.6222
log(Variance) ~ log(Longevity) + Habitat + log(Longevity)*Habitat	0.528	128.1723	2.707	0.1607
log(Variance) ~ log(Longevity)	0.466	130.2689	4.804	0.0671
log(Variance) ~ Habitat	0.224	142.9632	17.498	0.0001

Table S8. Mean fecundity values of marine sessile species (n = 28). Fecundity values correspond to the mean annual recruitment rate per adult and were computed based on the F values of each size-class of the population matrix (first row), weigthed by the proportion of each class at the Stable Stage Distribution. We only included species in which demographic data in the form of standar matrix population models, including fecundity were available. To allow standard comparisons, we did not include matrices in which the first stage corresponded to larvae or eggs.

Species Name	Taxa	Fecundity	Source
A. islandica	Mollusca	0.001	Ripley & Caswell 2008
P. abrupta	Mollusca	0.004	Ripley & Caswell 2008
X. muta	Mollusca	0.006	McMurray *et al.* 2010
T. gigas	Mollusca	0.013	Ripley & Caswell 2008
A. colbecki	Mollusca	0.040	Ripley & Caswell 2008
A. compressa	Mollusca	0.071	Mercado-Molina 2011
C. rubrum	Cnidaria	0.077	Present study
A. palmata	Cnidaria	0.077	Vardi *et al.* 2012
P. astreoides	Cnidaria	0.083	Edmunds 2010
L. digitata	Macroalgae	0.126	Chapman 1990
S. graminea	Porifera	0.135	Cropper 1999
G. demissa	Mollusca	0.254	Ripley & Caswell 2008
N. obscurata	Mollusca	0.261	Dudas. et al. 2007
H. iris	Mollusca	0.547	Somerville *et al*. 2014
H. sorenseni	Mollusca	0.727	Roggers-Bennett 2006
H. rufenses	Mollusca	0.794	Roggers-Bennett 2006
P. caesia	Cnidaria	0.847	Tanner 1997
B. annulata	Cnidaria	0.875	Nelsen 2008
A. nana	Macroalgae	0.966	Pfister 2005
L. notorcadensis	Mollusca	1.176	Ripley & Caswell 2008
L. miliaris	Mollusca	1.639	Ripley & Caswell 2008
H. laevigata	Mollusca	1.654	Fordham et al. 2013
M. mactroides	Mollusca	1.791	Brazeiro & Defeo 1999
M. californianus	Mollusca	2.314	Carson *et al*. 2011
M. galloprovincialis	Mollusca	2.768	Carson *et al.* 2011
Alcyonium sp.	Cnidaria	3.257	McFadden 1991
F. distichus	Macroalgae	8.001	Ang & De Wreede 1993
L. rubra	Mollusca	115.314	Ripley & Caswell 2008

References included in Table S8

1. Ang Jr, P. O., & De Wreede, R. E. (1993). Simulation and analysis of the dynamics of a Fucus distichus (Phaeophyceae, Fucales) population. Marine Ecology Progress Series, 253-265.

2. Brazeiro, A., & Defeo, O. (1999). Effects of harvesting and density dependence on the demography of sandy beach populations: the yellow clam Mesodesma mactroides of Uruguay. Marine Ecology Progress Series, 127-135.

3. Carson, H. S., Cook, G. S., López-Duarte, P. C., & Levin, L. A. (2011). Evaluating the importance of demographic connectivity in a marine metapopulation. *Ecology*, *92*(10), 1972-1984.

4. Chapman, A. R. (1993). 'Hard'data for matrix modelling of *Laminaria digitata* (Laminariales, Phaeophyta) populations. Hydrobiologia, 260(1), 263-267.

5. Cropper, W. P., & DiResta, D. (1999). Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after Hurricane Andrew. Ecological Modelling, 118(1), 1-15.

6. Dudas, S. E., Dower, J. F., & Anholt, B. R. (2007). Invasion dynamics of the varnish clam (*Nuttallia obscurata*): a matrix demographic modeling approach. Ecology, 88(8), 2084-2093.

7. Edmunds, P. J. (2010). Population biology of *Porites astreoides* and *Diploria strigosa* on a shallow Caribbean reef. Marine Ecology Progress Series, 418, 87-104.

8. Fordham, D. A., Mellin, C., Russell, B. D., Akçakaya, R. H., Bradshaw, C. J., Aiello Lammens, M. E., & Brook, B. W. (2013). Population dynamics can be more important than physiological limits for determining range shifts under climate change. Global Change Biology, 19(10), 3224-3237.

9. McFadden, C. S. (1991). A comparative demographic analysis of clonal reproduction in a temperate soft coral. Ecology, 72(5), 1849-1866.

10. McMurray, S. E., Henkel, T. P., & Pawlik, J. R. (2010). Demographics of increasing populations of the giant barrel sponge *Xestospongia muta* in the Florida Keys. Ecology, 91(2), 560-570.

11. Mercado-Molina, A. E., Sabat, A. M., & Yoshioka, P. M. (2011). Demography of the demosponge *Amphimedon compressa*: Evaluation of the importance of sexual versus asexual recruitment to its population dynamics. Journal of Experimental Marine Biology and Ecology, 407(2), 355-362.

12. Nelsen, M. (2008). Population dynamic modeling of the corkscrew sea anemone *Bartholomea annulata* on Caribbean coral reefs. Doctoral dissertation, Auburn University, Auburn, AL.

13. Pfister, C. A., & Wang, M. (2005). Beyond size: matrix projection models for populations where size is an incomplete descriptor. Ecology, 86(10), 2673-2683.

14. Ripley, B. J., & Caswell, H. (2008). Contributions of growth, stasis, and reproduction to fitness in brooding and broadcast spawning marine bivalves. Population Ecology, 50(2), 207-214.

15. Rogers-Bennett, L., & Leaf, R. T. (2006). Elasticity analyses of size-based red and white abalone matrix models: management and conservation. Ecological Applications, *16*(1), 213-224.

16. Somerville, G. J., Krkosek, M., & Hepburn, C. D. (2014). A matrix model and elasticity analysis for New Zealand's blackfoot pāua *Haliotis iris*. Fisheries Research, 151, 158-168.

17. Tanner, J. E. (1997). The effects of density on the zoanthid Palythoa caesia. Journal of Animal Ecology, 793-810.

18. Vardi, T., Williams, D. E., & Sandin, S. A. (2012). Population dynamics of threatened elkhorn coral in the northern Florida Keys, USA. Endangered Species Research, 19(2), 157-169.

Table S9. Source studies of longevity estimates and maximum occurrence depth for marine sessile species included in the comparative analysis (n = 241) (See completed references list below).

Name	Family	Taxa	Lifespan Method	Source Lifespan	Source Depth
Acropora cervicornis	Acroporidae	Hexacoral	Matrix/Survival	1	37, 44
Acropora hyacinthus	Acroporidae	Hexacoral	Matrix/Survival	2	38, 44
Acropora palmata	Acroporidae	Hexacoral	Matrix/Survival	3	37, 44
Agaricia agaricites	Agariciidae	Hexacoral	Matrix/Survival	4	37, 44
Leptoseris cucullata	Agariciidae	Hexacoral	Matrix/Survival	9	49, 50, 44
Bartholomea annulata	Aiptasiidae	Hexacoral	Matrix/Survival	19	42
Antipathes dendrochristos	Antipathidae	Hexacoral	Radiometric Age	69, 70	69
Antipathes dichotoma	Antipathidae	Hexacoral	Radiometric Age	58	NA
Antipathes griggi	Antipathidae	Hexacoral	Radiometric Age	70	NA
Caryophyllia inornata	Caryophylliidae	Hexacoral	Growth	76, 86	87
Desmophyllum cristagalli	Caryophylliidae	Hexacoral	Radiometric Age	60	NA
Lophelia pertusa	Caryophylliidae	Hexacoral	Radiometric Age	131	130
Solenosmilia variabilis	Caryophylliidae	Hexacoral	Radiometric Age	132	133
Leptosammia pruvoti	Dendrophylliidae	Hexacoral	Growth	84, 76	81
Balanophyllia elegans	Dendrophylliidae	Hexacoral	Matrix/Survival	79	78
Balanophyllia europea	Dendrophylliidae	Hexacoral	Growth	80	81, 82
Enallopsammia rostrata	Dendrophylliidae	Hexacoral	Radiometric Age	134	135136
Ctenactis echinata	Fungiidae	Hexacoral	Growth	52	44
Diaseris distorta	Fungiidae	Hexacoral	Growth	52	37,44
Fungia actiniformis	Fungiidae	Hexacoral	Growth	52	44
Fungia fungites	Fungiidae	Hexacoral	Growth	52	44
Fungia granulosa	Fungiidae	Hexacoral	Growth	52	49, 44
Fungia paumotensis	Fungiidae	Hexacoral	Growth	52	49, 44
Leiopathes glaberime	Leiopathidae	Hexacoral	Radiometric Age	58,70	70
Leiopathes sp.	Leiopathidae	Hexacoral	Radiometric Age	57	133
Goniastrea aspera	Merulinidae	Hexacoral	Matrix/Survival	7	44
Goniastrea favulus	Merulinidae	Hexacoral	Matrix/Survival	7	258
Orbicella annularis	Merulinidae	Hexacoral	Matrix/Survival	9	37, 44
Platygyra sinensis	Merulinidae	Hexacoral	Matrix/Survival	7	237
Diploria strigosa	Mussidae	Hexacoral	Matrix/Survival	6	45
Antipathella fiordensis	Myriopathidae	Hexacoral	Growth	71, 70	41
Plumapathes pennacea	Myriopathidae	Hexacoral	Growth	72,70	NA

Kulamanamana haumeaae	Parazoanthidae	Hexacoral	Radiometric Age	57, 59	59
Parazoanthus axinellae	Parazoanthidae	Hexacoral	Matrix/Survival	75	74
Pocillopora damicornis	Pocilloporidae	Hexacoral	Matrix/Survival	2	48, 44
Alveopora japonica	Poritidae	Hexacoral	Growth	181	181
Porites astreoides	Poritidae	Hexacoral	Matrix/Survival	6	49, 50, 44
Fannyella rossii	Primnoidae	Hexacoral	Radiometric Age	64	NA
Stauropathes artica	Schizopathidae	Hexacoral	Radiometric Age	62	NA
Palythoa caesia	Sphenopidae	Hexacoral	Matrix/Survival	11	41
Alcyonium acaule	Alcyoniidae	Octocoral	Matrix/Survival	75, 76	77
Anthomastus ritteri	Alcyoniidae	Octocoral	Growth	179	179
Gorgonia ventalina	Anthothelidae	Octocoral	Matrix/Survival	88	91
Chrysogorgia sp.	Chrysogorgiidae	Octocoral	Radiometric Age	177	177
Corallium niobe	Corallidae	Octocoral	Radiometric Age	67	NA
Corallium secundum	Corallidae	Octocoral	Radiometric Age	58	NA
Corallium rubrum	Coralliidae	Octocoral	Matrix/Survival	Present Study	55
Eunicella singularis	Gorgoniidae	Octocoral	Growth	66	73
Leptogorgia sarmentosa	Gorgoniidae	Octocoral	Growth	85	123
Leptogorgia virgulata	Gorgoniidae	Octocoral	Matrix/Survival	8	259
Pseudopterogorgia	Gorgoniidae	Octocoral	Matrix/Survival	14	NA
Pseudopterogorgia acerosa	Gorgoniidae	Octocoral	Matrix/Survival	88	41
Pseudopterogorgia americana	Gorgoniidae	Octocoral	Matrix/Survival	88	91
Halipteris willemoesi	Halipteridae	Octocoral	Radiometric Age	63	NA
Halipteris willemoesi	Halipteridae	Octocoral	Growth	176	176
Isidella tentaculum	Isididae	Octocoral	Radiometric Age	129	NA
Keratosis ornata	Isididae	Octocoral	Radiometric Age	62	NA
Keratosis sp.	Isididae	Octocoral	Radiometric Age	128	NA
Acanella arbuscula	Isididae	Octocoral	Radiometric Age	62	NA
Eunicea laxispica	Plexauridae	Octocoral	Matrix/Survival	88	NA
Eunicea succinea	Plexauridae	Octocoral	Matrix/Survival	88	92
Eunicea tourneforti	Plexauridae	Octocoral	Matrix/Survival	88	NA
Muricea californica	Plexauridae	Octocoral	Growth	83	NA
Muricea fruticosa	Plexauridae	Octocoral	Growth	83	NA
Muriceopsis flavida	Plexauridae	Octocoral	Matrix/Survival	88	92
Paramuricea biscaya	Plexauridae	Octocoral	Growth	177	177
Paramuricea clavata	Plexauridae	Octocoral	Matrix/Survival	12	56
Paramuricea spp.	Plexauridae	Octocoral	Radiometric Age	62	NA

Plexaura A	Plexauridae	Octocoral	Matrix/Survival	13	NA
Plexaura flexuosa	Plexauridae	Octocoral	Matrix/Survival	88	91
Plexaurella dichotoma	Plexauridae	Octocoral	Matrix/Survival	88	91
Pseudoplexaura porosa	Plexauridae	Octocoral	Matrix/Survival	88	91
Pseudoplexaura wagenaari	Plexauridae	Octocoral	Matrix/Survival	88	91
Primnoa resedaeformis	Primnoidae	Octocoral	Radiometric Age	60, 65	62
Thouarella variabilis	Primnoidae	Octocoral	Radiometric Age	64	NA
Fannyella abies	Primnoidae	Octocoral	Radiometric Age	64	NA
Aplysina cavernicola	Aplysinidae	Sponge	Growth	76	104
Amphimedon compressa	Chalinidae	Sponge	Matrix/Survival	5	102
Haliclona fulva	Chalinidae	Sponge	Growth	76	103
Chondrosia reniformis	Chondrosiidae	Sponge	Growth	76	99
Crambe crambe	Crambeidae	Sponge	Matrix/Survival	76	101
Desmapsamma anchorata	Desmacididae	Sponge	Matrix/Survival	105	106
Monorhaphis chuni	Monorhaphididae	Sponge	Radiometric Age	94	NA
Mycale fistulifera	Mycalidae	Sponge	Matrix/Survival	170	NA
Petrosia ficiformis	Petrosiidae	Sponge	Growth	76	97, 98, 100
Xestospongia muta	Petrosiidae	Sponge	Growth	89	124
Rhabdocalyptus dawsoni	Rossellidae	Sponge	Growth	96	NA
Rosella spp.	Rossellidae	Sponge	Oxigen_Size	93	NA
Rossella racovitzaeracovitzae	Rossellidae	Sponge	Radiometric Age	95	NA
Spirastrella cunctatrix	Spirastrellidae	Sponge	Growth	76	100
Spongia graminea	Spongiidae	Sponge	Matrix/Survival	32	261
Stylocordyla borealis	Stylocordylidae	Sponge	Oxigen_Size	93	NA
Cinachyra antarctica	Tetillidae	Sponge	Oxigen_Size	93	NA
Scalarispongia scalaris	Thorectidae	Sponge	Growth	76	100
Glossus humanus	Glossidae	Bivalve	Growth	212	213
Panopea generosa	Hiatellidae	Bivalve	Growth	216	190, 217
Perna perna	Mytilidae	Bivalve	Growth	236	2237
Pedum spondyloideum	Pectinidae	Bivalve	Growth	180	248
Anadara tuberculosa	Anadarinae	Bivalve	Growth	207	211
Arca noae	Arcidae	Bivalve	Growth	208	195, 209
Arctica islandica	Arcticidae	Bivalve	Growth	127	121
Astarte arctica	Astartidae	Bivalve	Growth	240	41
Astarte borealis	Astartidae	Bivalve	Growth	240	215
Astarte elliptica	Astartidae	Bivalve	Growth	240	241

Astarte montagui	Astartidae	Bivalve	Growth	240	215
Astarte sulcata	Astartidae	Bivalve	Growth	234	234
Clinocardium californiense	Cardiidae	Bivalve	Growth	240	241
Clinocardium ciliatum	Cardiidae	Bivalve	Growth	240	241
Serripes gloenlandicus	Cardiidae	Bivalve	Growth	240	215
Tridacna gigas	Cardiidae	Bivalve	Matrix/Survival	16	205
Cardita affinis	Carditidae	Bivalve	Growth	226	227
Cyclocardia ventricosa	Carditidae	Bivalve	Growth	240	41
Donax denticulatus	Donacidae	Bivalve	Growth	173	215
Donax denticulatus	Donacidae	Bivalve	Growth	233	215
Donax trunculus	Donacidae	Bivalve	Growth	235	225
Mytilopsis leucophaeata	Dreissenidae	Bivalve	Growth	228	215
Glycymeris bimaculata	Glycymerididae	Bivalve	Growth	210	195
Glycymeris pilosa	Glycymerididae	Bivalve	Growth	194	195
Neopycnodonte zibrowii	Gryphaeidae	Bivalve	Radiometric Age	246	246
Haliotis iris	Haliotidae	Bivalve	Matrix/Survival	24	157
Haliotis laevigata	Haliotidae	Bivalve	Matrix/Survival	33, 34	158
Haliotis rufescens	Haliotidae	Bivalve	Matrix/Survival	25	159
Haliotis sorenseni	Haliotidae	Bivalve	Matrix/Survival	171	160
Cyrtodaria kurriana	Hiatellidae	Bivalve	Growth	240	272, 41
Hiatella arctica	Hiatellidae	Bivalve	Growth	240	273
Panomya ampla	Hiatellidae	Bivalve	Growth	240	41
Panopea abrupta	Hiatellidae	Bivalve	Growth	16, 151	152, 168
Hiatella arctica	Hiatellidae	Bivalve	Growth	119	167
Lasaea rubra	Lasaeidae	Bivalve	Matrix/Survival	16	278
Mysella kurilensis	Lasaeidae	Bivalve	Growth	240	240
Laternula elliptica	Laternulidae	Bivalve	Growth	148	150
Keletistes rhizoecus	Lucinidae	Bivalve	Growth	245	245
Lyonsia arenosa	Lyonsiidae	Bivalve	Growth	240	274
Lyonsia vniroi	Lyonsiidae	Bivalve	Growth	240	NA
Mactromeris polynyma	Mactridae	Bivalve	Growth	240	243
Spisula sachalinensis	Mactridae	Bivalve	Growth	240	244
Spisula solidissima	Mactridae	Bivalve	Growth	172	NA
Spisula subtruncata	Mactridae	Bivalve	Matrix/Survival	224	225
Mesodesma mactroides	Mesodesmatidae	Bivalve	Growth	175	174
Mya arenaria	Myidae	Bivalve	Growth	148	149, 196
Mya baxteri	Myidae	Bivalve	Growth	240	NA

Mya pseudoarenaria	Myidae	Bivalve	Growth	240	41
Mya truncata	Myidae	Bivalve	Growth	240	215
Mytilus trossulus	Mytilidae	Bivalve	Growth	240	242
Arvella manshurica	Mytilidae	Bivalve	Growth	240	240
Crenella decussata	Mytilidae	Bivalve	Growth	240	215
Crenomytilus grayanus	Mytilidae	Bivalve	Growth	240	192
Geukensia demissa	Mytilidae	Bivalve	Matrix/Survival	16	156
Limnoperna fortunei	Mytilidae	Bivalve	Growth	218	219
Lithophaga lithophaga	Mytilidae	Bivalve	Growth	206	195
Lithophaga patagonica	Mytilidae	Bivalve	Growth	214	215
Musculus discors	Mytilidae	Bivalve	Growth	240	215
Musculus niger	Mytilidae	Bivalve	Growth	240	215
Mytilus californianus	Mytilidae	Bivalve	Matrix/Survival	35	161
Mytilus galloprovincialis	Mytilidae	Bivalve	Matrix/Survival	35	162
Perna viridis	Mytilidae	Bivalve	Growth	231	232
Adamussium colbecki	Pectinidae	Bivalve	Matrix/Survival	16	278
Aequipecten opercularis	Pectinidae	Bivalve	Radiometric Age	147	146
Argopecten irradians irradians	Pectinidae	Bivalve	Growth	137	143144
Argopecten purpuratus	Pectinidae	Bivalve	Growth	139140	145
Placopecten megellanicus	Pectinidae	Bivalve	Growth	141, 142	153
Siliqua alta	Pharidae	Bivalve	Growth	240	41
Lissarca miliaris	Philobryidae	Bivalve	Matrix/Survival	16	155
Lissarca notorcadensis	Philobryidae	Bivalve	Matrix/Survival	16	154
Zirfaea pilsbryi	Pholadidae	Bivalve	Growth	240	NA
Pinna nobilis	Pinnidae	Bivalve	Matrix/Survival	122	120
Nuttallia obscurata	Psammobiidae	Bivalve	Matrix/Survival	31, 164	241
Pinctada imbricata	Pteriidae	Bivalve	Growth	229	230
Abra alba	Semelidae	Bivalve	Growth	247	41
Macoma balthica	Tellinidae	Bivalve	Growth	240	241
Macoma calcarea	Tellinidae	Bivalve	Growth	240	241
Macoma lama	Tellinidae	Bivalve	Growth	240	241
Macoma loveni	Tellinidae	Bivalve	Growth	240	215
Macoma middendorffi	Tellinidae	Bivalve	Growth	240	41
Tellina lutea	Tellinidae	Bivalve	Growth	240	41
Tellina tenuis	Tellinidae	Bivalve	Growth	238	239
Thracia septentrionalis	Thraciidae	Bivalve	Growth	240	215
Tindaria callistifomis	Tindariidae	Bivalve	Radiometric Age	138	NA

Tindaria callistiformis	Tindariidae	Bivalve	Radiometric Age	169	NA
Diplodonta aleutica	Ungulinidae	Bivalve	Growth	240	240
Callista brevisiphonata	Veneridae	Bivalve	Growth	197, 200	17, 18
Callista chione	Veneridae	Bivalve	Growth	201	203, 204, 222
Gemma gemma	Veneridae	Bivalve	Matrix/Survival	16	215
Liocyma fluctuosum	Veneridae	Bivalve	Growth	240	272
Mercenaria mercenaria	Veneridae	Bivalve	Growth	101	215
Protothaca euglypta	Veneridae	Bivalve	Growth	221	220, 221
Ruditapes philippinarum	Veneridae	Bivalve	Growth	201, 223	202
Yoldia eightsi	Yoldiidae	Bivalve	Growth	191	193
Yoldia myalis	Yoldiidae	Bivalve	Growth	240	215
Yoldia seminuda	Yoldiidae	Bivalve	Growth	240	241
Alaria nana	Alariaceae	Macroalgae	Matrix/Survival	17	267
Leathesia difformis	Chordariaceae	Macroalgae	Matrix/Survival	263	270
Lithothamnium crassiusculum	Corallinaceae	Macroalgae	Radiometric Age	187	187
Ascophyllum nodosum	Fucaceae	Macroalgae	Matrix/Survival	18	41
Fucus distichus	Fucaceae	Macroalgae	Matrix/Survival	23	268
Pelvetia fastigiata	Fucaceae	Macroalgae	Matrix/Survival	264	116
Iridaea splendens	Gigartinaceae	Macroalgae	Matrix/Survival	26	NA
Gracilaria gracilis	Gracilariaceae	Macroalgae	Matrix/Survival	265	
Halimeda incrassata	Halimedaceae	Macroalgae	Matrix/Survival	182	249
Hormosira banksii	Hormosiraceae	Macroalgae	Matrix/Survival	183	NA
Laminaria digitata	Laminariaceae	Macroalgae	Matrix/Survival	27	NA
Laminaria hyperborea	Laminariaceae	Macroalgae	Growth	117	117
Laminaria hyperborea	Laminariaceae	Macroalgae	Matrix/Survival	184	41
Macrocystis pyrifera	Laminariaceae	Macroalgae	Matrix/Survival	30	266
Petrocelis middendorffii	Phyllophoraceae	Macroalgae	Growth	113	NA
Pterocladia capillacea	Pterocladiaceae	Macroalgae	Growth	112	269
Petrocellis middendorffi	Rhodymeniophycidae	Macroalgae	Growth	186	NA
Cystoseira zosteroides	Sargassaceae	Macroalgae	NA	114	115
Clathromorphum nereostratum	Hapalidiaceae	Macroalgae	Growth	185	188
Adeonellopsis sp	Adeonidae	Bryozoan	NA	189	NA
Cellepora pumicosa	Celleporidae	Bryozoan	Matrix/Survival	22	262
Mucropetraliella ellerii	Petraliellidae	Bryozoan	Matrix/Survival	10	10
Watersipora subtorquata	Watersiporidae	Bryozoan	Matrix/Survival	20	107
Semibalanus balanoides	Archaeobalanidae	Cirriped (Crustacea)	Matrix/Survival	21	NA

Onithochiton quercinus	Chitonidae	Cirriped (Crustacea)	Growth	271	41
Chthamalus montagui	Chthamalidae	Cirriped (Crustacea)	Matrix/Survival	21	NA
Plaxiphora albida	Mopaliidae	Cirriped (Crustacea)	Growth	271	41
Cantellius sp.	Pyrgomatidae	Cirriped (Crustacea)	NA	180	41
Botrylloides violaceous	Styelidae	Tunicate	Matrix/Survival	20	110
Botryllus schlosseri	Styelidae	Tunicate	Matrix/Survival	20	111
Campanularia everta	Campanulariidae	Hydrozoan	NA	125	NA
Campanularia flexuosa	Campanulariidae	Hydrozoan	NA	126	NA
Corymorpha nutans	Corymorphidae	Hydrozoan	NA	250	250
Corymorpha palma	Corymorphidae	Hydrozoan	NA	250	41
Eutima japonica	Eirenidae	Hydrozoan	NA	253	NA
Helecium petrosum	Haleciidae	Hydrozoan	Growth	108	NA
Helecium pusillum	Haleciidae	Hydrozoan	Growth	108	NA
Nemertesia antennina	Plumulariidae	Hydrozoan	NA	251	41,
Errina novaezelandiae	Stylasteridae	Hydrozoan	Growth	178	178, 41
Tubularia indivisa	Tubulariidae	Hydrozoan	NA	125	NA
Tubularia indivisa	Tubulariidae	Hydrozoan	NA	252	41
Galeolaria hystrix	Serpulidae	Polychaete	NA	255	276
Circeis armoricana	Serpulidae	Polychaete	NA	256	41
Ficopomatus enigmaticus	Serpulidae	Polychaete	NA	254	41
Hydroides elegans	Serpulidae	Polychaete	NA	256	NA
Janua pagenstecheri	Serpulidae	Polychaete	NA	256	277
Neodexiospira brasiliensis	Serpulidae	Polychaete	NA	256	41
Pomatoceros triqueter	Serpulidae	Polychaete	NA	256	257
Pseudochitinopoma occidentalis	Serpulidae	Polychaete	NA	256	41
Spirobranchus cariniferus	Serpulidae	Polychaete	NA	255	NA
Spirobranchus giganteus	Serpulidae	Polychaete	NA	256	41

Complete references list of Table S6

1. Mercado-Molina, A. E., Ruiz-Diaz, C. P., Pérez, M. E., Rodríguez-Barreras, R., & Sabat, A. M. (2015). Demography of the threatened coral Acropora cervicornis: implications for its management and conservation. Coral Reefs, 34(4), 1113-1124.
2. Tanner, J. E. (1997). Interspecific competition reduces fitness in scleractinian corals. Journal of Experimental Marine Biology and Ecology, 214(1), 19-34.

3. Vardi, T., Williams, D. E., & Sandin, S. A. (2012). Population dynamics of threatened elkhorn coral in the northern Florida Keys, USA. Endangered Species Research, 19(2), 157-169.
4. Hughes, T. P. (1984). Population dynamics based on individual size rather than age: a general model with a reef coral example. American Naturalist, 778-795.
5. Mercado-Molina, A. E., Sabat, A. M., & Yoshioka, P. M. (2011). Demography of the demosponge Amphimedon compressa: Evaluation of the importance of sexual versus asexual recruitment to its population dynamics. Journal of Experimental Marine Biology and Ecology, 407(2), 355-362.
6. Edmunds, P. J. (2010). Population biology of Porites astreoides and Diploria strigosa on a shallow Caribbean reef. Marine Ecology Progress Series, 418, 87-104.
7. Babcock, R. C. (1991). Comparative demography of three species of scleractinian corals using age and size dependent classifications. Ecological Monographs, 61(3), 225-244.
8. Gotelli, N. J. (1991). Demographic models for Leptogorgia virgulata, a shallow water gorgonian. Ecology, 72(2), 457-467.
9. Hughes, T. P., & Tanner, J. E. (2000). Recruitment failure, life histories, and long term decline of Caribbean corals. Ecology, 81(8), 2250-2263.
10. Linacre, N. A., & Keough, M. J. (2003). Demographic effects of fragmentation history in modular organisms: illustrated using the bryozoan Mucropetraliella ellerii (MacGillivray). Ecological modelling, 170(1), 61-71.
11. Tanner, J. E. (1997). The effects of density on the zoanthid Palythoa caesia. Journal of Animal Ecology, 793-810.
12. Linares, C., Doak, D. F., Coma, R., Diaz, D., & Zabala, M. (2007). Life history and viability of a long lived marine invertebrate: the octocoral Paramuricea clavata. Ecology, 88(4), 918-928.
13. Lasker, H. R. (1991). Population growth of a gorgonian coral: equilibrium and non-equilibrium sensitivity to changes in life history variables. Oecologia, 86(4), 503-509.
14. Yoshioka, P. M. (1994). Size-specific life history pattern of a shallow-water gorgonian. Journal of Experimental Marine Biology and Ecology, 184(1), 111-122.
15. McMurray, S. E., Henkel, T. P., & Pawlik, J. R. (2010). Demographics of increasing populations of the giant barrel sponge Xestospongia muta in the Florida Keys. Ecology, 91(2), 560-570.
16. Ripley, B. J., & Caswell, H. (2008). Contributions of growth, stasis, and reproduction to fitness in brooding and broadcast spawning marine bivalves. Population Ecology, 50(2), 207-214.
17. Pfister, C. A., & Wang, M. (2005). Beyond size: matrix projection models for populations where size is an incomplete descriptor. Ecology, 86(10), 2673-2683.
18. Aberg, P. (1992). A demographic study of two populations of the seaweed Ascophyllum nodosum. Ecology, 73(4), 1473-1487.
19. Nelsen, M. (2008). Population dynamic modeling of the corkscrew sea anemone Bartholomea annulata on Caribbean coral reefs. Doctoral dissertation, Auburn University, Auburn, AL.
20. Cockrell, M. L., & Sorte, C. J. (2013). Predicting climate-induced changes in population dynamics of invasive species in a marine epibenthic community. Journal of Experimental Marine Biology and Ecology, 440, 42-48.

21. Svensson, C. J., Johansson, E., & Åberg, P. (2006). Competing species in a changing climate: effects of recruitment disturbances on two interacting barnacle species. Journal of Animal Ecology, 75(3), 765-776.
22. Hughes, T. P. (1990). Recruitment limitation, mortality, and population regulation in open systems: a case study. Ecology, 71(1), 12-20.
23. Ang, P. O., & DeWreede, R. E. (1993). Simulation and analysis of the dynamics of a Fucus distichus (Phaeophyceae, Fucales) populations. Marine Ecology Progress Series, 93(3), 253-265.
24. Somerville, G. J., Krkosek, M., & Hepburn, C. D. (2014). A matrix model and elasticity analysis for New Zealand's blackfoot pāua Haliotis iris. Fisheries Research, 151, 158-168.
25. Rogers-Bennett, L., & Leaf, R. T. (2006). Elasticity Analyses of Size Based Red And White Abalone Matrix Models: Management And Conservation. Ecological Applications, 16(1), 213-224.
26. Ang Jr, P., De Wreede, R. E., Shaughnessy, F., & Dyck, L. (1990). A simulation model for an Iridaea splendens (Gigartinales, Rhodophyta) population in Vancouver, Canada. In Thirteenth International Seaweed Symposium (pp. 191-196). Springer Netherlands.
27. Chapman, A. R. (1993). 'Hard'data for matrix modelling of Laminaria digitata (Laminariales, Phaeophyta) populations. In Fourteenth International Seaweed Symposium (pp. 263-267). Springer Netherlands.
28. Ripley, B. J., & Caswell, H. (2006). Recruitment variability and stochastic population growth of the soft-shell clam, Mya arenaria. Ecological modelling,193(3), 517-530.
29. Brazeiro, A., & Defeo, O. (1999). Effects of harvesting and density dependence on the demography of sandy beach populations: the yellow clam Mesodesma mactroides of Uruguay. Marine Ecology Progress Series, 182, 127-135.
30. Nyman, M. A., Brown, M. T., Neushul, M., & Keogh, J. A. (1990). Macrocystis pyrifera in New Zealand: testing two mathematical models for whole plant growth. Journal of Applied Phycology, 2(3), 249-257.
31. Dudas, S. E., Dower, J. F., & Anholt, B. R. (2007). Invasion dynamics of the varnish clam (Nuttallia obscurata): a matrix demographic modeling approach. Ecology, 88(8), 2084-2093.
32. Cropper, W. P., & DiResta, D. (1999). Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after Hurricane Andrew. Ecological Modelling, 118(1), 1-15.
33. Fordham, D. A., Mellin, C., Russell, B. D. et al. (2013). Population dynamics can be more important than physiological limits for determining range shifts under climate change. Global Change Biology, 19(10), 3224-3237.
34. Salguero Gómez, R., Jones, O. R., Archer, C. R. R. et al. (2016). COMADRE: a global data base of animal demography. Journal of Animal Ecology, 85(2), 371-384.
35. Carson, H. S., Cook, G. S., López-Duarte, P. C., & Levin, L. A. (2011). Evaluating the importance of demographic connectivity in a marine metapopulation. Ecology, 92(10), 1972-1984.
36. Van Moorsel, G. W. N. M. (1983). Reproductive strategies in two closely related stony corals (Agaricia, Scleractinia). Mar Ecol Prog Ser, 13, 273-283.
37. Carpenter, K. E., Abrar, M., Aeby, G., Aronson, R. B., Banks, S. et al. (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321, 560-563

38. Muir, P. R., Wallace, C. C., Done, T., Aguirre, J. D. (2015) Limited scope for latitudinal extension of reef corals. Science 348, 1135-1138
39. Abele, D., Brey, T., & Philipp, E. (2009). Bivalve models of aging and the determination of molluscan lifespans. Experimental Gerontology, 44(5), 307-315.
40. Cattaneo-Vietti, R., Chiantore, M., & Albertelli, G. I. A. N. C. A. R. L. O. (1997). The population structure and ecology of the Antarctic scallop Adamussium colbecki (Smith, 1902) at Terra Nova Bay (Ross Sea, Antarctica). Scientia Marina, 61(2), 15-24.
41. Encyclopedia of Life (eol.org)
42. Colin, P. L., & Heiser, J. B. (1973). Associations of two species of cardinalfishes (Apogonidae: Pisces) with sea anemones in the West Indies. Bulletin of Marine Science, 23(3), 521-524.
43. Brandt, M. E. (2009) The effect of species and colony size on the bleaching response of reef-building corals in the Florida Keys during the 2005 mass bleaching event. Coral Reefs 28, 911-924
44. Madin, J. S., Anderson, K. D., Andreasen, M. H., Bridge, T. C., Cairns, S. D. et al. (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Scientific Data, 3.
45. Aronson, R., Bruckner, A., Moore, J., Precht, B. & E. Weil. 2008. Diploria strigosa. The IUCN Red List of Threatened Species 2008: e.T133155A3605234.
46. Veron, J. E. N. (2000) Corals of the World. Australian Institute of Marine Science and CCR Qld Pty Ltd.
47. Szmant, A. M., Weil, E., Miller, M. W. (1997) Hybridization within the species complex of the scleractinan coral Montastraea annularis. Marine Biology 129, 561-572
48. Bridge, T. C. L., Fabricius, K. E., Bongaerts, P., Wallace, C. C., Muir, P. R., Done, T. J., Webster, J. M. (2011) Diversity of Scleractinia and Octocorallia in the mesophotic zone of the Great Barrier Reef, Australia. Coral Reefs 31, 179-189
49. Kühlmann, D. H. H. (1983) Composition and ecology of deep-water coral associations. Helgoländer Meeresuntersuchungen 36, 183-204
50. Goreau, T. F., Wells, J. W. (1967) The shallow-water Scleractinia of Jamaica: Revised list of species and their vertical distribution range. Bulletin of Marine Science 17, 442-453
51. Miller, M., Williams, D. E., Huntington, B. E., Piniak, G. A., & Vermeij, M. J. (2016). Decadal comparison of a diminishing coral community: a study using demographics to advance inferences of community status. PeerJ, 4, e1643.
52. Chadwick-Furman, N. E., Goffredo, S., & Loya, Y. (2000). Growth and population dynamic model of the reef coral Fungia granulosa Klunzinger, 1879 at Eilat, northern Red Sea. Journal of Experimental Marine Biology and Ecology, 249(2), 199-218.
53. Hoeksema, B.W., Obura, D.O., Wood, E., Rogers, A. & Quibilan, M.C. 2014. Fungia fungites. The IUCN Red List of Threatened Species 2014. Downloaded on 23 September 2016.
54. Veron, J. E. N. (1986) Corals of Australia and the Indo-Pacific. University of Hawaii Press, Honolulu
55. Costantini, F., Taviani, M., Remia, A., Pintus, E., Schembri, P. J., & Abbiati, M. (2010). Deep water Corallium rubrum (L., 1758) from the Mediterranean Sea: preliminary genetic characterisation. Marine Ecology, 31(2), 261-269.
56. Weinberg, S., 1978. Mediterranean Octocorallian communities and the abiotic environment. Mar. Biol. 49, 41–57

57. Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA (2009) Extreme longevity in proteinaceous deep-sea corals. Proc Natl Acad Sci USA 106: 5204−5208
58. Roark EB, Guilderson TP, Dunbar RB, Ingram BL (2006) Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. Mar Ecol Prog Ser 327: 1−14
59. Druffel, E. R., Griffin, S., Witter, A., Nelson, E., Southon, J., Kashgarian, M., & Vogel, J. (1995). Gerardia: Bristlecone pine of the deep-sea?. Geochimica et Cosmochimica Acta, 59(23), 5031-5036.
60. Risk et al. 2002. Lifespans and growth patterns of two deep-sea corals: Primnoa resedaeformis and Desmophyllum cristagalli
61. Roark EB, Guilderson TP, Flood-Page S, Dunbar RB, Ingram BL, Fallon SJ, McCulloch M (2005) Radiocarbon-based ages and growth rates of bamboo corals from the Gulf of Alaska. Geophys Res Lett 32: L04606
62. Sherwood, O. A., & Edinger, E. N. (2009). Ages and growth rates of some deep-sea gorgonian and antipatharian corals of Newfoundland and Labrador.Canadian Journal of Fisheries and Aquatic Sciences, 66(1), 142-152.
63. Wilson, Matthew T., et al. Axial rod growth and age estimation of the sea pen, Halipteris willemoesi Kölliker. Hydrobiologia 471.1-3 (2002): 133-142.
64. Martinez-Dios, A., Dominguez-Carrió, C., Zapata-Guardiola, R., & Gili, J. M. (2016). New insights on Antarctic gorgonians' age, growth and their potential as paleorecords. Deep Sea Research Part I: Oceanographic Research Papers, 112, 57-67.
65. Sherwood, O. A., Scott, D. B.& Risk, M. J. (2006) Late Holocene radiocarbon and aspartic acid racemization dating of deep-sea octocorals. Geochimica et Cosmochimica Acta, 70(11): 2806-2814.
66. Weinberg, S., & Weinberg, F. (1979). The life cycle of a gorgonian: Eunicella singularis (Esper, 1794). Bijdragen tot de Dierkunde, 48(2), 127-137.
67. Druffel, E. R., King, L. L., Belastock, R. A., & Buesseler, K. O. (1990). Growth rate of a deep-sea coral using 210 Pb and other isotopes. Geochimica et Cosmochimica Acta, 54(5), 1493-1499.
68. Abele, D., Brey, T., & Philipp, E. (2009). Bivalve models of aging and the determination of molluscan lifespans. Experimental Gerontology, 44(5), 307-315.
69. Love, M. S., Yoklavich, M. M., Black, B. A., and Andrews, A. H. (2007). Age of black coral (Antipathes dendrochristos) colonies, with notes on associated invertebrate species. Bulletin of Marine Science 80, 391–400.
70. Wagner, D., Luck, D. G., & Toonen, R. J. (2012). 2 The Biology and Ecology of Black Corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). Advances in marine biology, 63, 67.
71. Grange, K. R., & Goldberg, W. M. (1993). Chronology of black coral growth bands: 300 years of environmental history. Battershill, CN; Schiel, DR; Jones, GP, 168-174.
72. Oakley, S. G. (1988). Settlement and growth of Antipathes pennacea on a shipwreck. Coral Reefs, 7(2), 77-79.
73. Carpine C, Grasshoff M. (1975) Les Gorgonaires de la Méditerranée. Bull Inst Océanography Fish. 71, 1–140.
74. Cerrano, C., Totti, C., Sponga, F., & Bavestrello, G. (2006). Summer disease in Parazoanthus axinellae (Schmidt, 1862) (Cnidaria, Zoanthidea). Italian Journal of Zoology, 73(4), 355-361.
75. Garrabou, J. (1999). Life-history traits of Alcyonium acaule and Parazoanthus axinellae (Cnidaria, Anthozoa), with emphasis on growth. Marine Ecology Progress Series, 178, 193-204.

76. Teixidó, N., Garrabou, J., & Harmelin, J. G. (2011). Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. PLoS One, 6(8), e23744.
77. Ambroso, S., Gori, A., Dominguez-Carrió, C., Gili, J. M., Berganzo, E., Teixidó, N., ... & Rossi, S. (2013). Spatial distribution patterns of the soft corals Alcyonium acaule and Alcyonium palmatum in coastal bottoms (Cap de Creus, northwestern Mediterranean Sea). Marine biology, 160(12), 3059-3070.
78. Hellberg, M. E. (1994). Relationships between inferred levels of gene flow and geographic distance in a philopatric coral, Balanophyllia elegans. Evolution, 1829-1854.
79. Fadlallah, Y. H. (1983). Population dynamics and life history of a solitary coral, Balanophyllia elegans, from Central California. Oecologia, 58(2), 200-207.
80. Goffredo, S., Mattioli, G., & Zaccanti, F. (2004). Growth and population dynamics model of the Mediterranean solitary coral Balanophyllia europaea (Scleractinia, Dendrophylliidae). Coral Reefs, 23(3), 433-443.
81. Zibrowius, H. (1980). Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mémoires de l'Institut océanographique, Monaco.
82. Goffredo, S., Mezzomonaco, L., & Zaccanti, F. (2004). Genetic differentiation among populations of the Mediterranean hermaphroditic brooding coral Balanophyllia europaea (Scleractinia: Dendrophylliidae). Marine Biology, 145(6), 1075-1083.
83. Grigg, R. W. (1977). Population dynamics of two gorgonian corals. Ecology,58(2), 278-290.
84. Caroselli, E., Zaccanti, F., Mattioli, G., Falini, G., Levy, O., Dubinsky, Z., & Goffredo, S. (2012). Growth and demography of the solitary scleractinian coral Leptopsammia pruvoti along a sea surface temperature gradient in the Mediterranean Sea. PLoS One, 7(6), e37848.
85. Mistri, M., & Ceccherelli, V. U. (1993). Growth of the Mediterranean gorgonian Lophogorgia ceratophyta (L., 1758). Marine Ecology, 14(4), 329-340.
86. Caroselli, E., Nanni, V., Levy, O., Falini, G., Dubinsky, Z., & Goffredo, S. (2015). Latitudinal variations in biometry and population density of a Mediterranean solitary coral. Limnology and Oceanography, 60(4), 1356-1370.
87. Morri, C., Vafidis, D., Peirano, A., Chintiroglou, C. C., & Bianchi, C. N. (2000). Anthozoa from a subtidal hydrothermal area of Milos Island (Aegean Sea), with notes on the construction potential of the scleractinian coral Madracis pharensis. Italian Journal of Zoology, 67(3), 319-325.
88. Yoshioka, P. M., & Yoshioka, B. B. (1991). A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. Marine ecology progress series. Oldendorf, 69(3), 253-260.
89. McMurray, S. E., Blum, J. E., & Pawlik, J. R. (2008). Redwood of the reef: growth and age of the giant barrel sponge Xestospongia muta in the Florida Keys. Marine Biology, 155(2), 159-171.
90. Armstrong, R. A., Singh, H., Torres, J., Nemeth, R. S., Can, A., Roman, C., ... & Garcia-Moliner, G. (2006). Characterizing the deep insular shelf coral reef habitat of the Hind Bank marine conservation district (US Virgin Islands) using the Seabed autonomous underwater vehicle. Continental Shelf Research, 26(2), 194-205.
91. Kinzie, I. I. I., & Robert, A. (1973). Coral Reef Project—Papers in Memory of Dr. Thomas F. Goreau. 5. The Zonation of West Indian Gorgonians. Bulletin of Marine Science, 23(1), 93-155.

92. Botero, L. (1987). Zonación de octocorales gorgonáceos en el área de Santa Marta y parque nacional Tayrona, costa Caribe colombiana. An. Inst. Inv. Mar. Punta de Betin, 17, 61-80.
93. Gatti, S. (2002). The rôle of sponges in high-Antarctic carbon and silicon cycling-a modelling approach= Die Rolle der Schwämme im hochantarktischen Kohlenstoff- und Silikatkreislauf-ein Modellierungsansatz. Berichte zur Polar-und Meeresforschung (Reports on Polar and Marine Research), 434.
94. Jochum, K. P., Wang, X., Vennemann, T. W., Sinha, B., & Müller, W. E. (2012). Siliceous deep-sea sponge Monorhaphis chuni: A potential paleoclimate archive in ancient animals. Chemical Geology, 300, 143-151.
95. Fallon, S. J., James, K., Norman, R., Kelly, M., & Ellwood, M. J. (2010). A simple radiocarbon dating method for determining the age and growth rate of deep-sea sponges. Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms, 268(7), 1241-1243.
96. Leys, S. P., & Lauzon, N. R. (1998). Hexactinellid sponge ecology: growth rates and seasonality in deep water sponges. Journal of Experimental Marine Biology and Ecology, 230, 111-129.
97. Ferretti, C., Vacca, S., De Ciucis, C., Marengo, B., Duckworth, A. R., Manconi, R., ... & Domenicotti, C. (2009). Growth dynamics and bioactivity variation of the Mediterranean demosponges Agelas oroides (Agelasida, Agelasidae) and Petrosia ficiformis (Haplosclerida, Petrosiidae). Marine Ecology, 30, 327-336.
98. Bavestrello, G., Bonito, M., & Sarà, M. (1993). Influence of depth on the size of sponge spicules. Scientia Marina(Barcelona), 57(4), 415-420.
99. Antoniadou, C., Voultsiadou, E., & Chintiroglou, C. (2006). Sublittoral megabenthos along cliffs of different profile (Aegean Sea, Eastern Mediterranean). Belgian journal of zoology, 136(1), 69.
100. Voultsiadou, E. (2005). Demosponge distribution in the eastern Mediterranean: a NW–SE gradient. Helgoland Marine Research, 59(3), 237.
101. Becerro, M. A., Turon, X., & Uriz, M. J. (1995). Natural variation of toxicity in encrusting spongeCrambe crambe (Schmidt) in relation to size and environment. Journal of Chemical Ecology, 21(12), 1931-1946.
102. Mercado-Molina, A. E., & Yoshioka, P. M. (2009). Relationships between water motion and size-specific survivorship and growth of the demosponge Amphimedon compressa. Journal of Experimental Marine Biology and Ecology, 375, 51-56.
103. Nuzzo, G., Ciavatta, M. L., Villani, G., Manzo, E., Zanfardino, A., Varcamonti, M., & Gavagnin, M. (2012). Fulvynes, antimicrobial polyoxygenated acetylenes from the Mediterranean sponge Haliclona fulva. Tetrahedron, 68, 754-760.
104. Cebrián, E., & Ballesteros, E. (2004). Zonation patterns of benthic communities in an upwelling area from the western Medierranean (La Herradura, Alboran Sea). Scientia Marina, 68(1), 69-84.
105. McLean, E. L. (2006). Ecology of the encrusting sponge Desmapsamma anchorata. Doctoral dissertation, University of Puerto Rico, Mayagüez Campus.
106. McLean, E. L., & Yoshioka, P. M. (2008). Substratum effects on the growth and survivorship of the sponge Desmapsamma anchorata. Caribbean Journal of Science, 44(1), 83-89.
107. Taylor P.D., D.P. Gordon (2002). Alcide d’Orbigny’s work on Recent and fossil bryozoans. Comptes Rendus Palevol 1:533-547

108. Coma, R., Llobet, I., Zabala Iturriagagoitia, J. M., Gili, J. M., & Hughes, R. G. (1992). The population dynamics of Halecium petrosum and Halecium pusillum (Hydrozoa, Cnidaria), epiphytes of Halimeda tuna in the nortwestern Mediterranean.
109. Delduca, E. (2011). New record of depth distribution for the cheilostome bryozoan Cauloramphus spinifer. Marine Biodiversity Records, 4, e71.
110. Yund, P. O. (1995). Gene flow via the dispersal of fertilizing sperm in a colonial ascidian (Botryllus schlosseri): the effect of male density. Marine Biology, 122, 649-654.
111. Paz, G., Douek, J., Mo, C., Goren, M., & Rinkevich, B. (2003). Genetic structure of Botryllus schlosseri (Tunicata) populations from the Mediterranean coast of Israel. Marine Ecology Progress Series, 250, 153-162.
112. Dixon (1965) Perennation, vegetative propagation and algal life histories, with special reference to Asparagopsis and other Rhodophyta. Bot. Gothoburgensia III, 67–74.
113. Paine, R.T., Slocum, C.J. and Duggins, D.O. (1979) Growth and longevity in the crustose red alga Petrocelis middendorffii. Mar. Biol. 51(2), 185–192
114. 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(6), 1799-1808.
115. Ballesteros, E., Garrabou, J., Hereu, B., Zabala, M., Cebrian, E., & Sala, E. (2009). Deep-water stands of Cystoseira zosteroides C. Agardh (Fucales, Ochrophyta) in the Northwestern Mediterranean: Insights into assemblage structure and population dynamics. Estuarine, coastal and shelf science, 82(3), 477-484.
116. Van Alstyne, K. L., McCarthy III, J. J., Hustead, C. L., & Duggins, D. O. (1999). Geographic variation in polyphenolic levels of Northeastern Pacific kelps and rockweeds. Marine Biology, 133(2), 371-379.
117. Pedersen, M. F., Nejrup, L. B., Fredriksen, S., Christie, H., & Norderhaug, K. M. (2012). Effects of wave exposure on population structure, demography, biomass and productivity of the kelp Laminaria hyperborea. Marine Ecology Progress Series, 451, 45-60.
118. Opresko, D.; Tracey, D.; Mackay, E. (2014). ANTIPATHARIA (BLACK CORALS) FOR THE NEW ZEALAND REGION. A field guide of commonly sampled New Zealand black corals including illustrations highlighting technical terms and black coral morphology. New Zealand Aquatic Environment and Biodiversity Report No. 131. 20 p.
119. Sejr, M. K., Sand, M. K., Jensen, K. T., Petersen, J. K., Christensen, P. B., & Rysgaard, S. (2002). Growth and production of Hiatella arctica (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland). Marine Ecology Progress Series, 244, 163-169.
120. Coppa, S. (2012). On the ecology and conservation of marine endangered species, Pinna nobilis (Linnaeus, 1758) and Patella ferruginea (Gmelin, 1791), in the Marine Protected Area of Penisola del Sinis-Isola di Mal di Ventre (western Sardinia, Italy).
121. Murawski, S. A., Ropes, J. W., & Serchuk, F. M. (1982). Growth of the ocean quahog, Arctica islandica, in the Middle Atlantic Bight. Fishery Bulletin, 80(1), 21-34.
122. Katsanevakis, S. (2009). Population dynamics of the endangered fan mussel Pinna nobilis in a marine lake: a metapopulation matrix modeling approach. Marine Biology, 156(8), 1715-1732.

123. Gori, A., Rossi, S., Berganzo, E., Pretus, J. L., Dale, M. R., & Gili, J. M. (2011). Spatial distribution patterns of the gorgonians Eunicella singularis, Paramuricea clavata, and Leptogorgia sarmentosa (Cape of Creus, Northwestern Mediterranean Sea). Marine biology, 158(1), 143-158.
124. Morrow, K. M., Fiore, C., & Lesser, M. (2016). Environmental drivers of microbial community shifts in the giant barrel sponge, Xestospongia muta, over a shallow to mesophotic depth gradient. Environmental Microbiology.
125. Gili, J. M., & Hughes, R. G. (1995). The ecology of marine benthic hydroids. Oceanography and Marine Biology, 33, 351-426.
126. Brock, M. A. (1974). Growth, developmental, and longevity rhythms in Campanularia flexuosa. American Zoologist, 14(2), 757-771.
127. Butler, P. G., Wanamaker, A. D., Scourse, J. D., Richardson, C. A., & Reynolds, D. J. (2013). Variability of marine climate on the North Icelandic Shelf in a 1357-year proxy archive based on growth increments in the bivalve Arctica islandica. Palaeogeography, Palaeoclimatology, Palaeoecology, 373, 141-151.
128. Andrews, A. H., Cailliet, G. M., Kerr, L. A., Coale, K. H., Lundstrom, C., & DeVogelaere, A. P. (2005). Investigations of age and growth for three deep-sea corals from the Davidson Seamount off central California. In Cold-water corals and ecosystems (pp. 1021-1038). Springer Berlin Heidelberg.
129. Andrews, A. H., Stone, R. P., Lundstrom, C. C., & DeVogelaere, A. P. (2009). Growth rate and age determination of bamboo corals from the northeastern Pacific Ocean using refined 210Pb dating. Marine Ecology Progress Series, 397, 173-185.
130. Frederiksen, R., Jensen, A., & Westerberg, H. (1992). The distribution of the scleractinian coral Lophelia pertusa around the Faroe Islands and the relation to internal tidal mixing. Sarsia, 77(2), 157-171.
131. Hall–Spencer, J., Allain, V., & Fosså, J. H. (2002). Trawling damage to Northeast Atlantic ancient coral reefs. Proceedings of the Royal Society of London B: Biological Sciences, 269(1490), 507-511.
132. Fallon, S. J., Thresher, R. E., & Adkins, J. (2014). Age and growth of the cold-water scleractinian Solenosmilia variabilis and its reef on SW Pacific seamounts. Coral Reefs, 33(1), 31-38.
133. Thresher, R. E., Tilbrook, B., Fallon, S., Wilson, N. C., & Adkins, J. (2011). Effects of chronic low carbonate saturation levels on the distribution, growth and skeletal chemistry of deep-sea corals and other seamount megabenthos. Marine Ecology Progress Series, 442, 87-99.
134. Houlbrèque, F., McCulloch, M., Roark, B., Guilderson, T., Meibom, A., Kimball, J., & Dunbar, R. (2010). Uranium-series dating and growth characteristics of the deep-sea scleractinian coral: Enallopsammia rostrata from the Equatorial Pacific. Geochimica et Cosmochimica Acta, 74(8), 2380-2395.
135. Cairns, S. D. (1984). New Records of Ahennatypic Corals (Scleractinia) from the Hawaiian and Line Islands. Bishop Museum Occasiollal Papers. Vol. XXV. 10. 1984
136. Cairns, S. D. (1996). The marine fauna of New Zealand: Scleractinia (Cnidaria: Anthozoa). Oceanographic Literature Review, 3(43), 293.
137. Estabrooks, S. L. (2007). The possible role of telomeres in the short life span of the bay scallop, Argopecten irradians irradians (Lamarck 1819). Journal of Shellfish Research, 26(2), 307-313.
138. Turekian, K. K., Cochran, J. K., Kharkar, D. P., Cerrato, R. M., Vaisnys, J. R., Sanders, H. L. & Allen, J. A. (1975). Slow growth rate of a deep-sea clam determined

by 228Ra chronology. Proceedings of the National Academy of Sciences USA, 72(7), 2829-2832.

139. Alarcón, E. & M. Wolff. 1991. Estudio biológico pesquero sobre el recurso de ostiones (Argopecten purpuratus) de bahia Tongoy durante el fenomeno El Niño 1982-83. Invest. Pesq. 32:167–173.
140. DiSalvo, L. H., E. Alarco´n, E. Martinez & E. Uribe. 1984. Progress in mass culture of Chlamys (Argopecten) purpuratus Lamarck (1819) with notes on its natural history. Rev. Chil. Hist. Nat. 57:34–45.
141. MacDonald, B. A. (1986). Production and resource partitioning in the giant scallop Placopecten magellanicus grown on the bottom and in suspended culture. Mar. Ecol. Prog. Ser, 34, 79-86.
142. MacDonald, B. A., & Thompson, R. J. (1988). Intraspecific variation in growth and reproduction in latitudinally differentiated populations of the giant scallop Placopecten magellanicus (Gmelin). The Biological Bulletin, 175(3), 361-371.
143. Garcia-Esquivel, Z., & Bricelj, V. M. (1993). Ontogenic changes in microhabitat distribution of juvenile bay scallops, Argopecten irradians irradians (L.), in eelgrass beds, and their potential significance to early recruitment. The Biological Bulletin, 185(1), 42-55.
144. Eckman, J. E. (1987). The role of hydrodynamics in recruitment, growth, and survival of Argopecten irradians (L.) and Anomia simplex (D'Orbigny) within eelgrass meadows. Journal of Experimental Marine Biology and Ecology,106(2), 165-191.
145. Jones, K. B., Hodgins, G. W., Dettman, D. L., Andrus, C. F. T., Nelson, A., & Etayo-Cadavid, M. F. (2007). Seasonal variations in Peruvian marine reservoir age from pre-bomb Argopecten purpuratus shell carbonate. Radiocarbon, 49(2), 877-888.
146. Hickson, J. A., Johnson, A. L., Heaton, T. H., & Balson, P. S. (1999). The shell of the Queen Scallop Aequipecten opercularis (L.) as a promising tool for palaeoenvironmental reconstruction: evidence and reasons for equilibrium stable-isotope incorporation. Palaeogeography, Palaeoclimatology, Palaeoecology, 154(4), 325-337.
147. Philipp, E., Brey, T., Heilmayer, O., Abele, D., & Pörtner, H. O. (2006). Physiological ageing in a polar and a temperate swimming scallop. Marine ecology-progress series, 307, 187-198.
148. Philipp, E., Brey, T., Pörtner, H. O., & Abele, D. (2005). Chronological and physiological ageing in a polar and a temperate mud clam. Mechanisms of ageing and Development, 126(5), 598-609.
149. Möller, P., & Rosenberg, R. (1983). Recruitment, abundance and production of Mya arenaria and Cardium edule in marine shallow waters, western Sweden. Ophelia, 22(1), 33-55.
150. Jażdżeski, K., Jurasz, W., Kittel, W., Presler, E., Presler, P., & Siciński, J. (1986). Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island, South Shetland Islands. Polar Biology, 6(1), 5-16.
151. Strom, A., Francis, R. C., Mantua, N. J., Miles, E. L., & Peterson, D. L. (2004). North Pacific climate recorded in growth rings of geoduck clams: a new tool for paleoenvironmental reconstruction. Geophysical Research Letters, 31(6).
152. Coan, E. V., Scott, P. V., & Bernard, F. R. (2000). Bivalve seashells of Western North America, Santa Barbara Museum of Natural History Monographs Number 2. Studies in Biodiversity, (2).

153. NOAA (2004). Sea Scallop, Placopecten magellanicus, life history and habitat characteristics (2 ed.). U. S. DEPARTMENT OF COMMERCE. pp. 1–6. Retrieved
154. Brey, T., & Hain, S. (1992). Growth, reproduction and production of Lissarca notorcadensis (Bivalvia Philobryidae) in the Weddell Sea, Antarctica. Marine Ecology Progress Series, 82, 219-226.
155. Dell RK (1964) Antarctic and sub-Antarctic Mollusca: Amphineura, Scaphapoda and Bivalvia. Discov Rep 33:93–250
156. Bertness, M. D., & Grosholz, E. (1985). Population dynamics of the ribbed mussel, Geukensia demissa: the costs and benefits of an aggregated distribution. Oecologia, 67(2), 192-204.
157. McShane, P. E., & Naylor, J. R. (1995). Depth can affect post-settlement survival of Haliotis iris (Mollusca: Gastropoda). Journal of Experimental Marine Biology and Ecology, 187(1), 1-12.
158. Shepherd, S. A. (1973). Studies on southern Australian abalone (genus Haliotis). I. Ecology of five sympatric species. Marine and Freshwater Research, 24(3), 217-258.
159. Cowles, D. (2005). Haliotis rufescens. Biological Department, Walla Walla University. Retrieved 25 February 2015.
160. Lafferty, K. D., Behrens, M. D., Davis, G. E., Haaker, P. L., Kushner, D. J., Richards, D. V. & Tegner, M. J. (2004). Habitat of endangered white abalone, Haliotis sorenseni. Biological Conservation, 116(2), 191-194.
161. Schmidt, D., A Review of California Mussel ("Mytilus californianus") Fisheries Biology and Fisheries Programs, Canadian Stock Assessment Secretariat Research Document 99/187
162. FAO Fisheries and Aquaculture Department [online]. Rome. Updated 1 January 2004. [Cited 14 October 2016].
163. Byers, J. E. (2005). Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. Ecology, 86(2), 487-500.
164. Kolpakov, E. V., & Kolpakov, N. V. (2005). Population Size-Age Structure and Growth of the Subtropical Bivalve Nuttallia obscurata in Primorye Waters at the North Boundary of Its Geographic Range. Russian Journal of Marine Biology, 31(3), 164-167.
165. Morton, J. E., Boney, A. D., & Corner, E. D. S. (1957). The adaptations of Lasaea rubra (Montagu), a small intertidal lamellibranch. Journal of the Marine Biological Association of the United Kingdom, 36(02), 383-405.
166. Witbaard, R. (1996). Growth variations in Arctica islandica L.(Mollusca): a reflection of hydrography-related food supply. ICES Journal of Marine Science: Journal du Conseil, 53(6), 981-987.
167. Sejr, M. K., Sand, M. K., Jensen, K. T., Petersen, J. K., Christensen, P. B., & Rysgaard, S. (2002). Growth and production of Hiatella arctica (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland). Marine Ecology Progress Series, 244, 163-169.
168. Jamison, D., R. Heggen, and J. Lukes. 1984. Underwater video in a regional benthos survey, p. 15-17. In Proceedings of the Pacific Congress on Marine Technology. Marine Technology Society, Honolulu, Hawaii
169. Turekian, K. K., Cochran, J. K., Kharkar, D. P., Cerrato, R. M., Vaisnys, J. R., Sanders, H. L. & Allen, J. A. (1975). Slow growth rate of a deep-sea clam determined by 228Ra chronology. Proceedings of the National Academy of Sciences, 72(7), 2829-2832.

170. Meroz, E., & Ilan, M. (1995). Life history characteristics of a coral reef sponge. Marine Biology, 124(3), 443-451.
171. Andrews, A. H., Leaf, R. T., Rogers-Bennett, L., Neuman, M., Hawk, H., & Cailliet, G. M. (2013). Bomb radiocarbon dating of the endangered white abalone (Haliotis sorenseni): investigations of age, growth and lifespan. Marine and Freshwater Research, 64(11), 1029-1039.
172. Jones, D. S., Thompson, I., & Ambrose, W. (1978). Age and growth rate determinations for the Atlantic surf clam Spisula solidissima (Bivalvia: Mactracea), based on internal growth lines in shell cross-sections. Marine Biology, 47(1), 63-70.
173. Wade, B. A. (1968). Studies on the biology of the West Indian beach clam, Donax denticulatus Linne. 2. Life-history. Bulletin of Marine Science, 18(4), 876-901.
174. Gutiérrez, D.; G. Darrigran & C. Damborenea (2015). Los Moluscos Marinos de Argentina y su Consumo. Serie Didáctica, N° 2. Sección Malacología. División Zoología Invertebrados. La Plata: Facultad de Ciencias Naturales y Museo, UNLP.
175. Fiori, S., & Defeo, O. (2006). Biogeographic patterns in life-history traits of the yellow clam, Mesodesma mactroides, in sandy beaches of South America. Journal of Coastal Research, 872-880.
176. Wilson, M. T., Andrews, A. H., Brown, A. L., & Cordes, E. E. (2002). Axial rod growth and age estimation of the sea pen, Halipteris willemoesi Kölliker. Hydrobiologia, 471(1), 133-142.
177. Prouty, N. G., Fisher, C. R., Demopoulos, A. W., & Druffel, E. R. (2016). Growth rates and ages of deep-sea corals impacted by the Deepwater Horizon oil spill. Deep Sea Research Part II: Topical Studies in Oceanography, 129, 196-212.
178. J Miller, K., Mundy, C. N., & Lindsay Chadderton, W. (2004). Ecological and genetic evidence of the vulnerability of shallow-water populations of the stylasterid hydrocoral Errina novaezelandiae in New Zealand's fiords. Aquatic Conservation: Marine and Freshwater Ecosystems, 14(1), 75-94.
179. Cordes, E. E., Nybakken, J. W., & VanDykhuizen, G. (2001). Reproduction and growth of Anthomastus ritteri (Octocorallia: Alcyonacea) from Monterey Bay, California, USA. Marine Biology, 138(3), 491-501.
180. Nishi, E., & Nishihira, M. (1999). Use of annual density banding to estimate longevity of infauna of massive corals. Fisheries Science, 65(1), 48-56.
181. Vieira, C., Keshavmurthy, S., Ju, S. J., Hyeong, K., Seo, I., Kang, C. K., ... & Choi, K. S. (2016). Population dynamics of a high-latitude coral Alveopora japonica Eguchi from Jeju Island, off the southern coast of Korea. Marine and Freshwater Research, 67(5), 594-604.
182. van Tussenbroek, B. I., & Santos, M. G. B. (2011). Demography of Halimeda incrassata (Bryopsidales, Chlorophyta) in a Caribbean reef lagoon. Marine Biology, 158(7), 1461-1471.
183. Kain, J. M. (2015). Hormosira banksii (Phaeophyceae): a tough survivor in the harsh conditions of high intertidal pools in southeast Australia. European Journal of Phycology, 50(4), 408-421.
184. Pedersen, M. F., Nejrup, L. B., Fredriksen, S., Christie, H., & Norderhaug, K. M. (2012). Effects of wave exposure on population structure, demography, biomass and productivity of the kelp Laminaria hyperborea. Marine Ecology Progress Series, 451, 45-60.
185. Frantz, B. R., Foster, M. S., & Riosmena-Rodríguez, R. (2005). Clathromorphum nereostratum (corallinales, rhodophyta): the oldest alga? Journal of Phycology, 41(4), 770-773.

186. Paine, R. T., Slocum, C. J., & Duggins, D. O. (1979). Growth and longevity in the crustose red alga Petrocelis middendorffii. Marine Biology, 51(2), 185-192.
187. Frantz, B. R., Kashgarlan, M., Coale, K. H., & Foster, M. S. (2000). Growth rate and potential climate record from a rhodolith using^ 1^ 4C accelerator mass spectrometry. Limnology and Oceanography, 45(8), 1773-1777.
188. Adey, W., Halfar, J., Humphreys, A., Suskiewicz, T., Belanger, D., Gagnon, P., & Fox, M. (2015). Subarctic rhodolith beds promote longevity of crustose coralline algal buildups and their climate archiving potential. Palaios, 30(4), 281-293.
189. Smith, A. M., Stewart, B., Key, M. M., & Jamet, C. M. (2001). Growth and carbonate production by Adeonellopsis (Bryozoa: Cheilostomata) in Doubtful Sound, New Zealand. Palaeogeography, Palaeoclimatology, Palaeoecology, 175(1), 201-210.
190. Bernard, F.R. 1983. Catalogue of the living Bivalvia of the eastern Pacific Ocean: Bering Strait to Cape Horn. Can. Spec. Publ. Fish. Aquat. Sci. No. 61.
191. Román-González, A., Scourse, J. D., Butler, P. G., Reynolds, D. J., Richardson, C. A., Peck, L. S., et al. (2017). Analysis of ontogenetic growth trends in two marine Antarctic bivalves Yoldia eightsi and Laternula elliptica: Implications for sclerochronology. Palaeogeography, Palaeoclimatology, Palaeoecology, 465, 300-306.
192. Ovsyannikov, V.P. and Sidyakov, Yu.V. 2005 Brief Information about the Stocks of Economically Valuable Mac robenthos Based on a Dredging Survey in the North-Western Tatar Strait, Morskie pribrezhnye ekosistemy: vodorosli, bespozvonochnye i produkty ikh pererabotki (Marine Coastal Ecosystems: Algae, Invertebrates and Their Processing Products), Moscow: VNIRO. pp. 74–73. 1
193. Cattaneo-Vietti, R., Chiantore, M., Schiaparelli, S., & Albertelli, G. (2000). Shallow- and deep-water mollusc distribution at Terra Nova Bay (Ross Sea, Antarctica). Polar Biology, 23(3), 173-182.
194. Peharda, M., Black, B. A., Purroy, A., & Mihanović, H. (2016). The bivalve Glycymeris pilosa as a multidecadal environmental archive for the Adriatic and Mediterranean Seas. Marine environmental research, 119, 79-87.
195. Demir, M. 2003 Shells of mollusca collected from the seas of Turkey. Turkey Journal of Zoology 27:101-140.
196. Bernard, F.R., Y.Y. Cai and B. Morton 1993 Catalogue of the living marine bivalve molluscs of China. Hong Kong University Press, Hong Kong. 121 p.
197. Selin, N. I. (2016). Spatial growth rate variability in Callista brevisiphonata (Carpenter, 1865) (Bivalvia: Veneridae). Russian Journal of Marine Biology, 42(4), 308-314.
198. Kitamura, A., Kawakami, I., Okamoto, F., et al., Distribution of mollusk shells in the Sea of Okhotsk, off Hokkaido, Bull. Geol. Surv. Jpn., 2002, vol. 53, nos. 5–6, pp. 483–558.
199. Semenikhina, O.Ya., Kolotukhina, N.K., and Evseev, G.A., Morphology of bivalve larvae of the Veneridae family (Bivalvia) of the Sea of Japan, Zool. Zh., 2006, vol. 85, no. 9, pp. 1067–1075
200. Zolotarev, V.N., Lifespan of bivalves from the Japan and Okhotsk Seas, Biol. Morya, 1980, no. 6, pp 3–12.
201. Treaster SB, Chaudhuri AR, Austad SN (2015) Longevity and GAPDH Stability in Bivalves and Mammals: A Convenient Marker for Comparative Gerontology and Proteostasis. PLoS ONE 10(11): e0143680.

202. Kasuya, T., Hamaguchi, M., & Furukawa, K. (2004). Detailed observation of spatial abundance of clam larva Ruditapes philippinarum in Tokyo Bay, central Japan. Journal of oceanography, 60(3), 631-636.
203. Gaspar, M.B., M.N. Santos, P. Vasconcelos and C.C. Monteiro 2002 Shell mophometric relationships of the most common bivalve species (Mollusca: Bivalvia) of the Algarve coast (southern Portugal). Hydrobiologia 477:73-80.
204. Leontarakis, P. K., & Richardson, C. A. (2005). Growth of the smooth clam, Callista chione (Linnaeus, 1758) (Bivalvia: Veneridae) from the Thracian Sea, northeastern Mediterranean. Journal of molluscan studies, 71(2), 189-192.
205. Bernard, F.R., Y.Y. Cai and B. Morton 1993 Catalogue of the living marine bivalve molluscs of China. Hong Kong University Press, Hong Kong. 121 p
206. Peharda, M., Puljas, S., Chauvaud, L., Schöne, B. R., Ezgeta-Balić, D., & Thébault, J. (2015). Growth and longevity of Lithophaga lithophaga: what can we learn from shell structure and stable isotope composition?. Marine biology, 162(8), 1531-1540.
207. Flores, L., Licandeo, R., Cubillos, L. A., & Mora, E. (2014). Intra-specific variability in life-history traits of Anadara tuberculosa (Mollusca: Bivalvia) in the mangrove ecosystem of the Southern coast of Ecuador. Revista de Biología Tropical, 62(2), 473-482.
208. Puljas, S., Peharda, M., Župan, I., & Bukša, F. (2015). Maximum recorded life span of Arca noae Linnaeus, 1758 in the marine protected area Telašćica, Adriatic Sea. Cah Biol Mar, 56, 163-168.
209. Morton, B., & Peharda, M. (2008). The biology and functional morphology of Arca noae (Bivalvia: Arcidae) from the Adriatic Sea, Croatia, with a discussion on the evolution of the bivalve mantle margin. Acta Zoologica, 89(1), 19-28.
210. Bušelić, I., Peharda, M., Reynolds, D. J., Butler, P. G., González, A. R., Ezgeta-Balić, D., & Richardson, C. A. (2015). Glycymeris bimaculata (Poli, 1795)—A new sclerochronological archive for the Mediterranean? Journal of Sea Research, 95, 139-148.
211. MacKenzie C. L. Jr. (2001). The Fisheries for Mangrove Cockles, Anadara spp., from Mexico to Peru, With Descriptions of Their Habitats and Biology, the Fishermen’s Lives, and the Effects of Shrimp Farming. Marine Fisheries Review 63(1).
212. Reynolds, D. J., Richardson, C. A., Scourse, J. D., Butler, P. G., Wanamaker Jr, A. D., Ridgway, I. & Gulliver, P. (2013). The potential of the marine bivalve mollusc Glossus humanus (L.) as a sclerochronological archive. The Holocene, 23(12), 1711-1720.
213. Owen, G. (1953). On the biology of Glossus humanus (L.) (Isocardia cor Lam.). Journal of the Marine Biological Association of the United Kingdom, 32(01), 85-106.
214. Bagur, M., Richardson, C. A., Gutiérrez, J. L., Arribas, L. P., Doldan, M. S., & Palomo, M. G. (2013). Age, growth and mortality in four populations of the boring bivalve Lithophaga patagonica from Argentina. Journal of sea research, 81, 49-56.
215. Rosenberg, G. 2009 Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca. [WWW database (version 4.1.1)] URL http://www.malacolog.org/.
216. Kastelle, C. R., Helser, T. E., Black, B. A., Stuckey, M. J., Gillespie, D. C., McArthur, J. & Khan, R. S. (2011). Bomb-produced radiocarbon validation of growth-increment crossdating allows marine paleoclimate reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology, 311(1), 126-135.
217. Gotshall, D.W. 2005 Guide to marine invertebrates: Alaska to Baja California, 2nd ed. (revised). Sea Challengers. 117 p.

218. Belz, C. E., Darrigran, G., Bonel, N., & Mäder Netto, O. S. (2010). Density, Recruitment, and Shell Growth of Limnoperna fortunei (Mytilidae), an lnvasive Mussel in Tropical South America. Journal of Freshwater Ecology, 25(2), 227-233.
219. Boltovskoy, D., & Cataldo, D. H. (1999). Population dynamics of Limnoperna fortunei, an invasive fouling mollusc, in the lower Paraná River (Argentina). Biofouling, 14(3), 255-263.
220. Lutaenko, K. A. (1999). Additional data on the fauna of bivalve mollusks of the Russian continental coast of the Sea of Japan: middle Primorye and Nakhodka Bay.
221. Selin, N. I. (2009). The effect of environmental conditions on distribution, growth and life span of Protothaca euglypta (Mollusca: Bivalvia). Russian Journal of Marine Biology, 35(1), 20-24.
222. Kasai, A., Horie, H., & Sakamoto, W. (2004). Selection of food sources by Ruditapes philippinarum and Mactra veneriformis (Bivalva: Mollusca) determined from stable isotope analysis. Fisheries science, 70(1), 11-20.
223. Ponurovskii, S. K. (2008). Population structure and growth of the Japanese littleneck clam Ruditapes philippinarum in Amursky Bay, Sea of Japan. Russian Journal of Marine Biology, 34(5), 329-332.
224. Deval, M. C., & Göktürk, D. (2008). Population structure and dynamics of the cut trough shell Spisula subtruncata (da Costa) in the Sea of Marmara, Turkey. Fisheries Research, 89(3), 241-247.
225. Gaspar, M.B., M.N. Santos and P. Vasconcelos 2001 Weight-length relationships of 25 bivalve species (Mollusca: Bivalvia) from the Algarve coast (southern Portugal). J. Mar. Biol. Ass. U.K. 81:805-807.
226. Riascos, J. M., Heilmayer, O., & Laudien, J. (2007). Population dynamics of the tropical bivalve Cardita affinis from Málaga Bay, Colombian Pacific related to La Niña 1999–2000. Helgoland Marine Research, 62(1), 63.
227. Lozano-Cortés, D., Londoño-Cruz, E., Izquierdo, V., Arias, F., Barona, M., & Zambrano, V. (2012). Checklist of benthonic marine invertebrates from Malaga Bay (Isla Palma and Los Negritos), Colombian Pacific. Check List, 8(4), 703-708.
228. Verween, A., Vincx, M., & Degraer, S. (2006). Growth patterns of Mytilopsis leucophaeata, an invasive biofouling bivalve in Europe. Biofouling, 22(4), 221-231.
229. Marcano, J. S., Prieto, A., Lárez, A., Alió, J., & Sanabria, H. (2005). Crecimiento y mortalidad de Pinctada imbricata (Mollusca: Pteriidae) en Guamachito, Península de Araya, Estado Sucre, Venezuela. Cien. Mar, 31(2), 387-397.
230. Turgeon, D.D., W.G. Lyons, P. Mikkelsen, G. Rosenberg and F. Moretzsohn 2009 Bivalvia (Mollusca) of the Gulf of Mexico. pp. 711-744 In Felder, D.L.; Camp, D.K. (eds.) Gulf of Mexico - Origins, Waters, and Biota. Biodiversity. Texas A&M University Press, College Station, Texas.
231. García, Y., Prieto, A., Marcano, J., Lodeiros, C., & Arrieche, D. (2005). Producción secundaria del mejillón verde (Perna viridis L. 1758), en la Península de Araya, Venezuela. Revista Científica, 15(3).
232. Poutiers, J.M. 1998 Bivalves. Acephala, Lamellibranchia, Pelecypoda. p. 123-362. In Carpenter, K. E. and V. H. Niem. 1998. FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 1. Seaweeds, corals, bivalves, and gastropods. Rome, FAO.
233. García, N., Prieto, A., Alzola, R., & Lodeiros, C. (2003). Crecimiento y distribución de tallas de Donax denticulatus (Mollusca: Donacidae) en playa Brava, península de Araya, estado Sucre, Venezuela. Revista Cientifica FCV-LUZ, 13.

234. Weber, A., Witbaard, R., & van Steenpaal, S. (2001). Patterns of growth and undetectable growth lines of Astarte sulcata (Bivalvia) in the Faroe-Shetland channel. Marine Biodiversity, 31(2), 235-244.
235. Zeichen, M. M., Agnesi, S., Mariani, A., Maccaroni, A., & Ardizzone, G. D. (2002). Biology and population dynamics of Donax trunculus L.(Bivalvia: Donacidae) in the South Adriatic coast (Italy). Estuarine, Coastal and Shelf Science, 54(6), 971-982.
236. McQuaid, C. D., & Lindsay, T. L. (2000). Effect of wave exposure on growth and mortality rates of the mussel Perna perna: bottom up regulation of intertidal populations. Marine Ecology Progress Series, 206, 147-154.
237. www.sealifebase.org

238. Wilson, J. G. (1997). Long-term changes in density, population structure and growth rate of Tellina tenuis from Dublin Bay, Ireland. Oceanolica Acta, 20(1), 267-274.
239. Alves, F., L. Chicharo, A. Nogueira and J. Regala 2003 Changes in benthic community structure due to clam dreging on the Algarve coast and the importance of seasonal analysis. J. Mar. Biol. Ass. U.K. 83:719-729.
240. Selin, N. I. (2010). The growth and life span of bivalve mollusks at the northeastern coast of Sakhalin Island. Russian journal of marine biology, 36(4), 258-269.
241. Harbo, R.M. 1997 Shells and shellfish of the Pacific Northwest, a field guide. Harbour Publishing, Canada, 270p.
242. Wołowicz, M., Sokołowski, A., Bawazir, A. S., & Lasota, R. (2006). Effect of eutrophication on the distribution and ecophysiology of the mussel Mytilus trossulus (Bivalvia) in southern Baltic Sea (the Gulf of Gdańsk). Limnology and Oceanography, 51(1part2), 580-590.
243. SAUP Database 2006 SAUP Database. www.seaaroundus.org.
244. Natural History Museum Rotterdam 2013 Spisula sachalinensis. [Accessed 4/29/2015].
245. Zabbey, N., Hart, A. I., & Wolff, W. J. (2010). Population structure, biomass and production of the West African lucinid Keletistes rhizoecus (Bivalvia, Mollusca) in Sivibilagbara swamp at Bodo creek, Niger Delta, Nigeria. Hydrobiologia, 654(1), 193-203.
246. Wisshak, M., Correa, M. L., Gofas, S., Salas, C., Taviani, M., Jakobsen, J., & Freiwald, A. (2009). Shell architecture, element composition, and stable isotope signature of the giant deep-sea oyster Neopycnodonte zibrowii sp. n. from the NE Atlantic. Deep Sea Research Part I: Oceanographic Research Papers, 56(3), 374-407.
247. Lastra, M., Palacio, J., & Mora, J. (1993). Population dynamics and secondary production of Abra alba (Wood)(Bivalvia) in the Santander Bay, northern Spain. Sarsia, 78(1), 35-42.
248. Dijkstra, H.H. 2013 Pectinoidea (Bivalvia: Propeamussiidae and Pectinidae) from the Panglao region, Philippine Islands. Vita Malacogica 10:1-108.
249. Bandeira-Pedrosa, M. E., Pereira, S., & Oliveira, E. C. (2004). Taxonomy and distribution of the green algal genus Halimeda (Bryopsidales, Chlorophyta) in Brazil. Brazilian Journal of Botany, 27(2), 363-377.
250. Svoboda, A. (1973). Underwater observations on the life cycle of Corymorpha nutans (Hydrozoa). Helgoland Wissenschaften Meeresuntersuchungen, 24, 145-150.
251. Hughes, R. G. (1977). Aspects of the biology and life-history of Nemertesia antennina (L.)(Hydrozoa: Plumulariidae). Journal of the Marine Biological Association of the United Kingdom, 57(03), 641-657.

252. Hughes, R. G. (1983). The life-history of Tubularia indivisa (Hydrozoa: Tubulariidae) with observations on the status of T. ceratogyne. Journal of the Marine Biological Association of the United Kingdom, 63(02), 467-479.
253. Kubota, S. (1997). A new form of the bivalve-inhabiting hydrozoan Eutima japonica (Leptomedusae, Eirenidae) in Japan.
254. Fox, H. M. (1963). Longevity in a polychaete and a coelenterate. Nature, 198(4886), 1222-1223.
255. Riedi, M. A., & Smith, A. M. (2015). Tube growth and calcification of two reef-building ecosystem engineers in southern New Zealand: Galeolaria hystrix and Spirobranchus cariniferus (Polychaeta: Serpulidae). Marine Geology, 367, 212-219.
256. Gibson, R. N., Barnes, M., & Atkinson, R. J. A. (2001). Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. Oceanography and Marine Biology, An Annual Review, Volume 39: An Annual Review, 39, 1-101.
257. Morri, C., C.N. Bianchi, S. Cocito, A. Peirano, A.M. De Biase, S. Aliani, M. Pansini, M. Boyer, F. Ferdeghini, M Pestarino and P. Dando 1999 Biodiversity of marine sessile epifauna at an Aegean island subject to hydrothermal activity: Milos, eastern Mediterranean Sea. Mar. Biol. 135:729-739.
258. Veron, J.E.N. 2000 Corals of the world. Volume 3. Australian Institute of Marine Science and CRR Qld. Pty. Ltd. Australia. 490 p.
259. Schellinger, J. (2017). Hardbottom Sessile Macroinvertebrate Communities of the Apalachee Bay Region of Florida's Northeastern Gulf of Mexico.
260. Cairns, S.D. and F.M. Bayer 2009 Octocorallia (Cnidaria) of the Gulf of Mexico. pp. 321-331 In Felder, D.L.; Camp, D.K. (eds.) Gulf of Mexico - Origins, Waters, and Biota. Biodiversity. Texas A&M University Press, College Station, Texas.
261. Rützler, K., R.W.M. van Soest and C. Piantoni 2009 Sponges (Porifera) of the Gulf of Mexico. pp. 285-313 In Felder, D.L.; Camp, D.K. (eds.) Gulf of Mexico - Origins, Waters, and Biota. Biodiversity. Texas A&M University Press, College Station, Texas.
262. Morri, C., Bianchi, C. N., Cocito, S., Peirano, A., De Biase, A. M., Aliani, S.,& Dando, P. (1999). Biodiversity of marine sessile epifauna at an Aegean island subject to hydrothermal activity: Milos, Eastern Mediterranean Sea. Marine Biology, 135(4), 729-739.
263. Chapman, A. R. O., & Goudey, C. L. (1983). Demographic study of the macrothallus of Leathesia difformis (Phaeophyta) in Nova Scotia. Canadian Journal of Botany, 61(1), 319-323.
264. Gunnill, F. C. (1980). Demography of the intertidal brown alga Pelvetia fastigiata in southern California, USA. Marine Biology, 59(3), 169-179.
265. Engel, C., Åberg, P., Gaggiotti, O. E., Destombe, C., & Valero, M. (2001). Population dynamics and stage structure in a haploid-diploid red seaweed, Gracilaria gracilis. Journal of Ecology, 89(3), 436-450.
266. Fischer, W. and J.-C. Hureau (eds.) 1985 FAO species identification sheets for fishery purposes. Southern Ocean (fishing areas 48, 58 and 88) (CCAMLR convention area). Prepared and published with the support of the Commission for the Conservation of Antarctic Marine Living Resources. FAO, Rome. 1:232 p.
267. Dyck, L. J. (1991). Some aspects of the demography of Iridaea splendens. Doctoral dissertation, University of British Columbia.
268. Pearson, G. A., & Brawley, S. H. (1996). Reproductive ecology, of Fucus distichus (Phaeophyceae): an intertidal alga with successful external fertilization. Marine Ecology Progress Series, 143, 211-223.

269. Coutinho, R., & Yoneshigue, Y. (1988). Diurnal variation in photosynthesis vs. irradiance curves from “sun” and “shade” plants of Pterocladia capillacea (Gmelin) Bornet et Thuret (Gelidiaciaceae: Rhodophyta) from Cabo Frio, Rio de Janeiro, Brazil. Journal of Experimental Marine Biology and Ecology, 118(3), 217-228.
270. Eriksson, B. K., Johansson, G., & Snoeijs, P. (2002). Long-term changes in the macroalgal vegetation of the inner Gullmar fjord, Swedish skagerrak coast. Journal of Phycology, 38(2), 284-296.
271. Otway, N. M. (1994). Population ecology of the low-shore chitons Onithochiton quercinus and Plaxiphora albida. Marine Biology, 121(1), 105-116.
272. Carey Jr, A. G., Scott, P. H., & Walter, K. R. (1984). Distributional ecology of shallow southwestern Beaufort Sea (Arctic Ocean) bivalve Mollusca. Marine Ecology Progress Series. Oldendorf, 17(2), 125-134.
273. Fyles, J. G., Marincovich Jr, L., Matthews Jr, J. V., & Barendregt, R. (1991). Unique mollusc find in the Beaufort Formation (Pliocene) on Meighen Island, Arctic Canada. Current Research, Part B. Geological Survey of Canada, pp. 461e468. Paper.
274. Wagner, F. J. (1977). Recent mollusc distribution patterns and palaeobathymetry, southeastern Beaufort Sea. Canadian Journal of Earth Sciences, 14(9), 2013-2028.
275. Buhl-Mortensen, L., & Høeg, J. T. (2006). Reproduction and larval development in three scalpellid barnacles, Scalpellum scalpellum (Linnaeus 1767), Ornatoscalpellum stroemii (M. Sars 1859) and Arcoscalpellum michelottianum (Seguenza 1876), Crustacea: Cirripedia: Thoracica): implications for reproduction and dispersal in the deep sea. Marine Biology, 149(4), 829-844.
276. Smith, A. M., McGourty, C. R., Kregting, L., & Elliot, A. (2005). Subtidal Galeolaria hystrix (Polychaeta: Serpulidae) reefs in Paterson Inlet, Stewart Island, New Zealand. New Zealand Journal of Marine and Freshwater Research, 39(6), 1297-1304.
277. Bianchi, C. N., & Morri, C. (2000). Serpuloidea (Annelida: Polychaeta) from Milos, an island in the Aegean Sea with submarine hydrothermalism. Journal of the Marine Biological Association of the UK, 80(02), 259-269.
278. Morton, J. E., Boney, A. D., & Corner, E. D. S. (1957). The adaptations of Lasaea rubra (Montagu), a small intertidal lamellibranch. Journal of the Marine Biological Association of the United Kingdom, 36(02), 383-405.
279. Schiaparelli, S., & Linse, K. (2006). A reassessment of the distribution of the common Antarctic scallop Adamussium colbecki (Smith, 1902). Deep Sea Research Part II: Topical Studies in Oceanography, 53(8), 912-920.

Table S10. Source studies of long-term demographic variability estimates included in the comparative analysis (n = 34) (See completed references list below).

Species Name	**Habitat**	**Study Period**	**# Populations**	**Source ID**
Actaea spicata	Terrestrial	1999 - 2005	2	1
Alliaria petiolata	Terrestrial	2003-2008	6	2
Arabis fecunda	Terrestrial	1987-1993, 2009	3	3, 4
Astragalus scaphoides	Terrestrial	1986-2009	3	3, 5
Astragalus tyghensis	Terrestrial	1991-1998, 2008	5	3, 6
Cimicifuga elata	Terrestrial	1992–1996, 1992–1997	3	3, 6
Cirsium pitcheri	Terrestrial	1998-2009	4	3, 7
Cypripedium fasciculatum	Terrestrial	1999-2007	3	3
Dicerandra frutescens	Terrestrial	1988-2008	6	3, 8, 9
Eryngium cuneifolium	Terrestrial	1990-2008	6	10
Gentiana pneumonanthe	Terrestrial	1987-1993, 2009	7	3, 11
Haplopappus radiatus	Terrestrial	1992-1999, 2009	4	3, 6
Horkelia congesta	Terrestrial	1994-1999, 2009	1	3, 12
Hypericum cumulicola	Terrestrial	1994-2007	6	3, 13
Lathyrus vernus	Terrestrial	1988-1991, 2009	10	3, 14
Liatris scariosa	Terrestrial	1995-2000, 2008	1	3
Lomatium cookii	Terrestrial	1994-1999, 2009	2	3, 6
Lomatium bradshawii	Terrestrial	1988–1994, 1996–1997	7	3, 6
Neobuxbaumia macrocephala	Terrestrial	1997-2002, 2009	1	3, 15, 16
Opuntia macrorhiza	Terrestrial	1999-2005	5	17
Phyllanthus emblica	Terrestrial	1999-2004, 2009	1	3
Phyllanthus indofischeri	Terrestrial	1999-2004, 2009	1	3
Silene acaulis	Terrestrial	1995-2000, 2009	4	3, 18
Silene spaldingii	Terrestrial	1987-2009	1	3, 19, 20
Trillium grandiflorum	Terrestrial	1998-2002, 2010	12	3, 21, 22
Plexaura A	Marine	1984-1987	1	23
Corallium rubrum	Marine	2003-2011	8	Present Study
Montastrea annularis	Marine	2001-2009	1	24

Porites astreoides	Marine	1999-2007	1	25
Diploria strigosa	Marine	2002-2007	1	25
Acropora palmata	Marine	2004-2010	1	26
Paramuricea clavata	Marine	1999-2003	1	27
Mesodesma mactroides	Marine	1983-1990	1	28
Yoldia notabilis	Marine	1973-1989, 1977-1989	2	29

Complete references list of Table S10

1. Fröborg, H., & Eriksson, O. (2003). Predispersal seed predation and population dynamics in the perennial understorey herb Actaea spicata. Canadian Journal of Botany, 81(11), 1058-1069.
2. Kalisz, S., Spigler, R. B., & Horvitz, C. C. (2014). In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. Proceedings of the National Academy of Sciences, 111(12), 4501-4506.
3. Ellis, M. M., J. L. Williams, P. Lesica, T. J. Bell, P. Bierzychudek, M. Bowles, E. E. Crone, D. F. Doak, J. Ehrlén, A. Ellis-Adam, K. McEachern, R. Ganesan, P. Latham, S. Luijten, T. N. Kaye, T. M. Knight, E. S. Menges, W. F. Morris, H. den Nijs, G. Oostermeijer, P. F. Quintana-Ascencio, J. Stephen Shelly, A. Stanley, A. Thorpe, T. Ticktin, T. Valverde, C. Weekley. (2012) Data Paper: Matrix population models from 20 studies of perennial plant populations. Ecology, 93:951
4. Lesica, P., & Shelly, J. S. (1995). Effects of reproductive mode on demography and life history in Arabis fecunda (Brassicaceae). American Journal of Botany, 752-762.
5. Lesica, P. (1995). Demography of Astragalus scaphoides and effects of herbivory on population growth. The Great Basin Naturalist, 142-150.
6. Kaye, T. N., & Pyke, D. A. (2003). The effect of stochastic technique on estimates of population viability from transition matrix models. Ecology, 84(6), 1464-1476.
7. Bell, T. J., Bowles, M. L., & McEachern, A. K. (2003). Projecting the success of plant population restoration with viability analysis. In Population viability in plants (pp. 313-348). Springer Berlin Heidelberg.
8. Menges, E. S., Ascencio, P. F. Q., Weekley, C. W., & Gaoue, O. G. (2006). Population viability analysis and fire return intervals for an endemic Florida scrub mint. Biological Conservation, 127(1), 115-127.
9. Menges, E. S. (2008). Demography of the endemic mint Dicerandra frutescens in Florida scrub. Ecology, 89(5), 1474-1474.
10. Menges, E. S., & Quintana-Ascencio, P. F. (2004). Population viability with fire in Eryngium cuneifolium: deciphering a decade of demographic data. Ecological Monographs, 74(1), 79-99.
11. Oostermeijer, J. G. B., Brugman, M. L., De Boer, E. R., & Den Nijs, H. C. (1996). Temporal and spatial variation in the demography of Gentiana pneumonanthe, a rare perennial herb. Journal of ecology, 153-166.
12. Kaye, T. N., Benfield, C., Cooperativ, A., & District, E. (2004). Population monitoring and viability analysis for Horkelia congesta ssp. congesta at the Long Tom Area of Critical Environmental Concern. Institute for Applied Ecology, Corvallis, Oregon, USA.

13. Quintana-Ascencio, P. F., Menges, E. S., & Weekley, C. W. (2003). A Fire-Explicit Population Viability Analysis of Hypericum cumulicola in Florida Rosemary Scrub. Conservation Biology, 17(2), 433-449.
14. Ehrlen, J. (1995). Demography of the perennial herb Lathyrus vernus. II. Herbivory and population dynamics. Journal of Ecology, 297-308.
15. Esparza-Olguın, L., Valverde, T., & Vilchis-Anaya, E. (2002). Demographic analysis of a rare columnar cactus (Neobuxbaumia macrocephala) in the Tehuacan Valley, Mexico. Biological Conservation, 103(3), 349-359.
16. Esparza-Olguín, L., Valverde, T., & Mandujano, M. C. (2005). Comparative demographic analysis of three Neobuxbaumia species (Cactaceae) with differing degree of rarity. Population Ecology, 47(3), 229-245.
17. Haridas, C. V., Keeler, K. H., & Tenhumberg, B. (2015). Variation in the local population dynamics of the short-lived Opuntia macrorhiza (Cactaceae). Ecology, 96(3), 800-807.
18. Morris, W. F., & Doak, D. F. (2005). How general are the determinants of the stochastic population growth rate across nearby sites? Ecological Monographs, 75(1), 119-137.
19. Lesica, P. (1997). Demography of the endangered plant, Silene spaldingii (Caryophyllaceae) in northwest Montana. Madrono, 347-358.
20. Lesica, P., & Crone, E. E. (2007). Causes and consequences of prolonged dormancy for an iteroparous geophyte, Silene spaldingii. Journal of Ecology, 95(6), 1360-1369.
21. Knight, T. M. (2004). The effects of herbivory and pollen limitation on a declining population of Trillium grandiflorum. Ecological Applications, 14(3), 915-928.
22. Knight, T. M., Caswell, H., & Kalisz, S. (2009). Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory. Forest Ecology and Management, 257(3), 1095-1103.
23. Lasker, H. R. (1990). Clonal propagation and population dynamics of a gorgonian coral. Ecology, 71(4), 1578-1589.
24. Hernández-Pacheco, R., Hernández-Delgado, E. A., & Sabat, A. M. (2011). Demographics of bleaching in a major Caribbean reef-building coral: Montastraea annularis. Ecosphere, 2(1), 1-13.
25. Edmunds, P. J. (2010). Population biology of Porites astreoides and Diploria strigosa on a shallow Caribbean reef. Marine Ecology Progress Series, 418, 87-104.
26. Vardi, T., Williams, D. E., & Sandin, S. A. (2012). Population dynamics of threatened elkhorn coral in the northern Florida Keys, USA. Endangered Species Research, 19(2), 157-169.
27. Linares, C., & Doak, D. F. (2010). Forecasting the combined effects of disparate disturbances on the persistence of long-lived gorgonians: a case study of Paramuricea clavata. Marine Ecology Progress Series, 402, 59-68.
28. Brazeiro, A., & Defeo, O. (1999). Effects of harvesting and density dependence on the demography of sandy beach populations: the yellow clam Mesodesma mactroides of Uruguay. Marine Ecology Progress Series, 182, 127-135.
29. Nakaoka, M. (1993). Yearly variation in recruitment and its effect on population dynamics inYoldia notabilis (Mollusca: Bivalvia), analyzed using projection matrix model. Researches on Population Ecology, 35(2), 199-213.

SUPPLEMENTARY METHODS

Integral Projection Model: data collection and model construction

Demographic monitoring of natural Corallium rubrum populations

A total of 1144 coral colonies from nine *C. rubrum* populations along the North-Western Mediterranean region were individually monitored using photographic techniques over periods ranging from 3 to 9 years between 2003 and 2011 (Montero-Serra *et al. in preparation*).

Six populations were located within Marine Protected Areas (MPA) where harvesting is not allowed but other human uses are allowed with some restrictions. Recreational diving is allowed in Parc Natural del Montgrí, Illes Medes i Baix Ter (Spain) and completely forbidden except for scientific studies in the Réserve Naturelle Marine Cerbère-Banyuls (France), in Parc Marine Côte Bleue (France), and the Réserve Naturelle de Scandola (France). The last three populations are located in the archipelago of Riou near Marseilles (France), where harvesting and recreational diving was allowed during the study (Fig. S1).

To individually identify and track each coral colony during the study period, two to four permanent transects were installed at each population. Transects were monitored once a year using a photographic sampling design. During sampling, a cord was deployed between permanently set screws and a 20 x 20 cm quadrat, sequentially positioned and photographed along the length of each transect. Two photographs were taken from each quadrat using different angles. This allowed us to obtain precise measurements of colony heights using photogrammetric techniques (Drap *et al.* 2013).

Estimation of vital rates

Vital rates (survival, growth, and reproduction) were estimated by fitting size-based continuous functions to long-term data on survival, post-recruit survival, growth and variance in growth (Easterling et al. 2000, Morris and Doak 2002). Survival was described by a logistic mixed effects model (GLMM) including colony size and year as fixed factors and population as a random factor.

Growth data from two populations over variable length periods (7 and 8 yrs) were used to fit a model characterizing annual growth rate depending on size. Processed height data from all annual photographs were not available, and growth is so slow in this species that even 7 to 8 year time periods only result in mean growth on the order of 10 to 40mm in maximum height ($2.74 \pm 0.19\ \mathrm{mm \cdot yr^{-1}}$, see Fig. S2). As for many other clonal species, red coral can both grow and shrink over time. Shrinkage or negative growth is a common process in plants and sessile invertebrates that is usually accounted for by assuming normally distributed variation in size changes around a mean rate (e.g., Easterling *et al.* 2000, Salguero-Gomez & Casper 2010). However, for many species assuming normally distributed growth variance is problematic, because a few individuals experience sporadic extreme shrinkage events and these results in a highly skewed distribution of growth rates (Shriver *et al*. 2012). We accounted for these two types of growth following the procedures proposed by Shriver and colleagues (2012), describing normal growth and extreme shrinkage as a two-part process. First, we estimated the probability of each colony undergoing "normal growth" (pn) and "extreme shrinkage" (1 - pn). These probabilities are size- and year-dependent according to the data.

For each type of growth (normal and extreme shrinkage) we first calculated mean annual change in size as.

$G = (Size_T - Size_0) / T$

where T is the time between the first and final census, $Size_0$ is the initial size measurement, and $Size_T$ is the final size measurement.

We then extracted the residuals from the best-fitting model and divided the residuals by the number of years to predict annual variance in growth:

$VAR = \{(Residuals) / T\}^2$

We then used a linear regression model to fit the squared residuals to size, which showed a marginally significant positive relationship for normal growth ($P = 0.08$) and shrinkage ($P < 0.001$).

Recruitment rates were annually quantified from 30 fixed quadrats for each population. We considered effective recruits to be the button-like colonies observed for the first time in a quadrat. We calculated post-recruitment survival by monitoring recruits that we observed for the first time within a quadrat and tracked during the study period. Our data allowed for a robust estimation of survival within the range from 1 to 4 years. Further, we estimated the probability of recruits growing to an adult stage by direct observations in three populations where this process could be clearly identified**.**

Molecular studies have revealed a fine-scale genetic structure within *C. rubrum* populations and almost negligible dispersal among populations (Ledoux *et al.* 2010). Thus, new recruits were assigned to past individual parents assuming a relationship between colony size and the relative rate of reproduction. Past work has shown that there is an exponential relationship between *C. rubrum* size and polyp number (Santangelo *et al.* 2003), proportion of fertile colonies, and frequency of larvae per polyp in *C. rubrum* (Torrents *et al*. 2005). Thus, we used the squared adult colony size (height) as an approximation for polyp number. We then corrected these data by the proportion of fertile colonies and percentage of fertile polyps, because both parameters have been shown to increase along with colony size (Torrents et al. 2005).

Fecundity was calculated as follows:

(1)

Recruits/Size = New Recruits per quadrat (t1) / ∑((Colony Size)^2)*Colony Fertility * Polyp Fertility) (t0) per quadrat

(2)

Fecundity values = [(Adult Colony Size)^2] * (Colony Fertility * Polyp Fertility)* (Rec/Size)

Model construction

We coupled continuous size-based vital rates estimates for adults to four age-based stages for recruits to build an IPM for red coral. We simulated the model using 60 classes (where the first four classes are age-based categories for recruits and the rest are size-based). The number of size classes was chosen after calculating asymptotic population growth under multiple matrices constructed using a range of size-classes from 3 to 200. The results of these simulations showed that matrices with a number of size-classes larger than 60 showed a consistent value for population growth rate (Fig S2).

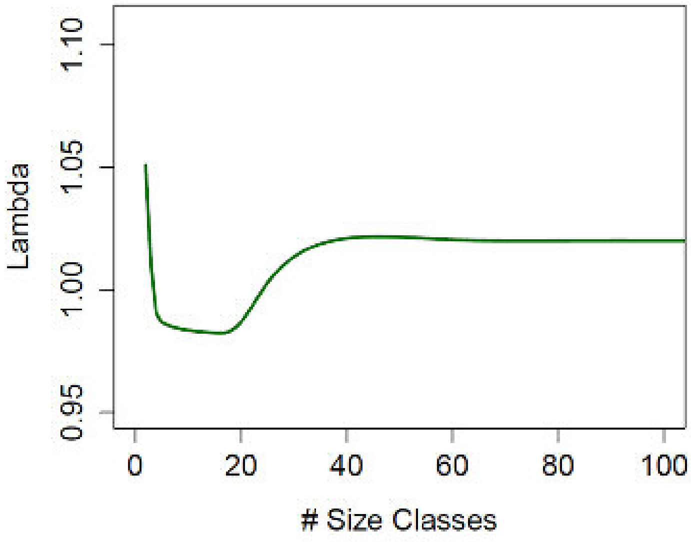


Figure S2. Asymptotic population growth rate (lambda) based on matrix approximations to a continuous IPM model constructed using a range of size-classes from 3 to 200.

We parameterized eight annual matrices that were derived based on the models previously fit; the fecundity and survival functions varied between these years, while growth was not estimated on an annual basis. All the a_{ji} matrix elements below the top row (the reproductive elements) were estimated as:

(3)

$$a_{ji} = s_i \,(p_{n,i}\, n_{ji} + (1 - p_{n,i})\, m_{ji})$$

where s_i is the probability of survival for the ith size class, $p_{n,i}$ is the probability of ‘‘normal growth or shrinkage’’ for the ith class, n_{ji} is the probability of normally growing or shrinking from the ith class to the jth class, and m_{ji} is the probability of moving from the ith to the jth class with extreme shrinkage. To estimate n_{ji} and m_{ji} values, we used the mid-point size for class i as the starting size, and a normal CDF to calculate the total probability of falling within the range of sizes in the jth class.

References included in the supplementary methods

1. Drap, P., Merad, D., Mahiddine, A., *et al.* (2013) Automating the measurement of red coral in situ using underwater photogrammetry and coded targets. XXIV International CIPA Symposium, Strasbourg, France. Vol. XL-5/W2, pp.231–236

2. Easterling, M.R., Ellner, S.P., and Dixon, P.M. (2000) Size-Specific Sensitivity: Applying a New Structured Population Model. *Ecology.*, 81(3) 694-708

3. Morris, W.F. & Doak, D.F. (2002) Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Inc. Publishers; Sunderland, Massachusetts U.S.A.

4. Torrents, O., Garrabou, J., Marschal, C. & Harmelin, J. G. (2005) Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) in the Marseilles area (France, NW Mediterranean). *Biol. Consv.,* 121(3) 391–397

5. Salguero-Gomez, R. & Casper, B. B. (2010) Keeping plant shrinkage in the demographic loop. *J. Ecol*., 98(2): 312–323

6. Santangelo, G., Carletti, E., Maggi, E. & Bramanti, L. (2003) Reproduction and population sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. *Mar. Eco. Prog. Ser.*, 248: 99–108, 2003

7. Shriver, R. K., Cutler, K., & Doak, D. F. (2012). Comparative demography of an epiphytic lichen: support for general life history patterns and solutions to common problems in demographic parameter estimation. *Oecologia*, 170(1), 137-146.

Supplementary Materials Chapter 2

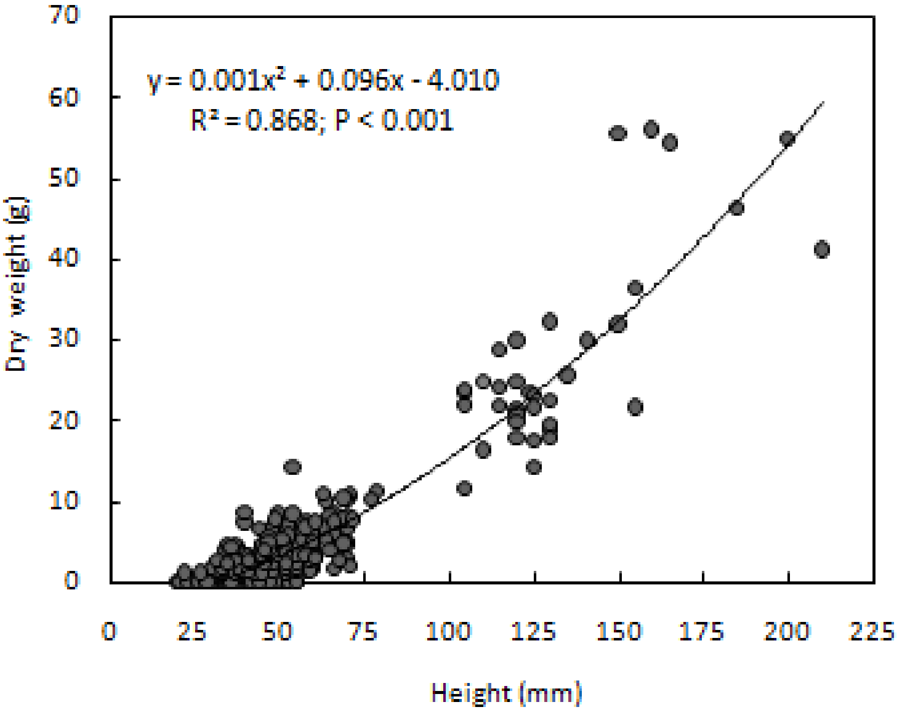


Figure S1. Height – weight relationship obtained from death corals (n = 300).

Supplementary Materials Chapter III

Table S1. Mediterranean red coral populations surveyed annually.

Table S2. Logistic Generalized Mixed Effects Models fitted to long-term demographic data on annual colony survival rates.

Table S3. Logistic Generalized Mixed Effects Models fitted to long-term demographic data on annual colony shrinkage rates.

Figure S1. Local disturbance levels used to simulate the interactive effects of warming and marine protected areas. To account for a continuous gradient of local disturbance intensity in Figure 5, we computed ten levels of local disturbance intensity by multiplying the protection factor in the shrinkage probability GLMM (Table S3) by ten levels. The maximum intensity (black line) corresponds to shrinkage probability outside MPAs, while the minimum probability (light grey) corresponds to shrinkage rates observed in populations within MPAs.

Figure S2. Annual transition probabilities of large red coral colonies (<100mm in height) in protected and unprotected populations. Large red coral colonies can survive and stay in the same size-class (stasis) or survive but transit to smaller size-classes due to partial mortality events (shrinkage). A total of 36 annual and

Table S1. Mediterranean red coral populations surveyed annually.

Name	**Depth (m)**	**Area**	**Protection Level**	**N**	**Years Surveyed**
Dofí	17-22	Catalan Sea (Spain)	Partial Protection	148	2006 to 2011
Reina	17-24	Catalan Sea (Spain)	Partial Protection	140	2007 to 2011
Banyuls	23 - 25	Catalan Sea (Spain)	Integral Protection	108	2005 to 2007
Maire	15 - 18	Marseille (France)	Unprotected	140	2002 to 2009
Riou	17-24	Marseille (France)	Unprotected	204	2005 to 2009
Plane	17-24	Marseille (France)	Unprotected	154	2003 to 2010
Passe	24 – 27	Corsica (France)	Integral Protection	145	2006 to 2016
Palazzu	19 – 22	Corsica (France)	Integral Protection	137	2003 to 2016

Table S2. Logistic Generalized Mixed Effects Models fitted to long-term demographic data on annual colony survival rates.

Model	AICc	ΔAICc	Parameter	Estimate	P-value
Survival ~ Colony Size + (1 | Population) + (1 | Year)	923.5	0	Intercept	4.360851 ± 0.508109	<0.0001
			Colony Size	0.015677 ± 0.003904	<0.0001
Survival ~ Colony Size + MPA + (1 | MPA/Population) + (1 | Year)	925.3	1.8	Intercept	4.177284 ± 0.675142	<0.0001
			Colony Size	0.015572 ± 0.003917	<0.0001
			MPA	0.316082 ± 0.769349	0.6810
Survival ~ Colony Size + MPA + Colony Size*MPA + (1 | MPA/Population) + (1 | Year)	927.3	3.8	Intercept	4.182451 ± 0.76020	<0.0001
			Colony Size	0.015398 ± 0.01244	0.2161
			MPA	0.310012 ± 0.87232	0.7223
			Colony Size*MPA	0.000193 ± 0.01307	0.9881

Table S3. Logistic Generalized Mixed Effects Models fitted to long-term demographic data on annual colony shrinkage rates.

Model	AIC	ΔAIC	Parameter	Estimate (±SE)	P-value
Shrinkage ~ Colony Size + MPA + Colony Size*MPA + (1 | MPA/Population) + (1 | Year)	1928.5	0	Intercept	-4.508317 ± 0.599878	<0.0001
			Colony Size	0.046478 ± 0.004421	<0.0001
			MPA	-0.580281 ± 0.763198	0.447
			Colony Size*MPA	-0.040954 ± 0.005398	<0.0001
Shrinkage ~ Colony Size + MPA + (1 | MPA/Population) + (1 | Year)	1987.9	59	Intercept	-3.457779 ± 0.458558	<0.0001
			Colony Size	0.020850 ± 0.002419	<0.0001
			MPA	-2.542601 ± 0.576368	<0.0001
Shrinkage ~ Colony Size + (1 | Population) + (1 | Year)	1994.5	66	Intercept	-5.319992 ± 0.748843	<0.0001
			Colony Size	0.020597 ± 0.002444	<0.0001

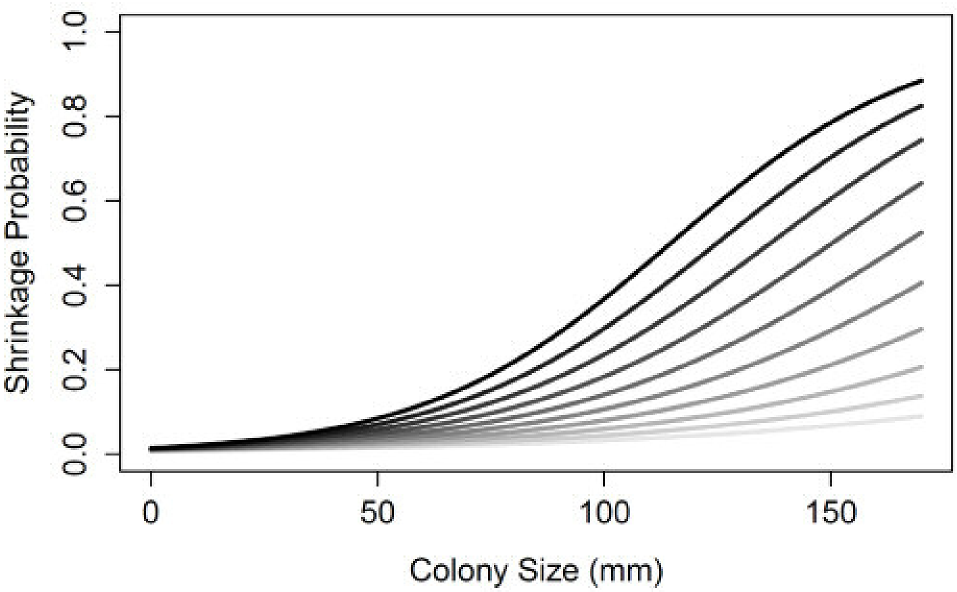


Figure S1. Local disturbance levels used to simulate the interactive effects of warming and marine protected areas. To account for a continuous gradient of local disturbance intensity in Figure 5, we computed ten levels of local disturbance intensity by multiplying the protection factor in the shrinkage probability GLMM (Table S3) by ten levels. The maximum intensity (black line) corresponds to shrinkage probability outside MPAs, while the minimum probability (light grey) corresponds to shrinkage rates observed in populations within MPAs.

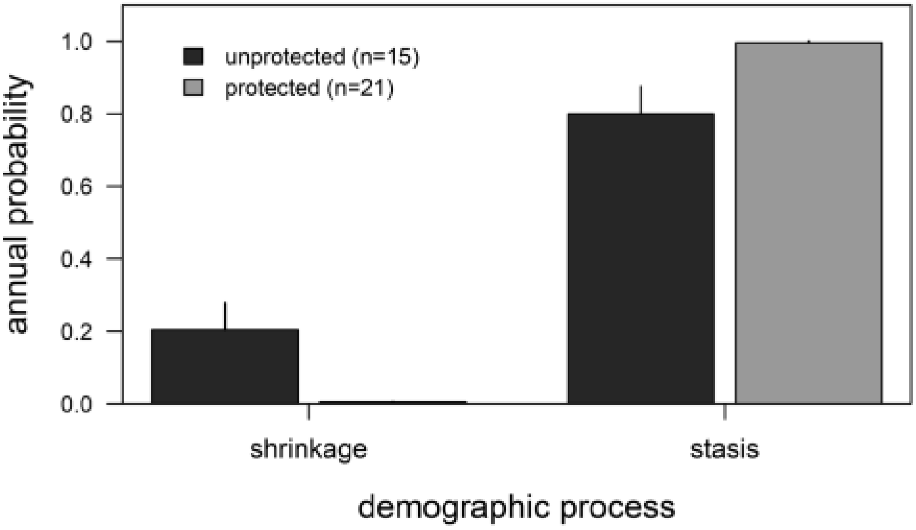


Figure S2. Annual transition probabilities of large red coral colonies (<100mm in height) in protected and unprotected populations. Large red coral colonies can survive and stay in the same size-class (stasis) or survive but transit to smaller size-classes due to partial mortality events (shrinkage). A total of 36 annual and population level matrices were constructed from field demographic data on four protected and three unprotected red coral populations in the NW Mediterranean Sea.

Supplementary Materials Chapter IV

Figure S1. Population size frequency distribution of the transplanted colonies represented by the brown bars and the brown line. Green lines represent the size-structure of three mature and well-preserved populations based on data from Linares *et al.* (2010): Carry, Banyuls, and Palazzu. In order to aid data visualization, we fitted a cubic smoothing spline to the colony-size frequency data of each population using the *Smoth.spline()* function in R.

Figure S2. Size-dependent growth of *C. rubrum* colonies based on data from two natural populations.

Figure S3. Growth rates in natural vs. transplanted coral colonies (log-scale) for 17 coral species.

Supplementary Methods. Full description of the demographic models.

Table S1. Summary statistics for the linear model fitted to the expected recovery periods.

Table S2. Source data of survival in transplant experiments and growth references of the marine sessile species included in the comparative analysis.

Table S3. Source data of population matrix models used to project potential recovery periods.

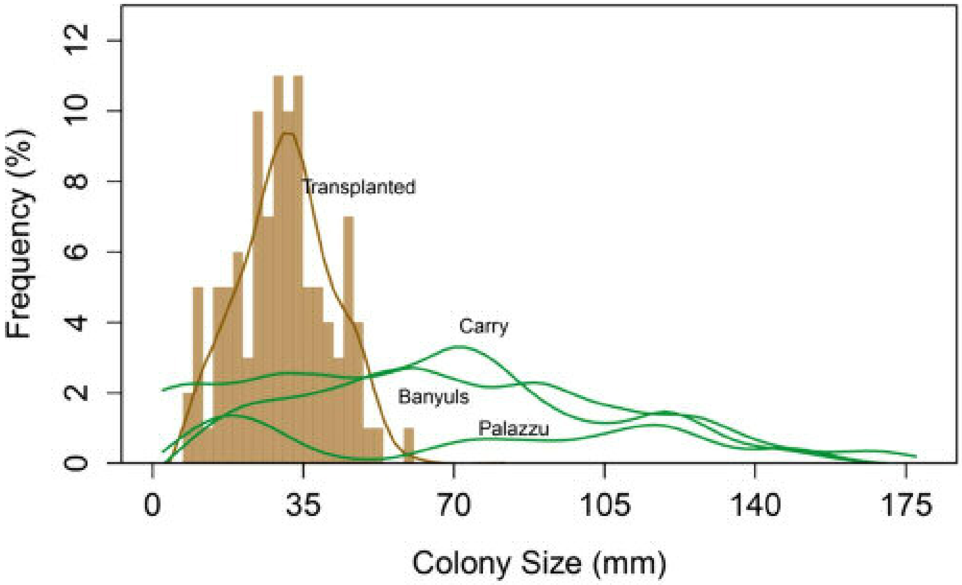


Figure S1. Population size frequency distribution of the transplanted colonies represented by the brown bars and the brown line. Green lines represent the size-structure of three mature and well-preserved populations based on data from Linares *et al.* (2010): Carry, Banyuls, and Palazzu. In order to aid data visualization, we fitted a cubic smoothing spline to the colony-size frequency data of each population using the *Smoth.spline()* function in R.

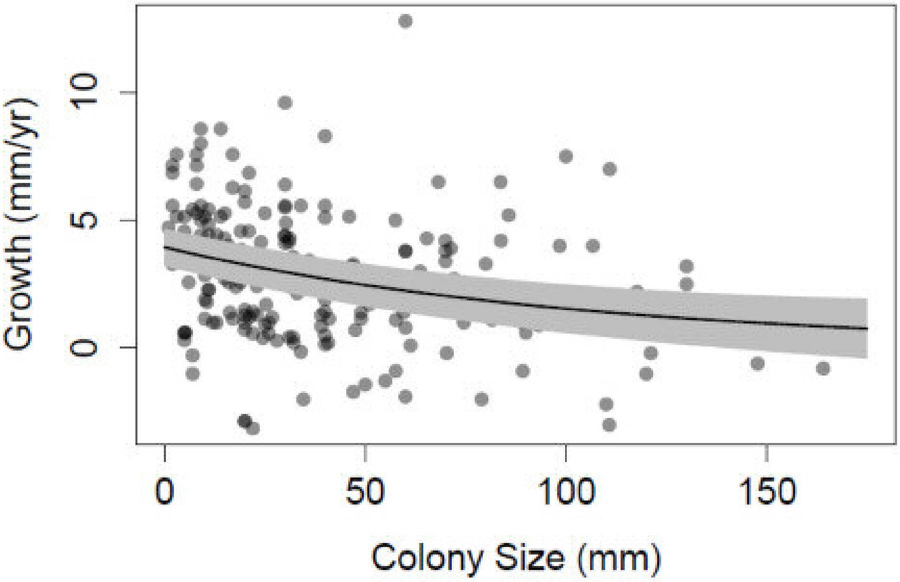


Figure S2. Size-dependent growth of *C. rubrum* colonies based on data from two natural populations.

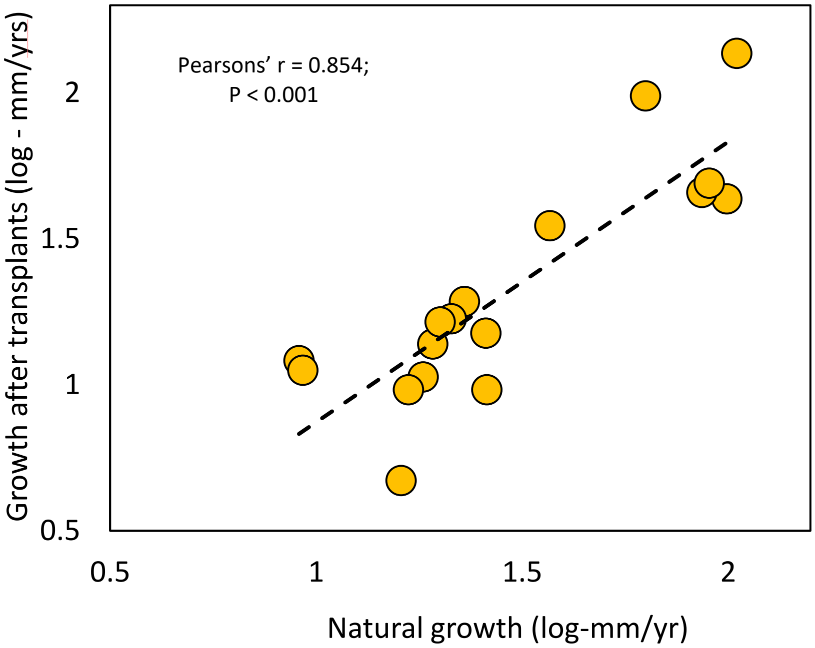


Figure S3. Growth rates in natural vs. transplanted coral colonies (log-scale) for 17 coral species.

Supplementary Methods Chapter IV

Integral Projection Model: data collection and model construction

Demographic monitoring of natural Corallium rubrum populations

A total of 1144 coral colonies from nine *C. rubrum* populations along the North-Western Mediterranean region were individually monitored using photographic techniques over periods ranging from 3 to 9 years between 2003 and 2011 (Montero-Serra *et al. in preparation*).

Six populations were located within Marine Protected Areas (MPA) where harvesting is not allowed but other human uses are allowed with some restrictions. Recreational diving is allowed in Parc Natural del Montgrí, Illes Medes i Baix Ter (Spain) and completely forbidden except for scientific studies in the Réserve Naturelle Marine Cerbère-Banyuls (France), in Parc Marine Côte Bleue (France), and the Réserve Naturelle de Scandola (France). The last three populations are located in the archipelago of Riou near Marseilles (France), where harvesting and recreational diving was allowed during the study (Fig. S1).

To individually identify and track each coral colony during the study period, two to four permanent transects were installed at each population. Transects were monitored once a year using a photographic sampling design. During sampling, a cord was deployed between permanently set screws and a 20 x 20 cm quadrat, sequentially positioned and photographed along the length of each transect. Two photographs were taken from each quadrat using different angles. This allowed us to obtain precise measurements of colony heights using photogrammetric techniques (Drap *et al.* 2013).

Estimation of vital rates

Vital rates (survival, growth, and reproduction) were described by fitting size-based continuous functions to long-term data on survival, post-recruit survival, growth and variance in growth (Easterling et al. 2000, Morris and Doak 2002). Survival was described by a logistic mixed effects model (GLMM) including colony size and year as fixed factors and population as a random factor.

Growth data from two populations over variable length periods (7 and 8 yrs) were used to fit a model characterizing annual growth rate depending on size. Processed height data from all annual photographs were not available, and growth is so slow in this species that even 7 to 8 year time periods only result in mean growth on the order of 10 to 40mm in maximum height (2.74 ± 0.19 mm·yr^{-1}, see Fig. S2). As for many other clonal species, red coral can both grow and shrink over time. Shrinkage or negative growth is a common process in plants and sessile invertebrates that is usually accounted for by assuming normally distributed variation in size changes around a mean rate (e.g., Easterling *et al.* 2000, Salguero-Gomez & Casper 2010). However, for many species assuming normally distributed growth variance is problematic, because a few individuals experience sporadic extreme shrinkage events and these results in a highly skewed distribution of growth rates (Shriver *et al*. 2012). We accounted for these two types of growth following the procedures proposed by Shriver and colleagues (2012), describing growth and shrinkage as a two-part process. First, we estimated the probability of each colony undergoing "normal growth" (pn) and "extreme shrinkage" (1 - pn). These probabilities are size- and year-dependent according to the data.

For each type of growth (normal and extreme shrinkage) we first calculated mean annual growth as.

$G = (Size_T - Size_0) / T$

where T is the time between the first and final census, $Size_0$ is the initial size measurement, and $Size_T$ is the final size measurement.

We then extracted the residuals from the best-fitting model and divided the residuals by the number of years to predict annual variance in growth:

$VAR = \{(Residuals) / T\}^2$

We then used a linear regression model to fit the squared residuals to size, which showed a marginally significant positive relationship for normal growth ($P = 0.08$) and shrinkage ($P < 0.001$).

Recruitment rates were annually quantified from 30 fixed quadrats for each population. We considered effective recruits to be the button-like colonies observed for the first time in a quadrat. We calculated post-recruitment survival by monitoring recruits that we observed for the first time within a quadrat and tracked during the study period. Our data allowed for a robust estimation of survival within the range from 1 to 4 years. Further, we estimated the probability of recruits growing to an adult stage by direct observations in three populations where this process could be clearly identified**.**

Molecular studies have revealed a fine-scale genetic structure within *C. rubrum* populations and almost negligible dispersal among populations (Ledoux *et al.* 2010). Thus, new recruits were assigned to past individual parents assuming a relationship between colony size and the relative rate of reproduction. Past work has shown that there is an exponential relationship between *C. rubrum* size and polyp number (Santangelo *et al.* 2003), proportion of fertile colonies, and frequency of larvae per polyp in *C. rubrum* (Torrents *et al*. 2005). Thus, we used the squared adult colony size (height) as an approximation for polyp number. We then corrected these data by the proportion of fertile colonies and percentage of fertile polyps, because both parameters have been shown to increase along with colony size (Torrents et al. 2005).

Fecundity was calculated as follows:

(1)

Recruits/Size = New Recruits per quadrat (t1) / ∑((Colony Size)^2)*Colony Fertility * Polyp Fertility) (t0) per quadrat

(2)

Fecundity values = [(Adult Colony Size)^2] * (Colony Fertility * Polyp Fertility)* (Rec/Size)

Model construction

We coupled continuous size-based vital rates estimates for adults to four age-based stages for recruits to build an IPM for red coral. We simulated the model using 60 classes (where the first four classes are age-based categories for recruits and the rest are size-based). The number of size classes was chosen after calculating asymptotic population growth under multiple matrices constructed using a range of size-classes from 3 to 200. The results of these simulations showed that matrices with a number of size-classes larger than 60 showed a consistent value for population growth rate (Fig S2).

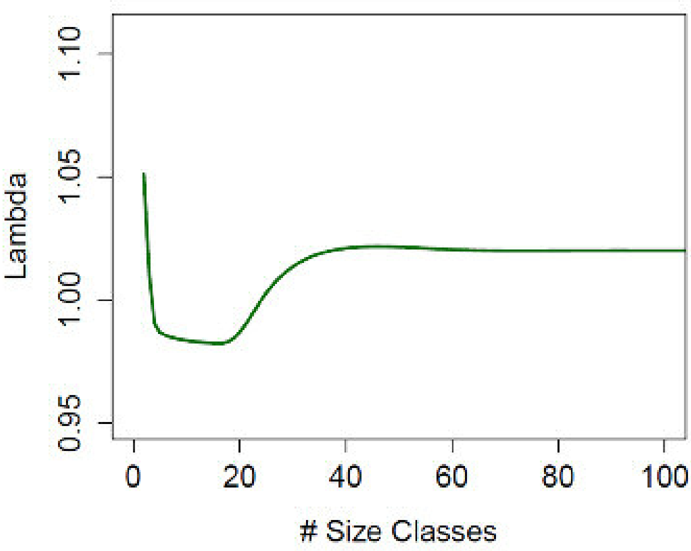


Figure S4. Asymptotic population growth rate (lambda) based on matrix approximations to a continuous IPM model constructed using a range of size-classes from 3 to 200.

We parameterized eight annual matrices that were derived based on the models previously fit; the fecundity and survival functions varied between these years, while growth was not estimated on an annual basis. All the a_{ji} matrix elements below the top row (the reproductive elements) were estimated as:

(3)

$$a_{ji} = s_i\,(p_{n,i}\,n_{ji} + (1 - p_{n,i})\,m_{ji})$$

where s_i is the probability of survival for the ith size class, $p_{n,i}$ is the probability of ‘‘normal growth or shrinkage’’ for the ith class, n_{ji} is the probability of normally growing or shrinking from the ith class to the jth class, and m_{ji} is the probability of moving from the ith to the jth class with extreme shrinkage. To estimate n_{ji} and m_{ji} values, we used the mid-point size for class i as the starting size, and a normal CDF to calculate the total probability of falling within the range of sizes in the jth class.

References included in the supplementary methods

1. Drap, P., Merad, D., Mahiddine, A., *et al.* (2013) Automating the measurement of red coral in situ using underwater photogrammetry and coded targets. XXIV International CIPA Symposium, Strasbourg, France. Vol. XL-5/W2, pp.231–236

2. Easterling, M.R., Ellner, S.P., and Dixon, P.M. (2000) Size-Specific Sensitivity: Applying a New Structured Population Model. *Ecology*., **81**(3) 694-708

3. Morris, W.F. & Doak, D.F. (2002) Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Inc. Publishers; Sunderland, Massachusetts U.S.A.

4. Torrents, O., Garrabou, J., Marschal, C. & Harmelin, J. G. (2005) Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) in the Marseilles area (France, NW Mediterranean). *Biol. Consv.,* **121**(3) 391–397

5. Salguero-Gomez, R. & Casper, B. B. (2010) Keeping plant shrinkage in the demographic loop. *J. Ecol*., **98**(2): 312–323

6. Santangelo, G., Carletti, E., Maggi, E. & Bramanti, L. (2003) Reproduction and population sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. *Mar. Eco. Prog. Ser*., **248**: 99–108, 2003

7. Shriver, R. K., Cutler, K., & Doak, D. F. (2012). Comparative demography of an epiphytic lichen: support for general life history patterns and solutions to common problems in demographic parameter estimation. *Oecologia*, **170**(1), 137-146.

TABLE S1. Summary statistics for the linear models fitted to the expected recovery periods (n = 41). A log transformation was previously applied to the response variable.

	Threshold at 20%					**Threshold at 80%**				
Model	**Estimate**	**DF**	**t**	**P**	**R²**	**Estimate**	**DF**	**t**	**P**	**R²**
Survival + Dimensions	2.50 ± 0.55	38	4.56	> 0.001	0.42	3.01 ± 0.53	38	5.63	> 0.001	0.50
(Dimensions)	0.03 ± 0.01	38	2.93	0.029	0.42	0.03 ± 0.01	38	1.98	0.055	0.50
Survival*Dimensions	-	-	-	0.274	-	-	-	-	0.243	-
Survival	2.73 ± 0.57	39	4.82	> 0.001	0.36	3.21 ± 0.43	39	5.44	> 0.001	0.46
Dimensions	0.05 ± 0.02	39	2.57	0.014	0.12	0.04 ± 0.02	39	2.30	0.027	0.10

TABLE S2. Source data of survival rates in transplant experiments and growth rates of the marine sessile species included in the comparative analysis. Numbers correspond to references listed below the table.

Species Name	**Family**	**Taxa**	**Survival Transplants**	**Growth Natural**	**Growth Transplants**
Acropora cervicornis	*Acroporidae*	Scleractinia	1, 2, 3, 4, 94	41, 42, 43, 44	92, 93, 94
Acropora digitifera	*Acroporidae*	Scleractinia	5	61	NA
Acropora divaricata	*Acroporidae*	Scleractinia	6	NA	6
Acropora echinata	*Acroporidae*	Scleractinia	88	88	88
Acropora abrolhosensis / A. gomezi	*Acroporidae*	Scleractinia	87, 90	NA	90
Acropora hemprichii	*Acroporidae*	Scleractinia	8, 9, 10	49, 50	NA
Acropora humilis	*Acroporidae*	Scleractinia	6, 9	47, 52, 54	6
Acropora hyacinthus	*Acroporidae*	Scleractinia	5, 6, 11, 53	51	6
Acropora intermedia/ A. nobilis	*Acroporidae*	Scleractinia	11, 53	52	NA
Acropora microphthalma	*Acroporidae*	Scleractinia	87	NA	NA
Acropora millepora	*Acroporidae*	Scleractinia	12,53	NA	NA
Acropora muricata/ A. formosa	*Acroporidae*	Scleractinia	7, 8, 10, 20, 111	46, 47, 48	99
Acropora nasuta	*Acroporidae*	Scleractinia	8, 10	47, 51	10
Acropora palmata	*Acroporidae*	Scleractinia	1, 2, 13, 14, 15, 16	47, 55, 56, 57, 58, 97	97
Acropora pulchra	*Acroporidae*	Scleractinia	NA	114	114
Acropora tenuis	*Acroporidae*	Scleractinia	17, 18	NA	NA

Acropora variabilis	*Acroporidae*	Scleractinia	19	NA	NA
Acropora verweyi	*Acroporidae*	Scleractinia	9	54	NA
Acropora yongei	*Acroporidae*	Scleractinia	20	98, 99	NA
Corallium rubrum	*Coralliidae*	Octocorallia	Present Study	Present Study	NA
Echinopora lamellosa	*Mussidae*	Scleractinia	24, 111	NA	NA
Eunicella cavolini	*Gorgoniidae*	Octocorallia	115	NA	NA
Eunicella singularis	*Gorgoniidae*	Octocorallia	115	116, 117, 118	NA
Eunicella verrucosa	*Gorgoniidae*	Octocorallia	115	119,120	NA
Favia stelligera	*Mussidae*	Scleractinia	9	62	NA
Isopora brueggemanni	*Acroporidae*	Scleractinia	20	63	NA
Leptoseris gardineri	*Agariciidae*	Scleractinia	88	88	88
Madracis mirabilis	*Astrocoeniidae*	Scleractinia	27	NA	NA
Merulina scabricula	*Merulinidae*	Scleractinia	24, 111	NA	NA
Montipora aequituberculata	*Acroporidae*	Scleractinia	111	113	NA
Montipora digitata	*Acroporidae*	Scleractinia	28, 29, 111, 112	100	28
Montipora foliosa	*Acroporidae*	Scleractinia	87	63	NA
Montipora pulcherrima	*Acroporidae*	Scleractinia	88	NA	88
Paramuricea clavata	*Plexauridae*	Octocorallia	30, 115	67, 121	NA
Pavona varians	*Agariciidae*	Scleractinia	19	68, 71, 73	NA
Pavona cactus	*Agariciidae*	Scleractinia	87, 88	88, 89	88
Pocillopora damicornis	*Pocilloporidae*	Scleractinia	9, 19, 31, 111	51, 68, 69, 70	NA
Pocillopora verrucosa	*Pocilloporidae*	Scleractinia	6, 8, 10, 20	51, 63, 73	NA

Porites astreoides	*Poritidae*	Scleractinia	32	73, 74	NA
Porites cylindrica	*Poritidae*	Scleractinia	8, 10, 33, 87	75,61	76, 91
Porites lobata	*Poritidae*	Scleractinia	6	77, 78, 79	6
Porites lutea	*Poritidae*	Scleractinia	6	80, 81	6
Porites nigrescens	*Poritidae*	Scleractinia	6	NA	6
Porites porites	*Poritidae*	Scleractinia	1, 2	82, 83, 84, 85	97
Porites rus	*Poritidae*	Scleractinia	111	76	76
Stylophora pistillata	*Pocilloporidae*	Scleractinia	9,19,31,40	101, 102, 103	104
Xestospongia muta	*Petrosiidae*	Sponge	41	86	NA
Cymodocea nodosa	*Cymodoceaceae*	Seagrass	21, 22	105	NA
Halodule wrightii	*Cymodoceaceae*	Seagrass	25, 110	105	NA
Posidonia australis	*Posidoniaceae*	Seagrass	26, 34	105	NA
Posidonia oceanica	*Posidoniaceae*	Seagrass	26, 35, 36, 37, 108	105	NA
Posidonia sinuosa	*Posidoniaceae*	Seagrass	26, 106	105	NA
Ruppia maritima	*Ruppiaceae*	Seagrass	38	NA	NA
Syringodium filiforme	*Cymodoceaceae*	Seagrass	25	105	NA
Thalassia testudinum	*Hydrocharitaceae*	Seagrass	25	105	NA
Zostera capricorni	*Zosteraceae*	Seagrass	26	NA	NA
Zostera marina	*Zosteraceae*	Seagrass	38, 109	105	NA
Zostera noltii	*Zosteraceae*	Seagrass	107	NA	NA
Cystoseira barbata	*Fucaceae*	Macroalgae	23	NA	NA
Cystoseira compressa	*Fucaceae*	Macroalgae	23	NA	NA

List of references included in Table S2

1. Garrison, V., & Greg, W. A. R. D. (2008). Storm-generated coral fragments–A viable source of transplants for reef rehabilitation. *Biological Conservation*, 141(12), 3089-3100.
2. Garrison, V. H., & Ward, G. (2012). Transplantation of storm-generated coral fragments to enhance Caribbean coral reefs: A successful method but not a solution. *Revista de Biología Tropical*, 60, 59-70.
3. Johnson, M. E., C. Lustic, E. Bartels, I. B. Baums, D. S. Gilliam, L. Larson, D. Lirman, M. W. Miller, K. Nedimyer, S. Schopmeyer. 2011. Caribbean *Acropora* Restoration Guide: Best Practices for Propagation and Population Enhancement. The Nature Conservancy, Arlington, VA
4. Quinn, N. J., Kojis, B. L., & Bowden-Kerby, W. A. (2005). Assessing the potential for natural recovery and coral restoration techniques for enhancing coral habitat in Jamaica. In Proceedings of OCEANS 2005 MTS/IEEE (pp. 2752-2759). IEEE.
5. Boch, C. A., & Morse, A. N. (2012). Testing the effectiveness of direct propagation techniques for coral restoration of *Acropora spp. Ecological Engineering*, **40**, 11-17.
6. Clark, S., & Edwards, A. J. (1995). Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldive Islands. *Coral reefs*, **14**(4), 201-213.
7. Okubo, N., Motokawa, T., & Omori, M. (2007). When fragmented coral spawn? Effect of size and timing on survivorship and fecundity of fragmentation in *Acropora formosa*. *Marine Biology*, 151(1), 353-363.
8. Mbije, N. E., Spanier, E., & Rinkevich, B. (2010). Testing the first phase of the ‘gardening concept’ as an applicable tool in restoring denuded reefs in Tanzania. *Ecological Engineering*, *36*(5), 713-721.
9. Ammar, M. S. A., Amin, E. M., Gundacker, D., & Mueller, W. E. (2000). One rational strategy for restoration of coral reefs: application of molecular biological tools to select sites for rehabilitation by asexual recruits. *Marine Pollution Bulletin*, 40(7), 618-627.
10. Mbije, N. E., Spanier, E., & Rinkevich, B. (2013). A first endeavour in restoring denuded, post-bleached reefs in Tanzania. *Estuarine, Coastal and Shelf Science*, 128, 41-51.
11. Edwards, A. J., & Clark, S. (1999). Coral transplantation: a useful management tool or misguided meddling? *Marine Pollution Bulletin*, 37(8), 474-487.
12. Guest, J. R., Baria, M. V., Gomez, E. D., Heyward, A. J., & Edwards, A. J. (2014). Closing the circle: is it feasible to rehabilitate reefs with sexually propagated corals? *Coral Reefs*, 33(1), 45-55.

13. Edwards A (2010) Reef rehabilitation manual (A Edwards, Ed.). Coral Reef Targeted Research & Capacity Building for Management Program, St Lucia, Australia
14. Forrester, G., O'Connell-Rodwell, C., Baily, P., Forrester, L., Giovannini, S., Harmon, L., Karis, R., Krumholz, J., Rodwell, T., Jarecki, L. (2011) Evaluating methods for transplanting endangered elkhorn corals in the Virgin Islands. *Restoration Ecology,* 19:299–306
15. Franklin, E., Hudson, J., Anderson, J., Schittone, J. (2006) M/V Jacquelyn L coral reef restoration monitoring report, monitoring events 2004-2005. Florida Keys National Marine Sanctuary Monroe County, Florida. Marine Sanctuaries Conservation Series NMSP-06-09. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, MD
16. Forrester, G., Dauksis, R., Ferguson, M. (2013) Should coral fragments collected for restoration be subdivided to create more, smaller pieces for transplanting? *Ecological Restoration,* 31:4-7
17. Nakamura, R., Ando, W., Yamamoto, H., Kitano, M., Sato, A., Nakamura, M., Kayanne, H., Omori, M. (2011) Corals mass-cultured from eggs and transplanted as juveniles to their native, remote coral reef. *Marine Ecology Progress Series*, 436:161–168
18. Omori, M., Iwao, K., Tamura, M. (2007) Growth of transplanted *Acropora* tenuis 2 years after egg culture. *Coral Reefs*, 27:165–165
19. van Treeck, P., & Schuhmacher, H. (1997). Initial survival of coral nubbins transplanted by a new coral transplantation technology-options for reef rehabilitation. *Marine Ecology Progress Series*, 150, 287-292.
20. Ferse, S. (2010) Poor performance of corals transplanted onto substrates of short durability. *Restoration Ecology*, 18:399–408
21. Balestri, E., Lardicci, C. (2014) Effects of sediment fertilization and burial on *Cymodocea nodosa* transplants; implications for seagrass restoration under a changing climate. *Restoration Ecology*, 22:240-247
22. Zarranz, M.E., González-Henríquez, N., García-Jiménez, P., Robaina, R.R. (2010) Restoration of *Cymodocea nodosa* seagrass meadows through seed propagation: Germination in vitro, seedling culture and field transplants. *Botanica Marina*, 53:173-181
23. Falace, A., Zanelli, E., & Bressan, G. (2006). Algal transplantation as a potential tool for artificial reef management and environmental mitigation. *Bulletin of Marine Science*, 78(1), 161-166.

24. dela Cruz, D.W., Rinkevich, B., Gomez, E.D., & Yap, H.T. (2015). Assessing an abridged nursery phase for slow growing corals used in coral restoration. *Ecological Engineering*, 84, 408-415.
25. Thorhaug, A. (1985). Large-scale seagrass restoration in a damaged estuary. *Marine Pollution Bulletin*, 16:55-62
26. Ganassin C, Gibbs P (2008) A review of seagrass planting as a means of habitat compensation following loss of seagrass meadow. In: NSW Department of Primary Industries - *Fisheries Final Report Series No. 96. NSW Department of Primary Industries, Cronulla Fisheries Research Centre of Excellence*, Cronulla, Australia, p 43
27. Nagelkerken, I., Bouma, S., Van Den Akker, S., & Bak, R. P. M. (2000). Growth and survival of unattached *Madracis mirabilis* fragments transplanted to different reef sites, and the implication for reef rehabilitation. *Bulletin of Marine Science*, 66(2), 497-505.
28. Shaish, L., Levy, G., Katzir, G., & Rinkevich, B. (2010). Employing a highly fragmented, weedy coral species in reef restoration. *Ecological Engineering*, 36(10), 1424-1432.
29. Gomez ED, Yap HT, Cabaitan PC, Dizon RM (2011) Successful transplantation of a fragmenting coral, *Montipora digitata*, for reef rehabilitation. *Coastal Management* 39:556-574
30. Linares, C., Coma, R., & Zabala, M. (2008). Restoration of threatened red gorgonian populations: an experimental and modelling approach. *Biological Conservation*, 141(2), 427-437.
31. Horoszowski-Fridman, Y. B., Brêthes, J. C., Rahmani, N., & Rinkevich, B. (2015). Marine silviculture: Incorporating ecosystem engineering properties into reef restoration acts. *Ecological Engineering,* 82, 201-213.
32. Gleason, D. F., Brazeau, D. A., & Munfus, D. (2001) Can self-fertilizing coral species be used to enhance restoration of Caribbean reefs? *Bulletin of Marine Science*, 69(2), 933-943.
33. Gomez, E. D., Cabaitan, P. C., Yap, H. T., & Dizon, R. M. (2014). Can coral cover be restored in the absence of natural recruitment and reef recovery? *Restoration Ecology*, 22(2), 142-150.
34. Bastyan, G. R., & Cambridge, M. L. (2008). Transplantation as a method for restoring the seagrass *Posidonia australis*. *Estuarine, Coastal and Shelf Science*, 79(2), 289-299.
35. Gobert, S., Lepoint, G., Bouquegneau, J.M., Vangeluwe, D., Eisinger, M., Paster, M., Schuhmaker, H., Van Treeck, P. (2005). Restoration of seagrass meadows: Means

and limitations. *Proc 7th International Conference on the Mediterranean Coastal Environment, MEDCOAST. Middle East Technical University*

36. NOMATEC Manual on the application of the electrochemical accretion technology for the restoration and rehabilitation of *Posidonia oceanica*. University of Duisburg, Essen, Germany and University of Liege, Belgium
37. Oceana (2010) Restoration of seagrass meadows. In: Sustainable development manuals. *Oceana - Protecting the World´s Oceans*, p 24
38. Bologna, P. A., & Sinnema, M. S. (2012). Restoration of Seagrass Habitat in New Jersey, United States. *Journal of Coastal Research*, 28(1A), 99-104.
39. Rinkevich B (2000) Steps towards the evaluation of coral reef restoration by using small branch fragments. *Marine Biology,* 136:807-812
40. Epstein N, Bak R, Rinkevich B (2001) Strategies for gardening denuded coral reef areas: The applicability of using different types of coral material for reef restoration. *Restoration Ecology* 9:432–443
41. McMurray, S.E. & Pawlic, J.R. (2009) A Novel Technique for the Reattachment of Large Coral Reef Sponges. *Restoration Ecology*. 17(2), 193-195
42. Lewis, J. B., Axelson, F., Goodbody, I., Page, C., Chislett, G. (1968) Comparative growth rates of some reef corals in the Caribbean. *Marine Science Center*, 10,1-26
43. Torres, J. L., Armstrong, R. A., Corredor, J. E., Gilbes, F. (2007) Physiological responses of *Acropora cervicornis* to increased solar irradiance. *Photochemistry and Photobiology*, 83, 839-850
44. Tunnicliffe, V. (1983) Caribbean staghorn coral populations: pre-hurricane Allen conditions in Discovery Bay, Jamaica. *Bulletin of Marine Science,* 33, 132-151
45. Crabbe, M. (2009) Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica. Marine Environmental Research, 67, 189-198
46. Suresh, V R and Mathew, K J (1993) Skeletal extension of staghorn coral *Acropora formosa* in relation to environment at Kavaratti atoll (Lakshadweep). *Indian Journal of Marine Sciences*, 22(3), 176-179.
47. Pratchett, M. S., Anderson, K. D., Hoogenboom, M. O., Widman, E., Baird, A. H., Pandolfi, J. M., Edmunds, P. J., Lough, J. M. (2015) Spatial, temporal and taxonomic variation in coral growth - implications for the structure and function of coral reef ecosystems. *Oceanography and Marine Biology: An Annual Review*, 53, 215-295
48. Edmunds, P. J., Burgess, S. C., Putnam, H. M., Baskett, M. L., Bramanti, L., Fabina, N. S., Han, X., Lesser, M. P., Madin, J. S., Wall, C. B., Yost, D. M., Gates, R. D. (2014) Evaluating the causal basis of ecological success within the scleractinia: an integral projection model approach. *Marine Biology*, 161, 2719-2734

49. Guzner, B., Novoplansky, A., & Chadwick, N. E. (2007) Population dynamics of the reef-building coral *Acropora hemprichii* as an indicator of reef condition. Marine Ecology Progress Series, 333, 143-150.
50. Ebeid, M. L., Hasan, M. H., and Geneid, Y. A. (2009) Response to increased sediment load by three coral species from the Gulf of Suez (Red Sea). *Journal of Fisheries and Aquatic Sciences* 4 (5) 328-245
51. Stimson, J. (1985) The effect of shading by the table coral *Acropora Hyacinthus* on understory corals. Ecology, 66, 40-53
52. Jokiel P.L., Tyler W.A. (1992) Distribution of stony corals in Johnston Atoll lagoon. Proceedings of the Seventh International Coral Reef Symposium, 2, 683–692
53. Smith, L. D., & Hughes, T. P. (1999). An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology*, 235(1), 147-164.
54. Hughes, R.N. Hughes, D.J., Smith, I. P. Dale A.C. *Oceanography and Marine Biology: An Annual Review*, Volume 53
55. Bak, R. P. M., Nieuwland, G., Meesters, E. H. (2009) Coral growth rates revisited after 31 years: What is causing lower extension rates in *Acropora palmata*? *Bulletin of Marine Science*, 84, 287-294
56. Shapiro, A. (1980) Growth rate, strength, and internal structure as environmental indicators in the reef-building coral, *Acropora palmata*. *Geol Soc Am Abst with Programs* 12(1)
57. Bak, R. P. M., (1983) Neoplasia, regeneration and growth in the reef-building coral *Acropora palmata*. *Marine Biology*, 77, 221-227
58. Crabbe, M. (2010) Topography and spatial arrangement of reef-building corals on the fringing reefs of North Jamaica may influence their response to disturbance from bleaching. *Marine Environmental Research*, 69, 158-162
59. Harriott, V. J. (1999). Coral growth in subtropical eastern Australia. *Coral Reefs*, 18(3), 281-291.
60. Ross, C. L., Falter, J. L., Schoepf, V., & McCulloch, M. T. (2015). Perennial growth of hermatypic corals at Rottnest Island, Western Australia (32 S). *PeerJ*, 3, e781.
61. Morgan, K. M., & Kench, P. S. (2012). Skeletal extension and calcification of reef-building corals in the central Indian Ocean. *Marine Environmental Research*, 81, 78-82.
62. Buddemeier, R., Maragos, J., Knutson, D. (1974) Radiographic studies of reef coral exoskeletons: Rates and patterns of coral growth. *Journal of Experimental Marine Biology and Ecology*, 14, 179-199

63. Gomez, E. D., Alcala, A. C., Yap, H. T., Alcala, L. C., Aline, P. M. (1985) Growth studies of commercially important scleractinians. *Proceedings of the Fifth International Coral Reef Congress*, Tahiti 199-204
64. Bruno, John F., Edmunds, Peter J. (1997) Clonal Variation for Phenotypic Plasticity in the Coral *Madracis Mirabilis*. *Ecology*, 78, 2177
65. Misti M & Ceccherelli VU (1994) Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*. *Marine Ecology Progress Series*, 103, 291-296, 1994
66. Coma R, Ribes M, Zabala M, Gili JM (1998a) Growth in a modular colonial marine invertebrate. *Estuarine & Coastal Shelf Science*, 47: 459-470
67. Linares, C., Doak, D. F., Coma, R., Díaz, D., Zabala, M. (2007) Life history and viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. *Ecology*, 88(4):918-28.
68. Glynn, P. W., Colley, S. B., Ting, J. H., Matá, J. L., Guzmán, H. M. (2000) Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá; and Galápagos Islands (Ecuador). IV. Agariciidae, recruitment and recovery of *Pavona varians* and *Pavona sp.a.*. *Marine Biology,* 136, 785-805
69. Richmond, R. H. (1987) Energetic relationships and biogeographical differences among fecundity, growth and reproduction in the reef coral *Pocillopora damicornis*. *Bulletin of Marine Science,* 41, 594-604
70. Ward, S. (1995) The effect of damage on the growth, reproduction and storage of lipids in the scleractinian coral *Pocillopora damicornis* (Linnaeus). *Journal of Experimental Marine Biology and Ecology,* 187, 193-206
71. Guzman, H. M., Cortes, J. (1989) Growth rates of eight species of scleractinian corals in the Eastern Pacific (Costa Rica). *Bulletin of Marine Science,* 44, 1186-1194
72. Mass, T., & Genin, A. (2008). Environmental versus intrinsic determination of colony symmetry in the coral *Pocillopora verrucosa*. *Marine Ecology Progress Series*, *369*, 131-137.
73. Manzelloa DP, Enochsa IC, Kolodzieja G, Carltona G (2015) Coral growth patterns of *Montastraea cavernosa* and *Porites astreoides* in the Florida Keys: The importance of stress and inimical waters thermal stress and inimical waters. *Journal of Experimental Marine Biology and Ecology*, 471, 198-207.
74. Elizalde-Rendón, E.M., Horta-Puga, G., González-Diaz, P., Carricart-Ganivet, J.P. (2010) Growth characteristics of the reef-building coral *Porites astreoides* under different environmental conditions in the Western Atlantic. *Coral Reefs*, 29:607–614
75. Neudecker, S. (1981) Growth and survival of scleractinian corals exposed to thermal effluents at Guam.Proc 4th Int Coral reef Symp 1,173-180

76. Custodio, H.P., Yap, H.T. (1997) Skeletal extension rates of *Porites cylindrica* and *Porites (Synaraea) rus* after transplantation to two depths. *Coral Reefs,* 16(4), 267-268.
77. Klein, R., Loya, Y. (1991) Skeletal growth and density patterns of two *Porites* corals from the Gulf of Eilat, Red Sea. *Marine Ecology Progress Series*, 77, 253-259
78. Barnes, D.J., Lough, J.M., (1989) The nature of skeletal density banding in scleractinian corals: fine banding and seasonal patterns. *Journal of Experimental Marine Biology and Ecology,* 126, 119-134
79. Grigg, R.W. (1982) Darwin Point: A threshold for atoll formation. *Coral Reefs,* 1, 29-34
80. Supriharyono, S. (2004). Growth rates of the massive coral *Porites lutea*, on the coast of Bontang, east Kalimantan, Indonesia. *Journal of Coastal Development*, 7(3), 143-155.
81. Tanzil J.T.I., Brown, B.E., Tudhope, A.W. and Dune, R.P. (2009) Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. *Coral Reefs,* 28(2), 519-528.
82. Edmunds, P. J., Davies, P. S. (1986) An energy budget for *Porites porites* (Scleractinia). *Marine Biology,* 92, 339-347
83. Vaughan, T. W. (1915) Growth rate of the Floridian and Bahaman shoal-water corals. *Year book - Carnegie Institution of Washington* 14, 221-231
84. Huston, M. (1985) Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs*, 4, 19-25
85. Lewis, J. B., Axelson, F., Goodbody, I., Page, C., Chislett, G. (1968) Comparative growth rates of some reef corals in the Caribbean. *Marine Science Center* 10,1-26
86. McMurray, S. E., Blum, J. E., & Pawlik, J. R. (2008) Redwood of the reef: growth and age of the giant barrel sponge Xestospongia muta in the Florida Keys. *Marine Biology*, 155:159–171
87. Palomar, M.J.S., Yap H.T., Gomez E.D. (2009) Coral Transplant Survival Over 3 Years under Different Environmental Conditions at the Hundred Islands, Philippines. The Philippine agriculturist 92(2):143-152

88. Plucer-Rosario, G. and Randall, R.H. (1987). Preservation of rare coral species by transplant action and examination of their recruitment and growth. *Bulletin of Marine Science*, 41(2): 585-593

89. Willis, B.L. (1985) Phenotypic plasticity versus phenotypic stability in the reef corals *Turbinaria mesenterina* and *Pavona cactus*. *Proceedings of the Fifth International Coral Reef Congress, Tahiti,* 107-112

90. Ferse S. C. E. & Kuznaman A. (2009) Effects of Concrete-Bamboo Cages on Coral Fragments: Evaluation of a Low-Tech Method Used in Artisanal Ocean-Based Coral Farming. *Journal of Applied Aquaculture*, 21:31–49
91. Dizon, R. M. & Yap, H. P. (2005) Coral responses in single- and mixed-species plots to nutrient disturbance. *Marine Ecology Progress Series*, 296: 165–172
92. Shinn, E. A. (1966). Coral growth-rate, an environmental indicator. *Journal of Paleontology*, 233-240.
93. Mercado-Molina, A. E., Ruiz-Diaz, C. P., & Sabat, A. M. (2016). Branching dynamics of transplanted colonies of the threatened coral *Acropora cervicornis*: Morphogenesis, complexity, and modeling. *Journal of Experimental Marine Biology and Ecology*, 482, 134-141.
94. Johnson M 2015 Staghorn Coral, *Acropora cervicornis*, Restoration in South Florida: Growth and Survivorship of Outplanted Nursery Corals. *Master's thesis. Nova Southeastern University*.
95. Mercado-Molina, A. E., Ruiz-Diaz, C. P., Pérez, M. E., Rodríguez-Barreras, R., & Sabat, A. M. (2015). Demography of the threatened coral *Acropora cervicornis*: implications for its management and conservation. *Coral Reefs*, 34(4), 1113-1124.
96. Putchim, L., Thongtham, N., Hewett, A., & Chansang, H. (2008, July). Survival and growth of Acropora spp. in mid-water nursery and after transplantation at Phi Phi Islands, Andaman Sea, Thailand. In *Proceeding of the 11thInternational Coral Reef Symposium, Ft Lauderdale, Florida* (pp. 1268-1261).
97. Cummings, K., Zuke, A., De Stasio, B., & Krumholz, J. (2015). Coral Growth Assessment on an Established Artificial Reef in Antigua. *Ecological Restoration*, 33(1), 90-95.
98. Harriott, V. J. (1999) Coral growth in subtropical eastern Australia. *Coral Reefs*, 18, 281-291
99. Marsh, L. M. (1992) The Occurrence and Growth of *Acropora* in Extra-tropical Waters off Perth, Western Australia. *Proceedings of the Seventh International Coral Reef Symposium, Guam*. 2, 1233-1238
100. Heyward, A. J., Collins, J. D. (1985) Growth and sexual reproduction in the scleractinian coral *Montipora digitata* (Dana). *Marine and Freshwater Research*. 36, 441
101. Liberman, T., Genin, A., Loya, Y. (1995) Effects on growth and reproduction of the coral *Stylophora pistillata* by the mutualistic damselfish *Dascyllus marginatus*. *Marine Biology,* 121, 741-746

102. Geneid, Y., Ebeid, M., Hassan, M. (2009) Response to Increased Sediment Load by Three Coral Species from the Gulf of Suez (Red Sea). *Journal of Fisheries and Aquatic Science* 4, 238-245
103. Kotb, M.M.A. (2001) Growth rates of three reef-building coral species in the northern Red Sea, Egypt. *Egyptian Journal of Aquatic Biology and Fisheries* 5, 165–185
104. Bongiorni, L., Shafir, S., Angel, D., & Rinkevich, B. (2003). Survival, growth and gonad development of two hermatypic corals subjected to in situ fish-farm nutrient enrichment. *Marine Ecology Progress Series*, 253, 137-144.
105. Marbà, N., & Duarte, C. M. (1998). Rhizome elongation and seagrass clonal growth. *Marine Ecology Progress Series*, 174, 269-280.
106. Paling, E. I., Van Keulen, M., & Tunbridge, D. J. (2007). Seagrass transplanting in Cockburn Sound, Western Australia: a comparison of manual transplantation methodology using *Posidonia sinuosa*. *Restoration Ecology*, 15(2), 240-249.
107. Martins, I., Neto, J. M., Fontes, M. G., Marques, J. C., & Pardal, M. A. (2005). Seasonal variation in short-term survival of *Zostera noltii* transplants in a declining meadow in Portugal. *Aquatic Botany*, 82(2), 132-142.
108. Piazzi, L., Balestri, E., Balata, D., and Cinelli, F. (2000). Pilot transplanting experiment of *Posidonia oceanica* (L.) Delile to restore a damaged coastal area in the Mediterranean Sea. *Biologia Marina Mediterranea*, 7: 409–411.
109. Davis, R. C., & Short, F. T. (1997). Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: the horizontal rhizome method. *Aquatic Botany*, 59(1), 1-15.
110. Sheridan, Pete, et al. (1998). Factors affecting restoration of *Halodule wrightii* to Galveston Bay, Texas. *Restoration Ecology*, 6.2 (1998): 144-158.
111. Shaish, L., Levy, G., Gomez, E., & Rinkevich, B. (2008). Fixed and suspended coral nurseries in the Philippines: Establishing the first step in the “gardening concept” of reef restoration. *Journal of Experimental Marine Biology and Ecology*, 358(1), 86-97.
112. Shaish, L., Levy, G., Katzir, G., & Rinkevich, B. (2010). Coral reef restoration (Bolinao, Philippines) in the face of frequent natural catastrophes. *Restoration Ecology*, 18(3), 285-299.
113. Browne, N. K. (2012). Spatial and temporal variations in coral growth on an inshore turbid reef subjected to multiple disturbances. *Marine environmental research*, 77, 71-83.
114. Yap, H. T., & Gomez, E. D. (1985). Growth of *Acropora pulchra*. *Marine Biology*, 87(2), 203-209.

115. Fava, F., Bavestrello, G., Valisano, L., & Cerrano, C. (2010). Survival, growth and regeneration in explants of four temperate gorgonian species in the Mediterranean Sea. *Italian Journal of Zoology*, 77(1), 44-52.
116. Weinberg, S., & Weinberg, F. (1979). The life cycle of a gorgonian: *Eunicella singularis* (Esper, 1794). Bijdragen tot de Dierkunde, 48(2), 127-137.
117. Munari, C., Serafin, G., & Mistri, M. (2013). Structure, growth and secondary production of two Tyrrhenian populations of the white gorgonian *Eunicella singularis* (Esper 1791). *Estuarine, Coastal and Shelf Science*, 119, 162-166.
118. Viladrich, N., Gori, A., & Gili, J. M. (2016). Fast growth rate in a young colony of the Mediterranean gorgonian *Eunicella singularis*. *Marine Biodiversity*, 1-2.
119. Sartoretto, S., & Francour, P. (2011). Bathymetric distribution and growth rates of *Eunicella verrucosa* (Cnidaria: Gorgoniidae) populations along the Marseilles coast (France*). Scientia Marina*, 76(2), 349-355.
120. Munro, L., & Munro, C. (2003). Reef Research. Determining the reproductive cycle of *Eunicella verrucosa*. *Interim report Nov*.
121. Mistri, M., & Ceccherelli, V. U. (1994). Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*. *Marine Ecology Progress Series*, 103, 291-291.

TABLE S3. Source data of matrix population models used to project recovery periods. Numbers correspond to references listed below the table. *Only matrices that included fecundity data (n = 41) were used to project recovery periods.

Name	Family	Taxa	Matrix Dimensions	Source ID
Acropora cervicornis	Acroporidae	Hexacoral	3	1
Acropora hyacinthus	Acroporidae	Hexacoral	4	2
Acropora palmata	Acroporidae	Hexacoral	4	3
Adamussium colbecki	Pectinidae	Bivalve	3	16
Agaricia agaricites	Agariciidae	Hexacoral	3	4
Alaria nana	Alariaceae	Algae	3	17
Amphimedon compressa	Chalinidae	Sponge	3	5
Artica islandica	Arcticidae	Bivalve	3	16
Ascophyllum nodosum	Fucaceae	Algae	5	18
Bartholomea annulata	Aiptasiidae	Hexacoral	5	19
Botrylloides schlosseri	Styelidae	Tunicate	3	20
Botrylloides violaceous	Styelidae	Tunicate	3	20
Cellepora pumicosa	Celleporidae	Bryozoan	3	22
Chthamalus montagui	Chthamalidae	Cirriped	4	21
Corallium rubrum	Coralliidae	Octocoral	60	Present Study
Diploria strigosa	Mussidae	Hexacoral	3	6
Fucus distichus	Fucaceae	Algae	9	23
Gemma gemma	Veneridae	Bivalve	3	16
Geukensia demissa	Mytilidae	Bivalve	3	16
Goniastrea aspera	Merulinidae	Hexacoral	5	7
Goniastrea favulus	Merulinidae	Hexacoral	5	7
Goniastrea favulus	Merulinidae	Hexacoral	5	7
Haliotis iris	Haliotidae	Bivalve	3	24
Haliotis laevigata	Haliotidae	Bivalve	7	33, 34
Haliotis rufenses	Haliotidae	Bivalve	4	25
Haliotis sorenseni	Haliotidae	Bivalve	8	25
Iridaea splendens	Gigartinaceae	Algae	8	26
Laminaria digitata	Laminariaceae	Algae	5	27
Lasaea rubra	Lasaeidae	Bivalve	3	16

Leptogorgia Virgulata	Gorgoniidae	Octocoral	5	8
Leptoseris cucullata	Agariciidae	Hexacoral	3	9
Lissarca miliaris	Philobryidae	Bivalve	3	16
Lissarca notorcadensis	Philobryidae	Bivalve	3	16
Macrocystis pyrifera	Laminariaceae	Algae	8	30
Mesodesma mactroides	Mesodesmatidae	Bivalve	5	29
Mucropetraliella ellerii	Petraliellidae	Bryozoan	5	10
Mya arenaria	Myidae	Bivalve	8	28
Mytilus californianus	Mytilidae	Bivalve	3	35
Mytilus galloprovincialis	Mytilidae	Bivalve	3	35
Nutallia obscurata	Psammobiidae	Bivalve	5	31
Orbicella annularis	Merulinidae	Hexacoral	3	9
Palythoa caesia	Sphenopidae	Hexacoral	4	11
Panopea abrupta	Hiatellidae	Bivalve	3	16
Paramuricea clavata	Plexaura A	Octocoral	7	12
Plexaura A	Plexaura A	Octocoral	3	13
Pocillopora damicornis	Pocilloporidae	Hexacoral	4	2
Goniastrea sinensis	Merulinidae	Hexacoral	5	8
Porites astreoides	Poritidae	Hexacoral	3	6
Pseudopterogorgia	Gorgoniidae	Octocoral	13	14
Semibalanus balanoides	Archaeobalanidae	Cirriped	3	21
Spongia graminea	Spongiidae	Sponge	10	32
Tridacna gigas	Cardiidae	Bivalve	3	16
Watersipora subtorquata	Watersiporidae	Bryozoan	3	20
Xestospongia muta	Petrosiidae	Sponge	6	15

List of references included in Table S3

1. Mercado-Molina, A.E., Ruiz-Diaz, C.P., Pérez, M.E., Rodríguez-Barreras, R., & Sabat, A.M. (2015). Demography of the threatened coral *Acropora cervicornis*: implications for its management and conservation. *Coral Reefs*, 34(4), 1113-1124.
2. Tanner, J.E. (1997). Interspecific competition reduces fitness in scleractinian corals. *Journal of Experimental Marine Biology and Ecology*, 214(1), 19-34.

3. Vardi, T., Williams, D.E., & Sandin, S.A. (2012). Population dynamics of threatened elkhorn coral in the northern Florida Keys, USA. *Endangered Species Research*, 19(2), 157-169.
4. Hughes, T.P. (1984). Population dynamics based on individual size rather than age: a general model with a reef coral example. *American Naturalist*, 778-795.
5. Mercado-Molina, A.E., Sabat, A.M., & Yoshioka, P.M. (2011). Demography of the demosponge *Amphimedon compressa*: Evaluation of the importance of sexual versus asexual recruitment to its population dynamics. *Journal of Experimental Marine Biology and Ecology*, 407(2), 355-362.
6. Edmunds, P. J. (2010). Population biology of *Porites astreoides* and *Diploria strigosa* on a shallow Caribbean reef. *Marine Ecology Progress Series*, 418, 87-104.
7. Babcock, R.C. (1991). Comparative demography of three species of scleractinian corals using age and size dependent classifications. *Ecological Monographs*, 61(3), 225-244.
8. Gotelli, N. J. (1991). Demographic models for *Leptogorgia virgulata*, a shallow water gorgonian. *Ecology*, 72(2), 457-467.
9. Hughes, T. P., & Tanner, J. E. (2000). Recruitment failure, life histories, and long term decline of Caribbean corals. *Ecology*, 81(8), 2250-2263.
10. Linacre, N. A., & Keough, M. J. (2003). Demographic effects of fragmentation history in modular organisms: illustrated using the bryozoan *Mucropetraliella ellerii* (MacGillivray). *Ecological modelling*, 170(1), 61-71.
11. Tanner, J. E. (1997). The effects of density on the zoanthid *Palythoa caesia*. *Journal of Animal Ecology*, 793-810.
12. Linares, C., Doak, D. F., Coma, R., Diaz, D., & Zabala, M. (2007). Life history and viability of a long lived marine invertebrate: the octocoral *Paramuricea clavata*. *Ecology*, 88(4), 918-928.
13. Lasker, H. R. (1991). Population growth of a gorgonian coral: equilibrium and non-equilibrium sensitivity to changes in life history variables. *Oecologia*, 86(4), 503-509.
14. Yoshioka, P. M. (1994). Size-specific life history pattern of a shallow-water gorgonian. *Journal of Experimental Marine Biology and Ecology*, 184(1), 111-122.
15. McMurray, S. E., Henkel, T. P., & Pawlik, J. R. (2010). Demographics of increasing populations of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Ecology*, 91(2), 560-570.
16. Ripley, B. J., & Caswell, H. (2008). Contributions of growth, stasis, and reproduction to fitness in brooding and broadcast spawning marine bivalves. *Population ecology*, 50(2), 207-214.

17. Pfister, C. A., & Wang, M. (2005). Beyond size: matrix projection models for populations where size is an incomplete descriptor. *Ecology*, 86(10), 2673-2683.
18. Aberg, P. (1992). A demographic study of two populations of the seaweed *Ascophyllum nodosum*. *Ecology*, 73(4), 1473-1487.
19. Nelsen, M. (2008). Population dynamic modeling of the corkscrew sea anemone *Bartholomea annulata* on Caribbean coral reefs. *Doctoral dissertation*, Auburn University, Auburn, AL.
20. Cockrell, M. L., & Sorte, C. J. (2013). Predicting climate-induced changes in population dynamics of invasive species in a marine epibenthic community. *Journal of Experimental Marine Biology and Ecology*, 440, 42-48.
21. Svensson, C. J., Johansson, E., & Åberg, P. (2006). Competing species in a changing climate: effects of recruitment disturbances on two interacting barnacle species. *Journal of Animal Ecology*, 75(3), 765-776.
22. Hughes, T. P. (1990). Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology*, 71(1), 12-20.
23. Ang, P. O. & DeWreede, R. E. (1993). Simulation and analysis of the dynamics of a *Fucus distichus* (Phaeophyceae, Fucales) populations. *Marine Ecology Progress Series*, 93(3), 253-265.
24. Somerville, G. J., Krkosek, M., & Hepburn, C. D. (2014). A matrix model and elasticity analysis for New Zealand's blackfoot pāua *Haliotis iris*. *Fisheries Research*, 151, 158-168.
25. Rogers-Bennett, L., & Leaf, R. T. (2006). Elasticity analyses of size based red and white abalone matrix models: management and conservation. *Ecological Applications*, 16(1), 213-224.
26. Ang Jr, P., De Wreede, R. E., Shaughnessy, F., & Dyck, L. (1990). A simulation model for an *Iridaea splendens* (Gigartinales, Rhodophyta) population in Vancouver, Canada. In Thirteenth International Seaweed Symposium (pp. 191-196). Springer Netherlands.
27. Chapman, A. R. (1993). 'Hard'data for matrix modelling of *Laminaria digitata* (Laminariales, Phaeophyta) populations. In Fourteenth International Seaweed Symposium (pp. 263-267). Springer Netherlands.
28. Ripley, B. J., & Caswell, H. (2006). Recruitment variability and stochastic population growth of the soft-shell clam, *Mya arenaria*. *Ecological modelling*, 193(3), 517-530.
29. Brazeiro, A., & Defeo, O. (1999). Effects of harvesting and density dependence on the demography of sandy beach populations: the yellow clam *Mesodesma mactroides* of Uruguay. *Marine Ecology Progress Series*, 182, 127-135.

30. Nyman, M. A., Brown, M. T., Neushul, M., & Keogh, J. A. (1990). *Macrocystis pyrifera* in New Zealand: testing two mathematical models for whole plant growth. *Journal of Applied Phycology*, 2(3), 249-257.
31. Dudas, S. E., Dower, J. F., & Anholt, B. R. (2007). Invasion dynamics of the varnish clam (*Nuttallia obscurata*): a matrix demographic modeling approach. *Ecology*, 88(8), 2084-2093.
32. Cropper, W. P., & Di Resta, D. (1999). Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after Hurricane Andrew. *Ecological Modelling*, 118(1), 1-15.
33. Fordham, D. A., Mellin, C., Russell, B. D. *et al.* (2013). Population dynamics can be more important than physiological limits for determining range shifts under climate change. *Global Change Biology*, 19(10), 3224-3237.
34. Salguero Gómez, R., Jones, O. R., Archer, C.R.R. *et al*. (2016). COMADRE: a global database of animal demography. *Journal of Animal Ecology*, 85(2), 371-384.
35. Carson, H. S., Cook, G. S., López-Duarte, P. C., & Levin, L. A. (2011). Evaluating the importance of demographic connectivity in a marine metapopulation. *Ecology*, 92(10), 1972-1984.

Supplementary Materials Chapter V

Table S1. Source data of distribution and depths of Corallium rubrum and Paramuricea clavata.

Table S2. Sample sizes of distribution and depth data for Corallium rubrum and Paramuricea clavata populations.

Table S3. Source data for environmental predictors included in the models.

Table S4. Collinearity among environmental predictors

Table S5. Logistic generalized additive mixed models fitted to presence/absence data for Paramuricea clavata and Corallium rubrum at five depth layers (from 5-15, 15-25, 25-35, 35-45, and 45-55).

Table S6. Clusters classification according to projected trajectories of change.

Figure S1. Correlations among environmental predictors

Figure S1. Examples of model validation comparing predicted probability of occurrence with independent presence and absence data.

Figure S2. Model validation results. Adjusted R squared values among 50 permutations comparing predicted probability of occurrence against independent presence and absence data for *C. rubrum* and *P. clavata*.

Figure S3. Projected changes by species.

Table S1. Sources of geographic distribution data of *Paramuricea clavata* and *Corallium rubrum* populations.

Source Type	**Project name (website)**	**Reference**
Citizen Science Program	ReefCheck (reefcheckmed.org)	Cerrano et al. 2017
	Cigesemed (cs.cigesmed.eu)	Gerovasileiou et al. 2016
	SeaWatchers (observadoresdelmar.es)	NA
Literature Review	NA	Di Camilo et al. 2018
Literature Review	NA	Boavida et al. 2016

REFERENCES

Boavida, J., Assis, J., Silva, I., & Serrão, E. A. (2016). Overlooked habitat of a vulnerable gorgonian revealed in the Mediterranean and Eastern Atlantic by ecological niche modelling. Scientific Reports, 6, 36460.

Cerrano, C., Milanese, M., & Ponti, M. (2017). Diving for science-science for diving: volunteer scuba divers support science and conservation in the Mediterranean Sea. Aquatic Conservation: Marine and Freshwater Ecosystems, 27(2), 303-323.

Di Camillo, C. G., Ponti, M., Bavestrello, G., Krzelj, M., & Cerrano, C. (2018). Building a baseline for habitat-forming corals by a multi-source approach, including Web Ecological Knowledge. Biodiversity and Conservation, 27(5), 1257-1276.

Gerovasileiou, V., Dailianis, T., Panteri, E., Michalakis, N., Gatti, G., Sini, M., ... & Doğan, A. (2016). CIGESMED for divers: Establishing a citizen science initiative for the mapping and monitoring of coralligenous assemblages in the Mediterranean Sea. Biodiversity Data Journal, (4).

Table S2. Total geographic and depth distribution data for *Corallium rubrum* and *Paramuricea clavata*. Filtering was done by randomly removing all duplicated data points and leaving only one for each location.

Species	PRESENCES						Filtered absences	TOTAL
	All data	Filtered presences*	No depth data	Single depth observation	Range of depths	Upper limit known		
Paramuricea clavata	1769	1019	199	242	186	392	199	1769
Corallium rubrum	1030	645	92	160	128	265	166	1277

Table S3. Total geographic and depth distribution data for *Corallium rubrum* and *Paramuricea clavata*.

Variable	Spatial Resolution	Source
Mean Annual Nitrate Concentration	0.083º x 0.083º	Ocean model (Macías et al. 2015)
Mean Annual Phosphate Concentration	0.083º x 0.083º	Ocean model (Macías et al. 2015)
Mean Annual Net Primary Productivity	0.083º x 0.083º	Ocean model (Macías et al. 2015)
Annual Mean Temperature	0.083º x 0.083º	Ocean model (Macías et al. 2015)
Mean August Temperature	0.083º x 0.083º	Ocean model (Macías et al. 2015)
Mean September Temperature	0.083º x 0.083º	Ocean model (Macías et al. 2015)
Max August Temperature	0.083º x 0.083º	Ocean model (Macías et al. 2015)
Max September Temperature	0.083º x 0.083º	Ocean model (Macías et al. 2015)
Concavity	0.0083 x 0.0083º	MARSPEC (Sbrocco et al. 2013)
Slope	0.0083 x 0.0083º	MARSPEC (Sbrocco et al. 2013)
NS Exposure	0.0083 x 0.0083º	MARSPEC (Sbrocco et al. 2013)
EW Exposure	0.0083 x 0.0083º	MARSPEC (Sbrocco et al. 2013)

Sbrocco, E. J., & Barber, P. H. (2013). MARSPEC: ocean climate layers for marine spatial ecology. Ecology, 94(4), 979-979.

Macias, D. M., Garcia-Gorriz, E., & Stips, A. (2015). Productivity changes in the Mediterranean Sea for the twenty-first century in response to changes in the regional atmospheric forcing. Frontiers in Marine Science, 2, 79.

Table S4. Collinearity among environmental predictors

	August Mean T^a	August Max T^a	September Max T^a	Annual Mean T^a	Annual Mean PPR	Annual Mean Pho
August Mean T^a	**0.963958**					
August Max T^a	**0.937181**	**0.908165**				
September Max T^a	**0.875857**	**0.803242**	0.**901352**			
Annual Mean T^a	-0.37764	-0.38413	-0.38215	-0.19237		
Annual Mean PPR	-0.35813	-0.34841	-0.39383	-0.25247	**0.856813**	
Annual Mean Pho	0.10049	0.06259	0.098412	0.122621	0.27999	0.386776

Table S5. Logistic generalized additive mixed models fitted to presence/absence data for *Paramuricea clavata* and *Corallium rubrum* at five depth layers (from 5-15, 15-25, 25-35, 35-45, and 45-55).

Species	**Forumula**	**Adjusted R^2**	**Sample Size**
P. clavata	Presence ~ Depth	0.344	n = 1198
	Presence ~ PPR	0.0589	
	Presence ~ Annual T^a	0.268	
	Presence ~ August T^a	0.343	
	Presence ~ Annual T^a + Depth	0.413	
	Presence ~ August T^a + Depth	0.342	
	Presence ~ August T^a + PPR	0.353	
	Presence ~ Annual T^a + PPR	0.266	
	Presence ~ August T^a + PPR + Depth	**0.402**	
	Presence ~ Annual T^a + PPR + Depth	**0.430**	
C. rubrum	**Forumula**	**Adjusted R^2**	**Sample Size**
	Presence ~ Depth	0.257	n = 497
	Presence ~ PPR	0.349	
	Presence ~ Annual T^a	0.418	
	Presence ~ August T^a	0.347	
	Presence ~ Annual T^a + Depth	0.333	
	Presence ~ August T^a + Depth	0.226	
	Presence ~ August T^a + PPR	0.238	
	Presence ~ Annual T^a + PPR	0.341	
	Presence ~ August T^a + PPR + Depth	**0.404**	
	Presence ~ Annual T^a + PPR + Depth	**0.424**	

Table S6. Number of sites classified in each cluster (K-means analysis) for each species and emission's scenario.

Species	**Scenario**	**Clusters according trajectories of change**							
		A	**B**	**C**	**D**	**E**	**F**	**G**	**H**
C. rubrum	RCP 4.5	35	68	193	60	19	138	50	30
	RCP 8.5	1	68	1	33	34	210	115	131
P. clavata	RCP 4.5	113	109	246	101	49	335	2	0
	RCP 8.5	4	109	97	15	228	487	15	0

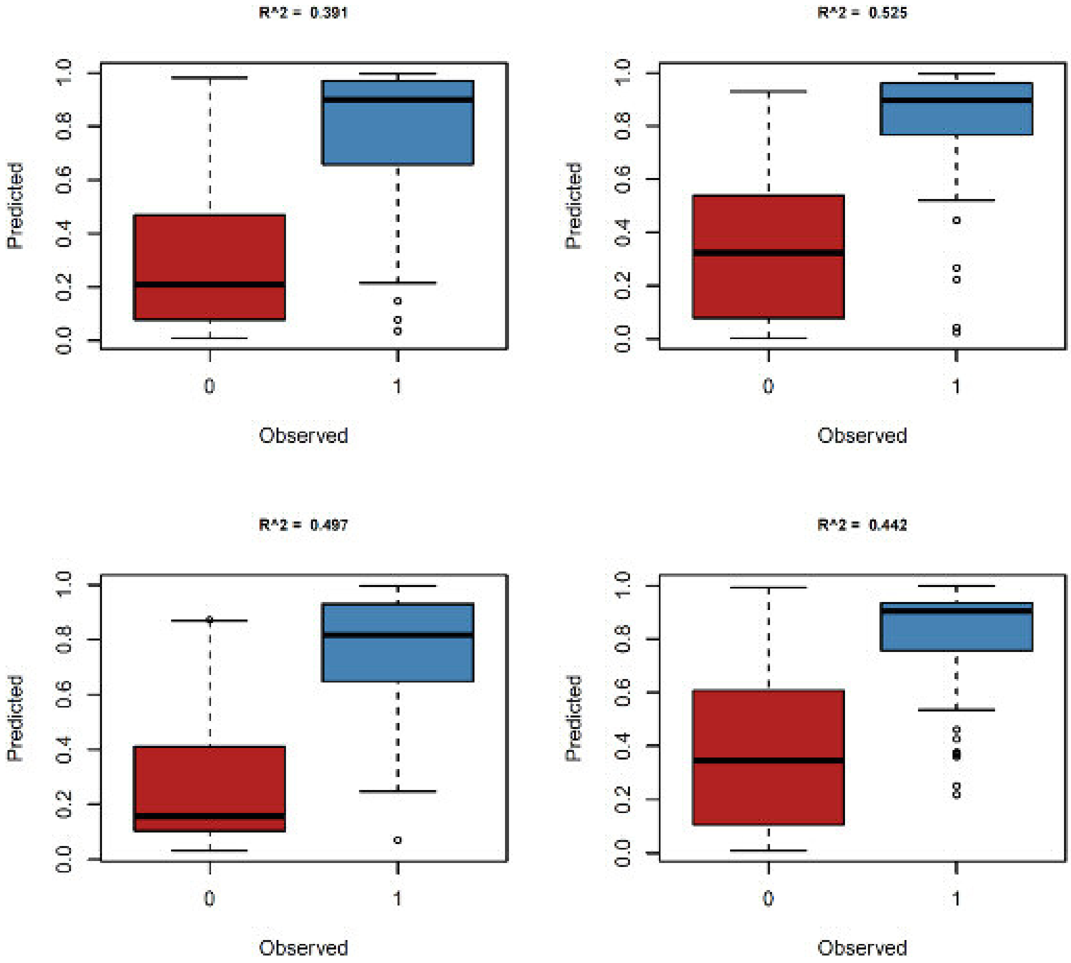


Figure S1. Examples of model validation comparing predicted probability of occurrence with independent presence and absence data.

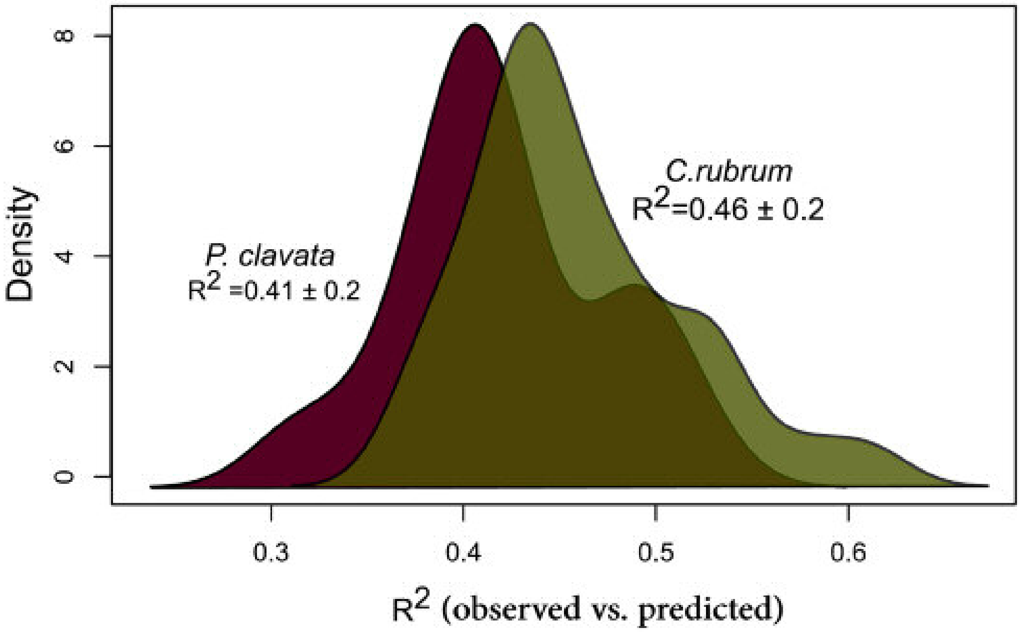


Figure S2. Model validation results. Adjusted R squared values among 50 permutations comparing predicted probability of occurrence against independent presence and absence data for *C. rubrum* and *P. clavata*.

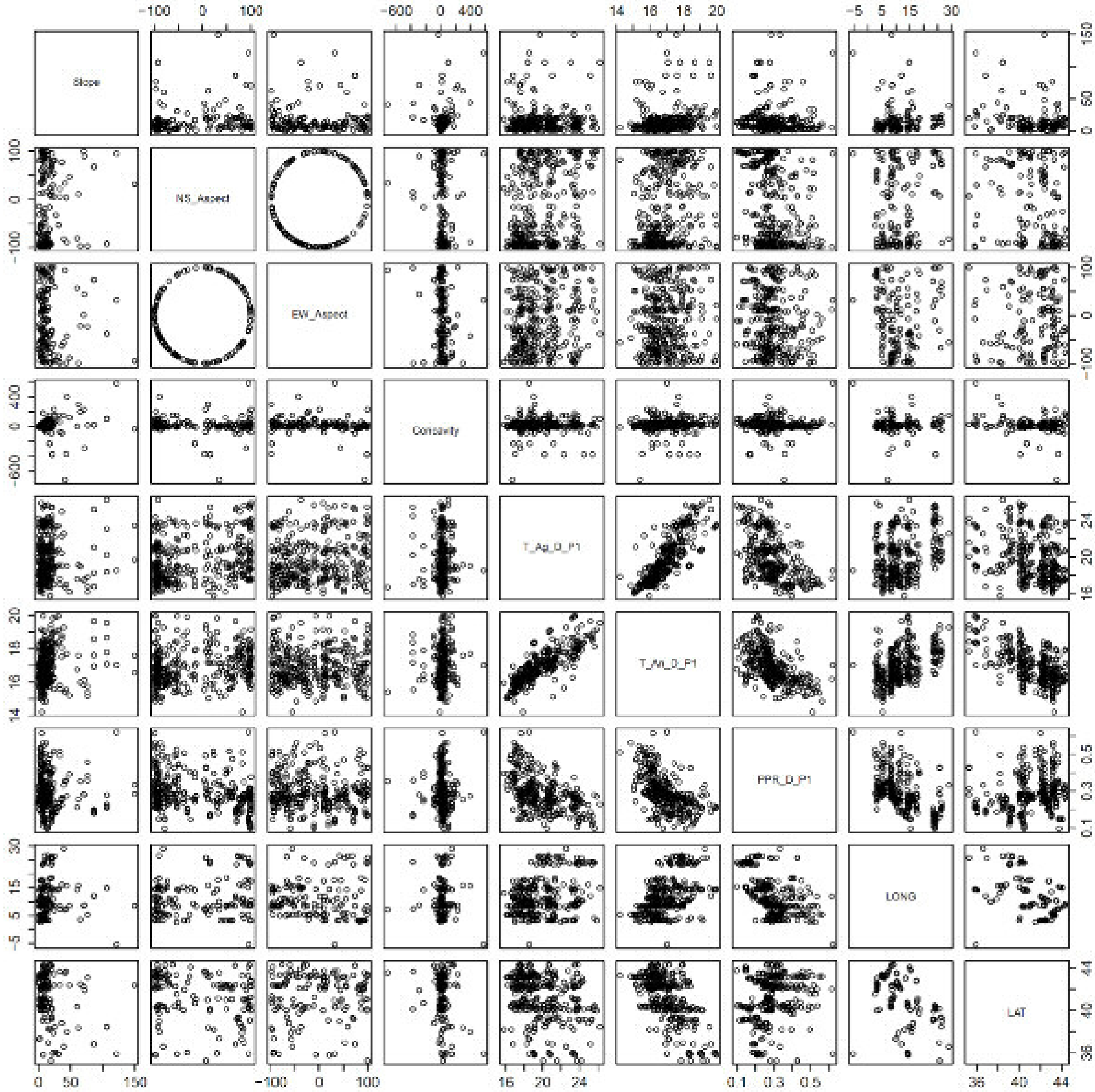


Figure S3. Correlations between environmental predictors**.** Only annual and August temperature showed a high correlation.

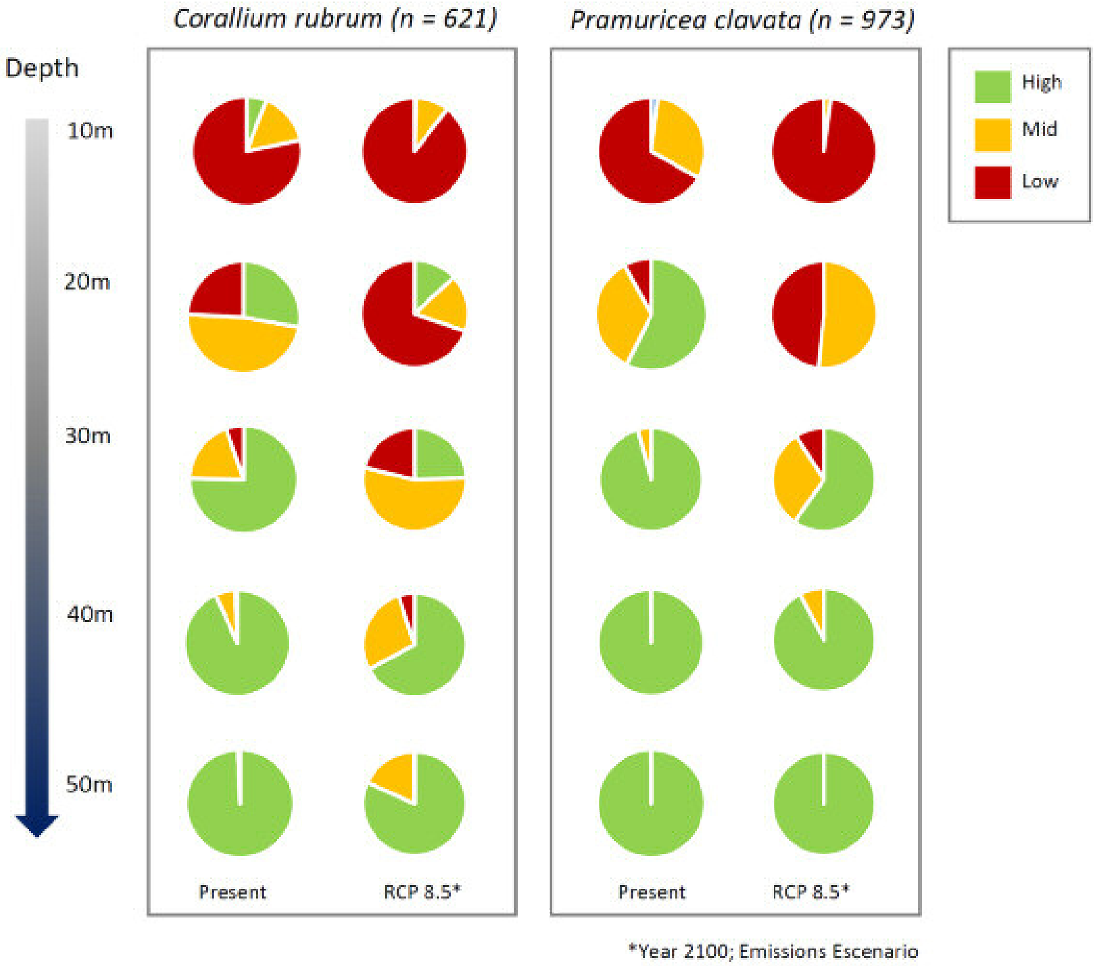


Figure S4. Species-specific predicted habitat suitability for present and future (2100) conditions according to RCP8.5. Suitability values were classified in three levels: high (>0.67), medium (0.34 to 0.67) and low (<0.34).

PROCEEDINGS B

rspb.royalsocietypublishing.org

Research

Cite this article: Montero-Serra I, Linares C, Doak DF, Ledoux JB, Garrabou J. 2018 Strong linkages between depth, longevity and demographic stability across marine sessile species. *Proc. R. Soc. B* **285**: 20172688. http://dx.doi.org/10.1098/rspb.2017.2688

Received: 1 December 2017
Accepted: 1 February 2018

Subject Category:
Ecology

Subject Areas:
ecology, evolution

Keywords:
comparative demography, *Corallium rubrum*, deep sea, integral projection models, life history, longevity

Author for correspondence:
I. Montero-Serra
e-mail: monteroserra@gmail.com

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4002595.

THE ROYAL SOCIETY
PUBLISHING

Strong linkages between depth, longevity and demographic stability across marine sessile species

I. Montero-Serra[1], C. Linares[1], D. F. Doak[2], J. B. Ledoux[3,4] and J. Garrabou[3,5]

[1]Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Avinguda Diagonal 643, 08028 Barcelona, Spain
[2]Environmental Studies Program, University of Colorado, Boulder, CO 80309, USA
[3]Institut de Ciències del Mar, CSIC, Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain
[4]CIIMAR/CIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental, Universidade do Porto, Porto, Portugal
[5]Aix-Marseille University, Mediterranean Institute of Oceanography (MIO), Université de Toulon, CNRS/IRD, Marseille, France

IM-S, 0000-0003-0284-0591; CL, 0000-0003-3855-2743; DFD, 0000-0001-8980-3392; JBL, 0000-0001-8796-6163; JG, 0000-0001-9900-7277

Understanding the role of the environment in shaping the evolution of life histories remains a major challenge in ecology and evolution. We synthesize longevity patterns of marine sessile species and find strong positive relationships between depth and maximum lifespan across multiple sessile marine taxa, including corals, bivalves, sponges and macroalgae. Using long-term demographic data on marine sessile and terrestrial plant species, we show that extreme longevity leads to strongly dampened population dynamics. We also used detailed analyses of Mediterranean red coral, with a maximum lifespan of 532 years, to explore the life-history patterns of long-lived taxa and the vulnerability to external mortality sources that these characteristics can create. Depth-related environmental gradients—including light, food availability, temperature and disturbance intensity—drive highly predictable distributions of life histories that, in turn, have predictable ecological consequences for the dynamics of natural populations.

1. Introduction

From sequoias to small desert shrubs to naked mole rats, the study of species with unusually long lifespans has long fascinated evolutionary ecologists [1–4]. Understanding the conditions where extreme life histories dominate and the potential consequences of these singular strategies for the dynamics of natural populations is central to ecology and evolution, and may also have important implications for conservation biology [5]. However, to date ecologists have only found weak correlations between extrinsic factors and longevity, and we still have relatively few full demographic descriptions for extremely long-lived species.

In terrestrial landscapes, high longevities are common in relatively inhospitable environments characterized by low availability of resources, such as desert and alpine ecosystems [6–8]. However, some species of extreme longevity inhabit highly productive habitats (e.g. the coastal redwood), and climate or habitat factors generally provide only weak predictions of life-history traits [9–12]. The marine realm is perhaps a more promising setting to examine the external factors driving life-history variation than are terrestrial habitats, owing to the set of physical–chemical properties that lead to strong and predictable depth-related gradients at smaller spatial scales than are observed in other systems [13]. The main abiotic factors controlling bottom-up processes in marine communities (light, food availability, temperature and disturbance intensity) all generally decrease with depth (e.g. [14,15]); these factors are also often invoked as likely selective agents favouring short or long lifespans [16]. If environment plays a role in shaping the evolution of longevity, we, therefore, expect an increase of lifespan along depth gradients. Yet, quantitative analyses addressing this hypothesis are scarce.

In this study, we first explore longevity patterns of marine habitat-forming species, asking how predictable longevity is across depths and whether there are consistent consequences of individual longevity for population dynamics. We discuss these results in the light of similar analyses for terrestrial plant species. Next, we conduct a focused analysis of the iconic Mediterranean red coral, examining aspects of population biology of an extremely long-lived species that may be general for high-longevity species. Our findings represent an important step towards a better understanding on the role of environmental conditions as drivers of the evolution and maintenance of longevity and have implications for the conservation of dominant structural species found at deep habitats, where demographic data are scarce.

2. Material and methods

(a) Review of demographic studies

Life-history strategies are complex combinations of multiple traits that describe the timing and magnitude of the species' reproduction, growth and survival, which in turn generate life-history metrics such as longevity, generation time and net reproductive rate. For two reasons, we have focused here on longevity as a proxy for this broader diversity in life-history strategies. First, several comparative demography studies have shown that longevity is highly correlated to many other demographic traits; in particular, longevity is positively correlated to age at maturity and generation time and negatively correlated to reproductive output and growth [17,18]. Second, unlike many complicated life-history traits that require detailed demographic study to estimate, longevity can be estimated in quite simple ways and is widely reported, making it especially suited to broad-scale comparisons.

To construct our dataset, we searched the literature for studies reporting longevity estimates and demographic data by using several combinations of keywords. We restricted our analysis to marine sessile species and used the terms 'marine sessile', 'coral', 'hexacoral', 'octocoral', 'macroalgae', 'seaweed', 'bivalve' and 'bryozoan'. These were combined with either 'demographic model' and 'matrix model' or 'longevity' and 'lifespan' in the Web of Knowledge. We found 144 suitable studies reporting data for 241 species (electronic supplementary material, table S9). We include studies of polycheates that form cemented tubes, and thus are effectively sessile, as well as studies of bivalves that are and are not strictly sessile.

Maximum longevity is estimated through different methodologies. Some studies directly report estimates of maximum observed lifespan using growth rings or geochemical analysis or both. Others report standard demographic data in the form of a matrix model or annual survival rates of adult individuals or colonies. The latter were used to derive potential maximum lifespan based on demographic simulations using the same methodology as for the red coral (see §2d(iii), Demographic analysis below). When demographic data were based on non-annual transitions, annual lifespan was calculated as $L_{\text{ann}} = L \times 12/T$, where L_{ann} is the annual lifespan, L is the non-corrected lifespan value and T is the period described by each transition in months.

As a proxy for habitat, we used depth of occurrence, quantified by the maximum depth reported for the species. While mean or median depth would be more informative, accurate information on these central depths is not available for a wide range of species. Maximum depth is more commonly reported and likely to be correlated with a species' characteristic depth range. Maximum depths were obtained by searching in the literature including the keywords 'depth', 'depth range' and 'maximum depth' combined to the species scientific name (electronic supplementary material, table S9).

(b) Demographic variability using matrix population models

To quantify temporal variance in population growth, we used stochastic demographic models based on at least 5-year study periods (four annual transition matrices) for marine sessile species ($n = 9$) and terrestrial plants ($n = 25$) (electronic supplementary material, table S10). For each species, we simulated the fate of 1000 initial individuals for 1000 years, assuming equal probabilities for each reported annual transition, and computed changes in population size by dividing the total number of individuals at each time (t) by the previous number ($t - 1$). We then log-transformed these realized annual lambda values and computed their variance. Two long-term demographic studies on bivalve species reported only observed annual lambdas, thus we computed variance in population growth directly from these observed lambdas after a log-transformation.

(c) Statistical analysis

We used Pearson's and Spearman's rank correlations and linear models to assess the relationships between depth and longevity as well as longevity and population growth variability. We also explored multiple combinations of potential predictors and their interactions by fitting a set of multiple linear models and using Akaike information criteria corrected for small sample sizes to select the best models. First, a set of linear models was fitted to the whole longevity dataset to test for effects of depth while accounting for different methodological differences in longevity calculations and also to explore potential significant interactions between depth and taxonomic class. We also ran a separate set of models to test if other taxomonic levels (Phylum or Order) had more explanatory power or shifted the results. A second set of models was fitted using only the species for which estimates were based on demographic models. For these species, we explored which longevity definition (see §2d(iii), Demographic analysis below) had a better fit with maximum depth. Finally, to assess the effect of longevity on demographic variability, a third set of models was fitted to sessile species for which four or more annual transition models were available, setting variance in population growth as a response variable and maximum longevity, habitat and their interaction as potential predictors. In these and all other statistical tests, longevity was log-transformed for analysis to achieve more linear results.

(d) Study case: the Mediterranean red coral *Corallium rubrum*

(i) Natural history

Precious corals are long-lived species found in several seas across the world. The red coral *Corallium rubrum* is a long-lived octocoral of the Mediterranean Sea. It is a depth-generalist species commonly observed in the northwestern Mediterranean at shallower depths in overhangs and caves but its bathymetrical distribution can reach up to 1000 m deep [19]. Owing to the high value of its carbonate skeleton for the ornamental jewellery industry, *C. rubrum* has been intensively harvested for millennia. Exploitation—both legal and illegal—as well as ongoing climate change are current threats to this species [20–25].

(ii) Study area and demographic monitoring

A total of 1144 coral colonies from eight *C. rubrum* populations along the northwestern Mediterranean region were individually monitored using photographic techniques ($n = 30$ photoquadrats of 20×20 cm at each population) over periods ranging from 3 to 10 years between 2003 and 2011 (electronic supplementary material, table S1; see [26] for detailed information).

(iii) Demographic analysis

Based on the photographic time-series data, we could estimate size-dependent annual survival, fecundity and growth rates. We used a set of generalized mixed effects models (GLMMs) to describe annual survival and fecundity rates. Because the goal was to describe the general life history of the red coral, population and year were included in the models as random factors. Growth rates are extremely low for this species [27,28], thus a nonlinear growth/shrinkage model was fitted to data of initial and final colony sizes measured for 247 colonies in two populations over periods of 7–8 years. Owing to relatively rare ‘extreme shrinkage’ of some colonies, we divided the growth/shrinkage process into normal growth and extreme retrogression, each with their own mean change of size (see the electronic supplementary material). The growth/shrinkage rates model and the fixed effects from the survival and reproduction GLMMs, which included colony size as a fixed effect and population and year as random factors, were then used to construct a deterministic integral projection model (hereafter IPM). We analysed this model as a large matrix based on 80 colony size-classes (see [26]; electronic supplementary material for a full description on model construction).

Maximum potential lifespan was estimated by deterministic simulations using the demographic IPMs. Specifically, we simulated the fate of 100 individuals starting at the same stage and recording the number of years until 50% (mean lifespan) and 5% (maximum potential lifespan) of individuals were still alive. To explore the expected mean and maximum lifespan conditional on starting at different life-stages, we ran three set of simulations: starting with 100 recruits, starting with 100 of the smallest size-class adults (first reproductive individuals [29]), and starting with 100 largest size-class adults. In all results reported in the main text, we use adult maximum longevity. To explore how robust these longevity metrics are to changes in the dimension of the transition matrix derived from the IPMs, we computed all these metrics using matrices constructed with 10 to 200 size-classes.

To assess the elasticity of deterministic population growth to each vital rate, we performed a perturbation analysis of size-dependent survival, fecundity, and mean normal growth and mean extreme shrinkage, using an 80 size-class model. Each size-dependent vital rate was separately increased or decreased (by 1% and 5%). A mean demographic model was derived that included each perturbation and its deterministic population growth rate (dominant eigenvalue) was computed. Finally, the size-dependent elasticity of each vital rate to λ was calculated using:

$$e_{a_j} = \frac{a_j}{\lambda} \cdot \frac{\partial \lambda}{\partial a_j},$$

where a is the vital rate, j the size-specific interval, λ the deterministic population growth and e_{a_j} is the elasticity for vital rate a_j. Since underlying vital rates were perturbed separately (e.g. mean growth, mean extreme shrinkage and survival), no compensation to control for shifting effects on other vital rates was required (see approach 4 in [30]).

We calculated mean age-specific survival and fecundity rates by simulating a cohort of 1000 new recruits and computing at each time step the survival rate (N_t/N_{t-1}) and the fecundity (R_t/N_{t-1}), where N is the total adult abundance and R is the total number of recruits.

3. Results

(a) Depth, longevity and population stability

The comparison of maximum lifespan revealed a great diversity of life histories across marine sessile species (figure 1). Hydrozoans, bryozoans, cirripeds and polychaetes displayed the shortest lifespans, ranging from weeks to several decades. These generally short-lived taxa have received significantly less attention in the literature compared with other major taxa such as bivalves and corals. The other groups had a great range of lifespans, up to hundreds of years for some calcareous macroalgae and bivalves and to thousands of years for cnidarians and sponges. Most macroalgae species ranged from less than 1 year to several decades, but an outlier with exceptional longevity is the Antarctic calcareous algae *Clathromorphum nereostratum*. Marine bivalve’s lifespans ranged from less than 1 year to more than 500 years for the Antarctic scallop *Arctica islandica* and the giant deep-sea oyster *Neopycnodonte zibrowii*, which is the longest-lived known non-clonal animal. Modular and structural taxa such octocorals, hexacorals and sponges were dominated by longer-lived species. Extreme cases were the deep-sea coral *Gerardia* sp., found in Hawaii, with an estimated age of 4700 years and the longest-lived known marine species, the sponge *Monorhaphis chuni*, observed at 1000 m depth with an estimated age of 11000 years [31,32].

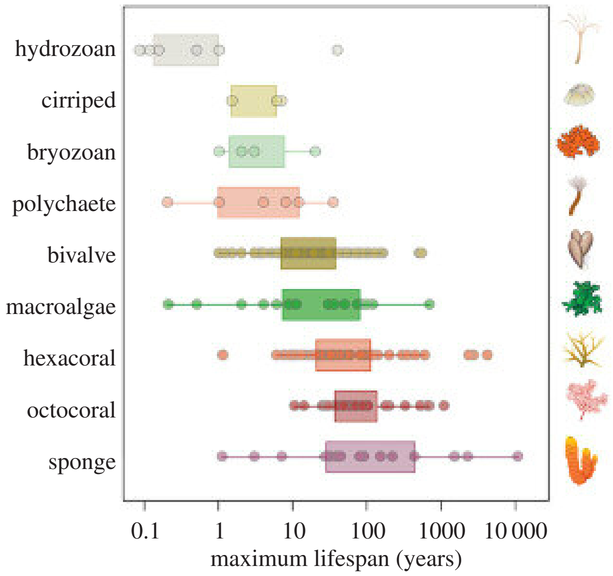


Figure 1. Longevity patterns across marine sessile species ($n = 241$). Data were obtained from the literature and correspond to the maximum potential lifespan reported for each species for the main marine sessile taxa. See the electronic supplementary material, table S9 for specific species data. (Online version in colour.) Images: Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

We correlated log(maximum lifespan) with log(maximum depth) and found strong positive relationships in the five main taxa for which enough data were available to perform meaningful analyses: octocorals (Spearman’s $\rho = 0.673$; $p < 0.001$; $n = 35$), hexacorals (Spearman’s $\rho = 0.592$; $p < 0.001$; $n = 40$), sponges (Spearman’s $\rho = 0.647$; $p < 0.001$; $n = 17$), macroalgae (Spearman’s $\rho = 0.600$; $p = 0.023$; $n = 14$) and bivalves (Spearman’s $\rho = 0.491$; $p < 0.001$; $n = 93$) (figure 2; electronic supplementary material, table S2). The positive relationship between depth and lifespan was consistent across different measures of longevity, although adult maximum longevity showed the strongest relationships with depth (electronic supplementary material, table S3). This relationship is also consistent when accounting for taxon or matrix dimension; the best supported model includes an interaction between depth and taxon, with significantly larger slopes for sponges ($p = 0.0131$) and macroalgae ($p = 0.0308$) than for the other taxa (electronic supplementary material, table S4; overall model statistics: $R^2 = 0.511$; $F_{185} = 18.12$; $p < 0.001$). Use of other taxonomic levels does not change this qualitative result,

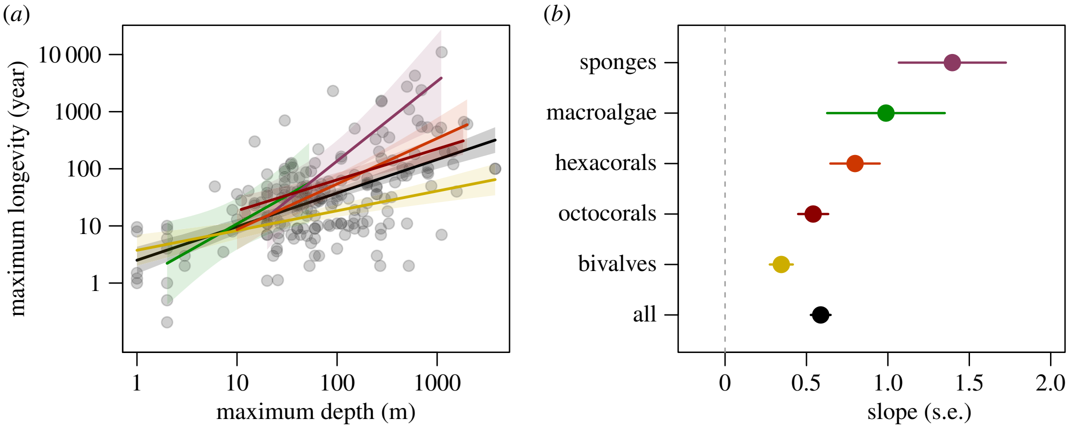


Figure 2. (*a*) Relationship between maximum depth of occurrence and maximum longevity across marine sessile species. Colours correspond to the labels in (*b*), and lines show the best fit linear model for each taxon. Black line shows the linear relationship for all taxa. Shaded areas represent standard errors. (*b*) Slope corresponds to the estimated slope of maximum depth on maximum longevity for each taxon, with error bars showing ±1 s.e. (Online version in colour.)

and model fit is best for Class (electronic supplementary material, table S5). We also ran quantile regressions between log(depth) and log(longevity) to see if depth is a more powerful regulator of extreme life-history values, but found no significant differences in the slope of the depth–longevity relationship for 10% up to 90% quantiles (electronic supplementary material, table S6).

To assess population consequences of longevity, we regressed variance in realized log-lambda on longevity across marine sessile invertebrates and terrestrial plants and found a similar, strongly negative relationship for both. Short-lived species displayed higher variability in population growth over time than did longer-lived species ($n = 34$; Spearman's $\rho = -0.73$; $p < 0.001$). The pattern was consistent in terrestrial plants ($n = 25$, Spearman's $\rho = -0.68$; $p = 0.0002$) and marine sessile invertebrates ($n = 9$; Spearman's $\rho = -0.67$, $p = 0.0214$) (figure 3; electronic supplementary material, table S7).

(b) The extreme life-history of *Corallium rubrum* and its population dynamics

The red coral *C. rubrum* displayed slow dynamics over the eight populations studied along the northwestern Mediterranean (electronic supplementary material, figure S1), a pattern driven by extremely high adult survival, ranging between 98.05% and 99.76% from the smallest to the largest reproductive *C. rubrum* colonies (figure 4*a*). Monitoring of post-recruitment survival revealed that relative to later survival rates, annual survival is low during the first years after recruitment with a mean of 69.5% (figure 4*c*). However, by the age of four, young colonies already displayed a high survival probability of 92.2%. Overall, mortality rates decreased rapidly during the early stages of the red coral lifetime, following a type III survivorship curve, and then decreased steadily, more similar to type II survivorship (figure 5*a*). Recruitment was very limited; from 246 quadrats (about 30 per population) individually monitored for recruitment at the eight studied populations, 83.7% showed no annual recruitment. The remaining 16.3% of quadrats were divided into 10.7% with only a single recruit present, 5.1% with two to four recruits and only 0.5 with five or more recruits (figure 4*b*,*d*). Mean annual *per capita* recruitment, weighted by the relative abundance of different sized individuals, was 0.077. This is considerably lower than the average *per capita* recruitment for a range of marine sessile invertebrates for which there is standard demographic data available ($n = 28$, median = 0.547–0.727, mean = 5.14 ± 4.02 (s.d.); electronic supplementary material, table S8), although higher than the same estimate for six other species (electronic supplementary material, table S8).

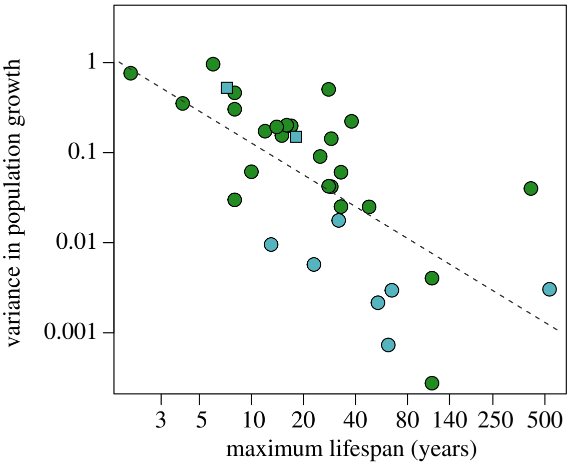


Figure 3. Relationship between temporal variability in population growth and maximum longevity in terrestrial plants (green, $n = 25$, Spearman's $\rho = -0.68$; $p = 0.0002$) and marine sessile (light blue, $n = 9$; Spearman's $\rho = -0.67$, $p = 0.0214$) species, and overall ($n = 34$; Spearman's $\rho = -0.73$; $p < 0.0001$). Squared light blue dots correspond to two bivalve species whose variance was computed directly from observed annual lambdas. (Online version in colour.)

Demographic simulations revealed high maximum potential future longevity for *C. rubrum* colonies, ranging from 501 to 532 years for small and large adult, respectively (figure 5*a*; electronic supplementary material, figure S2). The mean expected lifespan was also relatively high for adult red coral colonies and ranged from 98 years for small adult colonies to 129 years for the larger red coral colonies. Our simulations also revealed potential artefacts owing to matrix dimensionality. When using relatively small transition matrices (less than 60 size-classes) simulations underestimated values of maximum and mean longevity, the values stabilized around 60–80 size-classes and were consistent thereafter (electronic supplementary material, figure S2).

Perturbation analysis revealed a disproportionately large influence of survival rates on asymptotic population growth

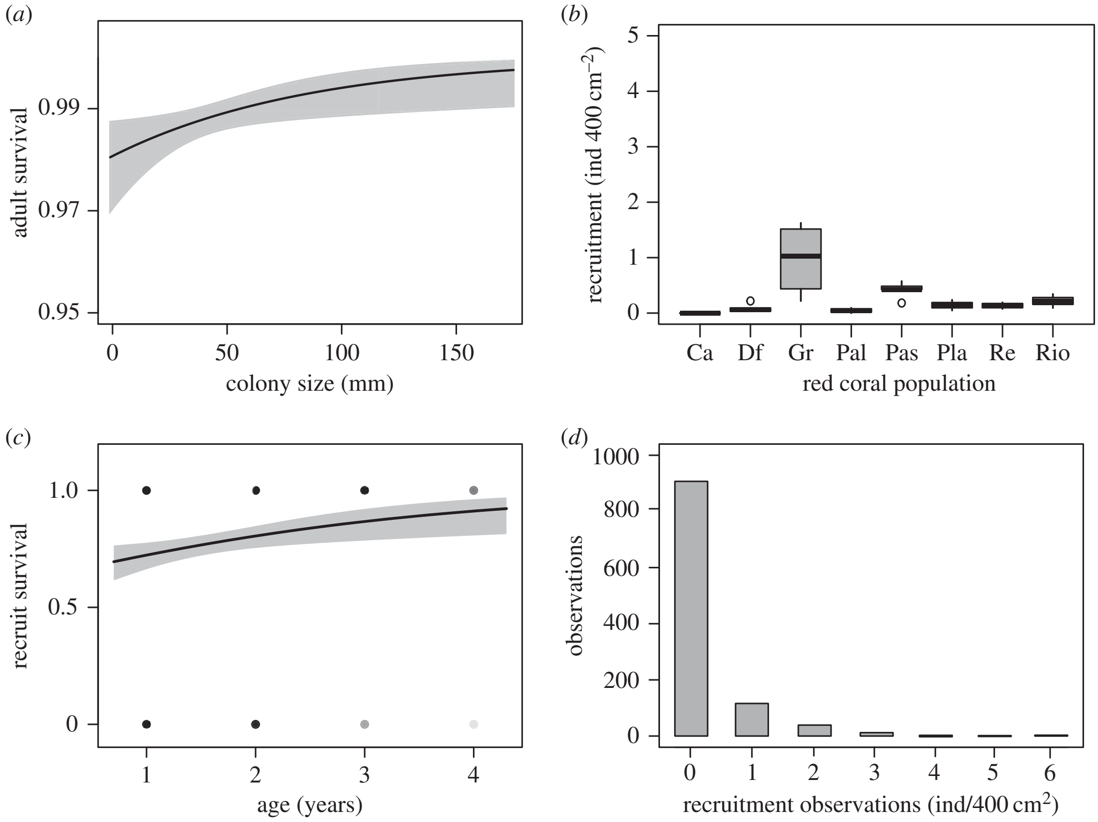


Figure 4. Long-term demographic traits of the red coral *Corallium rubrum*. (*a*) Adult survival probability depending on colony size. The line represents a logistic generalized linear mixed effects model including population and year as random effects and colony size as a fixed effect. (*b*) Mean recruitment rates in eight *C. rubrum* populations. (*c*) Age-dependent post-recruitment survival probability. (*d*) Frequency of annual recruitment observations in eight *C. rubrum* populations. In (*a,c*) grey areas show ±1 s.e.

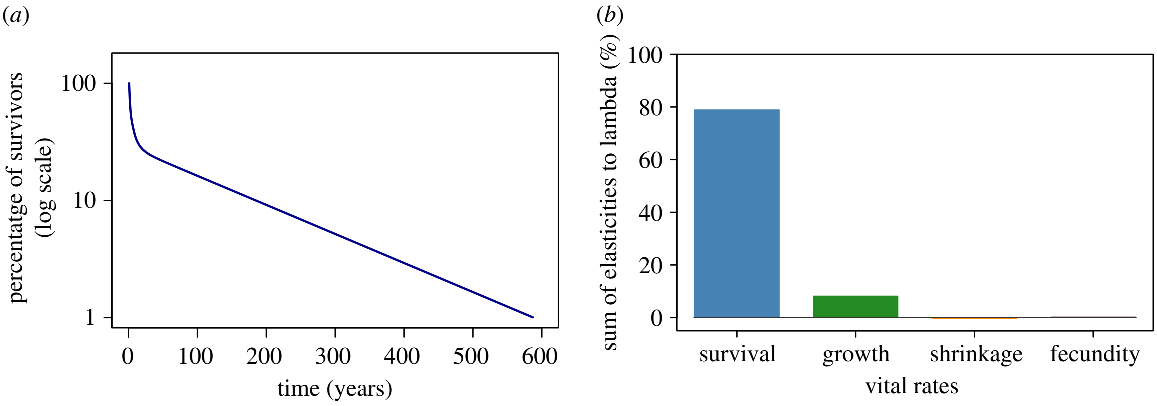


Figure 5. Demographic analyses for the red coral *Corallium rubrum*. (*a*) Survivorship curve based on a deterministic simulation of 100 individuals. (*b*) Patterns of elasticity to the asymptotic population growth rates of different vital rates, with each bar indicating elasticity summed across all size-classes. Other vital rates have even lower elasticities (electronic supplementary material, figure S4). (Online version in colour.)

(figure 5*b*). Elasticity of lambda to fecundity, mean growth and mean extreme shrinkage, as well as all other vital rates, was markedly lower (electronic supplementary material, figure S4). Model fitting of age- or size-dependent fecundity and survival showed no evidence of senescence (electronic supplementary material, figure S3).

4. Discussion

Demography is a powerful tool to understand the evolution of life histories and has provided important insights into plant, mammal and bird's strategies [5,33]. However, a lack of long-term and broad spatial-scale data on the dominant species of marine ecosystems, particularly those living at deeper depths, hinders our understanding of the processes shaping the dynamics of these threatened ecosystems [34]. In this study, we analysed the long-term dynamics of the long-lived red coral *C. rubrum* and published data for a broad range of marine sessile invertebrates and macroalgae. The results revealed strong positive relationships between depth, longevity and demographic stability, showing strong habitat-determined predictability of key demographic processes in marine ecosystems.

Marine sessile species have a wide range of maximum lifespans across taxa and habitats, ranging from weeks in some intertidal species to hundreds of years for the red coral *C. rubrum*, and several thousands of years for some deep-sea corals and sponges (figure 1). Our most striking finding was that maximum lifespan was strongly and positively correlated with a species' maximum depth occurrence in hexacorals, octocorals, sponges, and although weaker, also in bivalves (figure 2). These results demonstrate a strong role of habitat features at shaping the distribution of longevity patterns.

In the shallowest waters, short-lived species dominate (figure 2), perhaps owing to high disturbance rates and competition in high-energy environments where fast-growing species have a distinct advantage. By contrast, species displaying diverse life-history strategies coexist at intermediate depths, including short-lived invertebrates that also occur intertidally and longer-lived massive corals, macroalgae and seagrasses [35,36]. The high energy availability owing to constant solar irradiation may allow the presence of a large spectrum of life-history strategies that have diversified to occupy multiple niches, following analogous processes than those shaping tropical rainforest plant communities [37]. Finally, in deeper waters, environmental constraints seem to favour the dominance of slower life histories and longer lifespans. Depth gradient determines changes in environmental factors such as light and food availability, temperature and disturbance intensities. In turn, these factors are likely to control the evolution of lifespans through several mechanisms. First, deeper habitats are generally less productive, limiting food supply for consumers and favouring slow growth and longer lifespans [38]. Empirical studies exploring physiological trade-offs have shown that the elevated metabolic costs of fast strategies can be detrimental in the absence of high availability of resources [39]. Also, as light is strongly depth-dependent, organisms dwelling at deeper habitats may experience a 'competition release', mainly by the absence of macroalgae and other fast-growing autotroph organisms that are constrained to the photic zone [40]. Similarly, deeper habitats are less diverse and thus organisms could face less predation pressure, pushing selective forces to favour somatic maintenance and, therefore, life extension [41]. Finally, the relative predictability of deep environments may enable species to survive with lower reproductive and mortality rates. Shallow habitats are more exposed to external sources of mortality owing to extreme physical disturbances (i.e. hurricanes and storms) and temperature fluctuations [13,42], making them less suitable for organisms whose long-term success relay on extremely high survival of adult stocks [43].

Previous anecdotal data on longevity in sessile and mobile marine organisms support our findings. For instance, the highest longevity reported to date corresponds to the sponge *M. chuni*, found at 1000 m depth with an estimated age of 11000 years [32]. A similar pattern has been also observed in marine fishes [44]. Indeed, a recent study based on radiocarbon dating on eye tissue revealed that the deep-resident Greenland shark *Somniosus microcephalus*, which can live up to 400 years, may be the longest-lived vertebrate on the Earth [45]. Overall, these results demonstrate a strong role of depth-related environmental gradients in shaping life-history strategies across marine taxa. The strength of this pattern is striking and contrasts with the weak environmental correlates of longevity or other life-history traits that seem typical in terrestrial systems [9–12]. Nonetheless, our findings open new questions regarding the existence of potentially analogous processes driving the evolution of life-history strategies along elevation and/or productivity gradients in terrestrial landscapes. Further analyses exploring the relationship between depth and different environmental parameters could provide a more mechanistic understanding of this general pattern of increasing species maximum longevity towards deeper marine waters.

At least three demographic mechanisms may contribute to the strong relationship observed between depth and longevity in marine sessile organisms. First, species may show relatively indiscriminate settlement. Under this scenario, the longevity pattern may arise because faster-growing, shorter-lived species outcompete slow species in productive, shallow sites, while at deeper sites only slow-growing species with high longevity may persist. Second, species may have evolved specific settlement cues so that larvae of long-lived species preferentially settle in either deep or shallow sites. Finally, to some extent these life-history patterns could result from demographic compensation, reflecting phenotypic plasticity in life histories (i.e. fecundity, growth or survival rates) as a function of local constraints on population growth rates [46]. In reality, all three mechanisms are likely to contribute to this matching of life history to environment.

(a) The extreme life-history features of the red coral *Corallium rubrum*

While our survey shows that mesophotic and deep-sea ecosystems are predictably inhabited by species of extreme longevity, we have few detailed studies of the population ecology of these taxa. We found that *C. rubrum*, a widely distributed Mediterranean red coral, showed a consistent pattern of slow population dynamics driven by extremely high survival, recruitment limitation and apparently negligible senescence (figure 5; electronic supplementary material, figure S3a). The species revealed a maximum potential longevity of up to 532 years, overlapping with lifespan ranges of other deep-sea organisms. Although previous research had shown that *C. rubrum* settlement can be highly heterogeneous [47,48], in this study, we observed a much more homogeneous pattern of low recruitment in the long term (figure 4*b*,*d*; electronic supplementary material, table S8). Recruitment limitation has been observed in other long-lived temperate invertebrates [49–51] and can seriously hinder the ability of populations to recover after intense perturbations [52].

For species with limited recruitment, adult survival becomes of paramount importance to ensure their persistence [43]. We found extremely high survival for *C. rubrum* (figures 4*a* and 5*a*), with estimated mortality even lower than found in previous experimental studies [27,50]. In agreement with previous observations in long-lived gorgonians [43], the perturbation analysis supported that survival is the vital rate demonstrating the highest effect on population growth in *C. rubrum* (figure 5*b*). The absence of detectable senescence is common in sessile marine species and terrestrial plants [2,53], and may be related to high investments in structural tissues, although some authors have suggested that modularity may also play an important role [53]. It should also be noted that our data, like that for most other studies of extremely long-lived species, lack the precision necessary to carefully test for senescence. Precious corals build an energetically demanding hard carbonate skeleton; while preventing a fast rate of colony growth, it may provide the structural basis that allows for an extremely high survival.

The shallow occurrences of the monitored populations of this long-lived species could seem to make it an outlier in the depth-longevity pattern. However, this coral is distributed from shallow to deep waters up to 1000 m depth [19] and its shallow occurrences are exclusively found in dim-light and dark habitats where it cannot be outcompeted by fast-growing organisms [40]. Given the overall pattern observed for marine species, the dynamics of red coral populations dwelling at deeper habitats are likely to be even slower and more dependent on adult survival. However, we must be cautious with these extrapolations and note that demographic data on deeper locations is not available owing to logistical constraints. Exceptional shallow presence has been also observed in other important cold-water corals, such as *Lophelia pertusa*, which can occur at 25 m in sediment laden fjords where light attenuation reduces the abundances of autotroph organisms, and thus competition; while at the other end of the scale this species may be found as deep as 3300 m [54].

(b) Population-level consequences of extreme life histories

As important as unravelling the drivers of extreme longevities are the implications of these strategies for dynamics of natural populations. We show that maximum longevity strongly predicts temporal stability in population growth across terrestrial and marine sessile species (figure 3). This finding agrees with previous studies suggesting that long-lived species can strongly buffer environmental stochasticity [55,56]. As observed for the red coral *C. rubrum*, this buffering capacity relies on high adult survival and low reproductive success. While conferring stability under natural conditions, this extreme life history will also hinder the ability of long-lived species to overcome increased mortality rates, but whether these species will be able to cope with rapidly changing perturbation regimes driven by the ongoing global change is still unclear. For instance, while the red coral has persisted after millennia of historical overharvesting owing to the combination of consistent survival of partially harvested colonies [25] and small size at maturity [29], new human-related stressors such as global warming have increased mortality rates and put some shallow populations at risk [20,21,57]. Worryingly, although declines may already be driving populations of some long-lived species towards collapse, in some cases, these trajectories may be too subtle to be noticed by ecologists and managers [58]. The consistent depth relationship for longevity also implies greater sensitivity of species and communities occurring at greater depths to human perturbations, amplifying recent calls to better monitor and protect these vulnerable ecosystems [34].

Data accessibility. All data are deposited in Dryad: http://dx.doi.org/10.5061/dryad.p0b6b [59].

Authors' contributions. I.M.-S., C.L., D.F.D. and J.G. designed the study. C.L., J.B.L. and J.G. collected the demographic data in the field. I.M.-S. extracted data from the literature. I.M.-S. and D.F.D. performed analyses. I.M.-S. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Competing interests. We declare we have no competing interests.

Funding. This study was partially funded by the Spanish Ministry of Economy and Innovation Biorock project (CTM2009-08045), the Smart project (CGL2012-32194), the TOTAL Foundation Perfect project and the European Union's Horizon 2020 research and innovation programme under grant agreement no 689518 (MERCES). This output reflects only the authors' view and the European Union cannot be held responsible for any use that may be made of the information contained therein. I.M.-S. was supported by a FPI grant (BES-2013-066150), C.L. by a Ramon y Cajal (RyC-2011-08134) and J.B.L. by a postdoctoral grant (SFRH/BPD/74400/2010) from the Portuguese Foundation for Science and Technology. Support for D.F.D. came from National Science Foundation awards 1340024 and 1242355. I.M.-S., C.L., J.B.L. and J.G. are part of the Marine Conservation research group (2014 SGR 1297) from the Generalitat de Catalunya.

Acknowledgements. We thank K. Kaplan, M. Pages, A. Griffith and one anonymous reviewer for their valuable comments on early versions of this manuscript.

References

1. Buffenstein R. 2005 The naked mole-rat? A new long-living model for human aging research. *J. Gerontol. A. Biol. Sci. Med. Sci.* **60**, 1369–1377. (doi:10.1093/gerona/60.11.1369)
2. Baudisch A, Salguero-Gómez R, Jones OR, Wrycza T, Mbeau-Ache C, Franco M, Colchero F, Hutchings M. 2013 The pace and shape of senescence in angiosperms. *J. Ecol.* **101**, 596–606. (doi:10.1111/1365-2745.12084)
3. Jones OR *et al.* 2014 Diversity of ageing across the tree of life. *Nature* **505**, 169–173. (doi:10.1038/nature12789)
4. Colchero F *et al.* 2016 The emergence of longevous populations. *Proc. Natl Acad. Sci. USA* **113**, E7681–E7690. (doi:10.1073/pnas.1612191113)
5. Griffith AB, Salguero-Gómez R, Merow C, McMahon S. 2016 Demography beyond the population. *J. Ecol.* **104**, 271–280. (doi:10.1111/1365-2745.12547)
6. Vasek FC. 1980 Creosote bush: long-lived clones in the Mojave Desert. *Am. J. Bot.* **67**, 246–255. (doi:10.1002/j.1537-2197.1980.tb07648.x)
7. Forbis TA, Doak DF. 2004 Seedling establishment and life history trade-offs in alpine plants. *Am. J. Bot.* **91**, 1147–1153. (doi:10.3732/ajb.91.7.1147)
8. García MB, Pico FX, Ehrlén J. 2008 Life span correlates with population dynamics in perennial herbaceous plants. *Am. J. Bot.* **95**, 258–262. (doi:10.3732/ajb.95.2.258)
9. Stearns SC. 1977 The evolution of life history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Evol. Syst.* **8**, 145–171. (doi:10.1146/annurev.es.08.110177.001045)
10. McIntyre S, Lavorel S, Tremont RM. 1995 Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J. Ecol.* **83**, 31–44. (doi:10.2307/2261148)
11. Morrison C, Hero JM. 2003 Geographic variation in life-history characteristics of amphibians: a review. *J. Anim. Ecol.* **72**, 270–279. (doi:10.1046/j.1365-2656.2003.00696.x)
12. Moles AT *et al.* 2007 Global patterns in seed size. *Glob. Ecol. Biogeogr.* **16**, 109–116. (doi:10.1111/j.1466-8238.2006.00259.x)
13. Garrabou J, Ballesteros E, Zabala M. 2002 Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. *Coast. Shelf. Sci.* **55**, 493–508. (doi:10.1006/ecss.2001.0920)
14. Barnes RSK, Hughes RN. 1999 *An introduction to marine ecology*. New York, NY: John Wiley and Sons.
15. Smith KF, Brown JH. 2002 Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. *Glob. Ecol. Biogeo.* **11**, 313–322. (doi:10.1046/j.1466-822X.2002.00286.x)
16. Munch SB, Salinas S. 2009 Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proc. Natl Acad. Sci. USA* **106**, 13 860–13 864. (doi:10.1073/pnas.0900300106)

17. Gaillard JM *et al.* 2016 Life history axes of variation. In *Encyclopedia of evolutionary biology* (ed. RM Kliman), pp. 312–323. Oxford, UK: Academic Press.
18. Salguero-Gómez R *et al.* 2016 Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proc. Natl Acad. Sci. USA* **113**, 230–235. (doi:10.1073/pnas.1506215112)
19. Knittweis L *et al.* 2016 New depth record of the precious red coral *Corallium rubrum* for the Mediterranean. *Rapp. Comm. Int. Mer Médit.* **41**, 467.
20. Garrabou J, Perez T, Sartoretto S, Harmelin JG. 2001 Mass mortality event in red coral *Corallium rubrum* populations in the Provence region (France, NW Mediterranean). *Mar. Ecol. Prog. Ser.* **217**, 263–272. (doi:10.3354/meps217263)
21. Garrabou J *et al.* 2009 Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Glob. Change Biol.* **15**, 1090–1103. (doi:10.1111/j.1365-2486.2008.01823.x)
22. Garrabou J *et al.* 2017 Re-shifting the ecological baseline for the overexploited Mediterranean red coral. *Sci. Rep.* **7**, 42404. (doi:10.1038/srep42404)
23. Linares C, Garrabou J, Hereu B, Diaz D, Marschal C, Sala E, Zabala M. 2012 Assessing the effectiveness of marine reserves on unsustainably harvested long-lived sessile invertebrates. *Conserv. Biol.* **26**, 88–96. (doi:10.1111/j.1523-1739.2011.01795.x)
24. Bramanti L *et al.* 2013 Detrimental effects of ocean acidification on the economically important Mediterranean red coral (*Corallium rubrum*). *Glob. Change Biol.* **19**, 1897–1908. (doi:10.1111/gcb.12171)
25. Montero-Serra I *et al.* 2015 Harvesting effects, recovery mechanisms, and management strategies for a long-lived and structural precious coral. *PLoS ONE* **10**, e0117250. (doi:10.1371/journal.pone.0117250)
26. Montero-Serra I *et al.* 2017 Accounting for life-history strategies and timescales in marine restoration. *Conserv. Lett.* 1–9.
27. Garrabou J, Harmelin JG. 2002 A 20-year study on life-history traits of a harvested long-lived temperate coral in the NW Mediterranean: insights into conservation and management needs. *J. Anim. Ecol.* **71**, 966–978. (doi:10.1046/j.1365-2656.2002.00661.x)
28. Marschal C, Garrabou J, Harmelin JG, Pichon M. 2004 A new method for measuring growth and age in the precious red coral *Corallium rubrum* (L.). *Coral Reefs* **23**, 423–432. (doi:10.1007/s00338-004-0398-6)
29. Torrents O, Garrabou J, Marschal C, Harmelin JG. 2005 Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) in the Marseilles area (France, NW Mediterranean). *Biol. Conserv.* **121**, 391–397. (doi:10.1016/j.biocon.2004.05.010)
30. Griffith AB. 2017 Perturbation approaches for integral projection models. *Oikos* **126**, 1675–1686. (doi:10.1111/oik.04458)
31. Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA. 2009 Extreme longevity in proteinaceous deep-sea corals. *Proc. Natl Acad. Sci. USA* **106**, 5204–5208. (doi:10.1073/pnas.0810875106)
32. Jochum KP, Wang X, Vennemann TWSB, Müller WE. 2012 Siliceous deep-sea sponge *Monorhaphis chuni*: a potential paleoclimate archive in ancient animals. *Chem. Geol.* **300**, 143–151. (doi:10.1016/j.chemgeo.2012.01.009)
33. McDonald JL, Franco M, Townley S, Ezard TH, Jelbert K, Hodgson DJ. 2017 Divergent demographic strategies of plants in variable environments. *Nat. Ecol. Evol.* **1**, 0029. (doi:10.1038/s41559-016-0029)
34. Danovaro R *et al.* 2017 An ecosystem-based deep-ocean strategy. *Science* **355**, 452–454. (doi:10.1126/science.aah7178)
35. Arnaud-Haond S, Duarte CM, Diaz-Almela E, Marbà N, Sintes T, Serrão EA. 2012 Implications of extreme life span in clonal organisms: millenary clones in meadows of the threatened seagrass *Posidonia oceanica*. *PLoS ONE* **7**, e30454. (doi:10.1371/journal.pone.0030454)
36. Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM. 2012 Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* **15**, 1378–1386. (doi:10.1111/j.1461-0248.2012.01861.x)
37. Connell JH. 1978 Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310. (doi:10.1126/science.199.4335.1302)
38. Larson DW. 2001 The paradox of great longevity in a short-lived tree species. *Exp. Gerontol.* **36**, 651–673. (doi:10.1016/S0531-5565(00)00233-3)
39. Reznick DN, Tessier A. 2000 Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol. Evol.* **15**, 421–425. (doi:10.1016/S0169-5347(00)01941-8)
40. Zabala M, Ballesteros E. 1989 Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean. *Sci. Mar.* **53**, 3–17.
41. Healy K, Guillerme T, Finlay S, Kane A, Kelly SB. 2014 Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. B* **281**, 20140298. (doi:10.1098/rspb.2014.0298)
42. Bridge TC *et al.* 2014 Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. *F1000Res* **2**, 187. (doi:10.12688/f1000research.2-187.v3)
43. Linares C, Doak DF, Coma R, Diaz D, Zabala M. 2007 Life history and viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. *Ecology* **88**, 918–928. (doi:10.1890/05-1931)
44. Cailliet GM, Andrews AH, Burton EJ, Watters DL, Kline DE, Ferry-Graham LA. 2001 Age determination and validation studies of marine fishes: do deep-dwellers live longer? *Exp. Gerontol.* **36**, 739–764. (doi:10.1016/S0531-5565(00)00239-4)
45. Nielsen J *et al.* 2016 Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*). *Science* **353**, 702–704. (doi:10.1126/science.aaf1703)
46. Villellas J, Doak DF, García MB, Morris WF. 2015 Demographic compensation among populations: what is it, how does it arise and what are its implications? *Ecol. Lett.* **18**, 1139–1152. (doi:10.1111/ele.12505)
47. Bramanti L, Magagnini G, De Maio L, Santangelo G. 2005 Recruitment, early survival and growth of the Mediterranean red coral *Corallium rubrum* (L 1758), a 4-year study. *J. Exp. Mar. Bio. Ecol.* **314**, 69–78. (doi:10.1016/j.jembe.2004.08.029)
48. Santangelo G, Bramanti L, Rossi S, Tsounis G, Vielmini I, Lott C, Gili JM. 2012 Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral *Corallium rubrum*. *J. Exp. Mar. Bio. Ecol.* **411**, 7–13. (doi:10.1016/j.jembe.2011.10.030)
49. Grigg RW. 1988 Recruitment limitation of a deep benthic hard-bottom octocoral population in the Hawaiian Islands. *Mar. Ecol. Prog. Ser.* **45**, 121–126. (doi:10.3354/meps045121)
50. Teixidó N, Garrabou J, Harmelin JG. 2011 Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. *PLoS ONE* **6**, e23744. (doi:10.1371/journal.pone.0023744)
51. Kersting DK, Teixidó N, Linares C. 2014 Recruitment and mortality of the temperate coral *Cladocora caespitosa*: implications for the recovery of endangered populations. *Coral Reefs* **33**, 403–407. (doi:10.1007/s00338-014-1144-3)
52. Hughes TP, Tanner JE. 2000 Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* **81**, 2250–2263. (doi:10.1890/0012-9658(2000)081[2250:RFLHAL]2.0.CO;2)
53. Tanner JE. 2001 The influence of clonality on demography: patterns in expected longevity and survivorship. *Ecology* **82**, 1971–1981. (doi:10.1890/0012-9658(2001)082[1971:TIOCOD]2.0.CO;2)
54. Squires DF. 1959 Results of the puritan-American museum of natural history expedition to western Mexico. *Bull. Am. Museum Nat. Hist.* **118**, 371–431.
55. Morris WF *et al.* 2008 Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* **89**, 19–25. (doi:10.1890/07-0774.1)
56. Garcia MB, Dahlgren JP, Ehrlén J. 2011 No evidence of senescence in a 300-year-old mountain herb. *J. Ecol.* **99**, 1424–1430. (doi:10.1111/j.1365-2745.2011.01871.x)
57. Cerrano C *et al.* 2000 A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-western Mediterranean), summer 1999. *Ecol. Lett.* **3**, 284–293. (doi:10.1046/j.1461-0248.2000.00152.x)
58. Hughes TP, Linares C, Dakos V, van de Leemput IA, van Nes EH. 2013 Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends Ecol. Evol.* **28**, 149–155. (doi:10.1016/j.tree.2012.08.022)
59. Montero-Serra I, Linares C, Doak DF, Ledoux JB, Garrabou J. 2018 Data from: Strong linkages between depth, longevity and demographic stability across marine sessile species. Dryad Digital Repository. (http://dx.doi.org/10.5061/dryad.p0b6b)

PLOS | ONE

RESEARCH ARTICLE

Harvesting Effects, Recovery Mechanisms, and Management Strategies for a Long-Lived and Structural Precious Coral

Ignasi Montero-Serra[1]*, Cristina Linares[1], Marina García[2], Francesca Pancaldi[2], Maša Frleta-Valić[2], Jean-Baptiste Ledoux[2,5], Frederic Zuberer[3], Djamel Merad[4], Pierre Drap[4], Joaquim Garrabou[2,6]

1 Departament d'Ecologia, Universitat de Barcelona, Barcelona, Spain, **2** Institut de Ciències del Mar (ICM-CSIC), Barcelona, Spain, **3** Institut Pytheas, UMS 3470, Station Marine d'Endoume, Marseille, France, **4** LSIS UMR CNRS 7296, Centre National de la Recherche Scientifique, Marseille, France, **5** CIMAR /CIIMAR Centro Interdisciplinar de Investigação Marinha e Ambiental, Universidade do Porto, Porto, Portugal, **6** UM110, CNRS/INSU, IRD, Aix-Marseille Université, Université du Sud Toulon Var, Mediterranean Institute of Oceanography (MIO), Marseille, France

* monteroserra@gmail.com

Abstract

Overexploitation is a major threat for the integrity of marine ecosystems. Understanding the ecological consequences of different extractive practices and the mechanisms underlying the recovery of populations is essential to ensure sustainable management plans. Precious corals are long-lived structural invertebrates, historically overfished, and their conservation is currently a worldwide concern. However, the processes underlying their recovery are poorly known. Here, we examined harvesting effects and recovery mechanisms of red coral *Corallium rubrum* by analyzing long-term photographic series taken on two populations that were harvested. We compared the relative importance of reproduction and re-growth as drivers of resilience. Harvesting heavily impacted coral populations causing large decreases in biomass and strong size-class distribution shifts towards populations dominated by small colonies. At the end of the study (after 4 and 7 years) only partial recovery was observed. The observed general pattern of low recruitment and high mortality of new recruits demonstrated limited effects of reproduction on population recovery. Adversely, low mortality of partially harvested adults and a large proportion of colonies showing new branches highlighted the importance of re-growth in the recovery process. The demographic projections obtained through stochastic models confirmed that the recovery rates of *C. rubrum* can be strongly modulated depending on harvesting procedures. Thus, leaving the basal section of the colonies when harvesting to avoid total mortality largely enhances the resilience of *C. rubrum* populations and quickens their recovery. On the other hand, the high survival of harvested colonies and the significant biomass reduction indicated that abundance may not be an adequate metric to assess the conservation status of clonal organisms because it can underestimate harvesting effects. This study highlights the unsustainability of current harvesting practices of *C. rubrum* and provides urgently needed data to improve management practices that are still largely based on untested assumptions.

Citation: Montero-Serra I, Linares C, García M, Pancaldi F, Frleta-Valić M, Ledoux J-B, et al. (2015) Harvesting Effects, Recovery Mechanisms, and Management Strategies for a Long-Lived and Structural Precious Coral. PLoS ONE 10(2): e0117250. doi:10.1371/journal.pone.0117250

Academic Editor: Chaolun Allen Chen, Biodiversity Research Center, Academia Sinica, TAIWAN

Received: August 12, 2014

Accepted: December 19, 2014

Published: February 23, 2015

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: Support for this work was provided by a FPI grant (BES-2013-066150) to I. Montero-Serra and by a Ramon y Cajal research contract (RyC-2011-08134) to C. Linares. This study was partially funded by the Spanish Ministry of Economy and Innovation Biorock project (CTM2009-08045) and Smart project (CGL2012-32194). The authors are part of the Marine Conservation research group (2009 SGR 1174) from the Generalitat de Catalunya. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Overfishing is a major threat to the integrity of world's marine ecosystems. Historical exploitation of marine resources has resulted in drastic population declines, species extinctions and the general simplification of marine food webs [1], [2]. This structural impoverishment has also hindered the resilience of marine populations, lowering their ability to recover after recurrent natural and human disturbances [3], [4]. Understanding the ecological consequences of different extractive practices on the structure and function of populations, especially of those organisms exhibiting a long life span and slow dynamics, is therefore one of the greatest challenges in conservation biology [5].

Precious corals have been harvested and traded worldwide since ancient times due to the high economic value of their carbonate axial skeleton [6], [7], [8]. These sessile invertebrates are considered habitat forming species with a keystone role on coastal systems because they provide structural complexity and host high levels of biodiversity [9]. Additionally, they can enhance fisheries by providing shelter during early stages for some commercially important species of rock fishes, shrimps and crabs [10]. The red coral *Corallium rubrum* is a precious octocoral endemic to the Mediterranean rocky bottoms and adjacent Atlantic waters. Available data showed recent large declines in the Mediterranean yields, suggesting that this fishery is unsustainably managed following boom and bust cycles [11], [7]. Intensive harvesting has resulted in significant shifts in the size structure of current *C. rubrum* populations [12], [7], causing a decrease in biomass and mean and maximum colony size [13], [14]. Moreover, current warming and acidification trends associated to global change are major threats for shallow red coral populations [15], [16], [17], [18]. Consequently, there is a growing concern for the conservation of *C. rubrum* and the rest of the precious corals worldwide as evidenced by the recent struggle to include the Genus *Corallium* in the Appendix II of Cites [7], [19], [20], [21].

The need for a responsible fishery for *C. rubrum* and the negative effects of current practices are widely accepted [11], [21], [22]. However, given the fragility and vulnerability to different threats of this species, all studies addressing harvesting effects and recovery have been carried out by comparing size-class distribution of different populations and periods. [11], [23], [24], [25]. To date, biomass reduction has been only quantified once after a poaching event [26]. Beyond the reported shifts in size structures of *C. rubrum* populations [11], [24], sound field and experimental data on the effects of different extractive practices and the recovery process are essentially lacking in the literature.

Due to their low population dynamics and limited dispersal capacities [27], [28], precious corals are considered to have low resilience to disturbances that cause high adult mortality such as harvesting. Paradoxically, *C. rubrum* has not undergone extinction despite being exposed to intensive harvesting since ancient times. In fact, the biological processes underlying coral populations' persistence are largely unknown. The early maturity of *C. rubrum* (2.4 cm in height) corresponding to an age of 6–10 yr [29, 30], could partially explain this persistence. It allows the colonies to contribute to reproductive output before they reach the size of interest for harvesters. On the other hand, colonial organisms have the capacity to recover after events of partial mortality (e.g. breakage of a branch). Indeed, red coral colonies with signs of breakage and recent re-growth of new branches have been observed [29], [31]. The resilience to harvesting will therefore depend on two main mechanisms: (1) re-growth or clonal growth of colonies suffering partial mortality (i. e. when leaving the basal section) and (2) recruitment by sexual or asexual reproduction (i. e. when eradicating the whole colony). Yet, there is no assessment on the relative contribution to recovery of these two mechanisms from a long-term perspective. This assessment would provide a scientific basis for new management measures that enhance the sustainability of this natural resource.

In this study, we examined harvesting effects and the recovery processes of *C. rubrum* using 5–7 years photographic series on two populations located on the coast of Marseilles (France, NW Mediterranean). Fishermen unexpectedly harvested two *C. rubrum* populations that were already being studied by our research team and this represented a unique opportunity to establish before / after comparisons as well as to explore directly the recovery mechanisms by following individually affected as well as unaffected *C. rubrum* colonies. Our overall goal was to elucidate the demographic process underlying the recovery of *C. rubrum* after harvesting events with a particular focus on the relative contribution of re-growth of harvested colonies and reproduction. More precisely we quantified (1) survival and re-growth rates of harvested colonies, (2) survival of non-affected colonies and (3) recruitment rates and survival of recruits. Based on these data, we developed biomass projections to compare population trajectories under different harvesting practices. We contend that the results provide meaningful insights to inform new legislation measures to promote resilience and ensure the conservation of this threatened species and other precious corals also at deeper depths, where most of fishing efforts are concentrated and this type of data is more difficult to obtain.

Methods

1 Study Area

We monitored two Mediterranean red coral populations located along the rocky coast of Massif des Calanques in the SE of Marseilles, France. Due to the specific habitat characteristics of the area, such as submerged cavities and overhangs, along with instability of the water column during summer [32], the development of red coral populations at shallow depths (15–22m) is favored. The studied populations are located in a vertical wall at Riou Island (43° 10' 23.47" N i 5° 23' 13.24" E) (hereafter Riou) and in a cave-like tunnel at Maire Island (43°12'32.34"N; 5°20' 14.01"E) (hereafter Maire).

2 Coral Population Monitoring

In each population we monitored 30 quadrants (20 x 20 cm) by setting up 2 permanent plots using PVC screws fixed to holes in the rocky substratum. Each plot was variable in length, depending on the complexity of the substratum, and 40 cm wide. In each sampling, a cord was deployed between the screws and quadrats assembled with a scale were sequentially positioned and photographed above and below the cord throughout the length of each transect. Two photographs from each quadrat (using 2 slightly different angles, ~30°) were used for analysis with photogrammetric techniques which allowed measuring the height of colonies [33]. Transects were photographed using a NIKON D70 with a housing and 2 electronic strobes.

At Maire, permanent plots were installed at 15 m after a harvesting event was observed during June 2002 and monitored till 2009 but due to logistic constraints, pictures were not taken during 2007 and 2008. Colonies that suffered partial mortality were evident because fishermen remove the branches leaving a wide colony basis, short in height with injuries (naked tissue), that unequivocally belongs to an older red coral colony that was recently pruned. In contrast, at Riou the permanent plots were installed in 2005 just before the harvesting event. Between April and June 2006 fishermen were observed in the area and subsequent surveys clearly detected their impact in the permanent plots (Fig. 1).

Our study did not involve any sampling of or damage to red coral colonies. The authors had all the permits provided by the French authority Affaire Maritimes to perform scientific surveys in the study area.

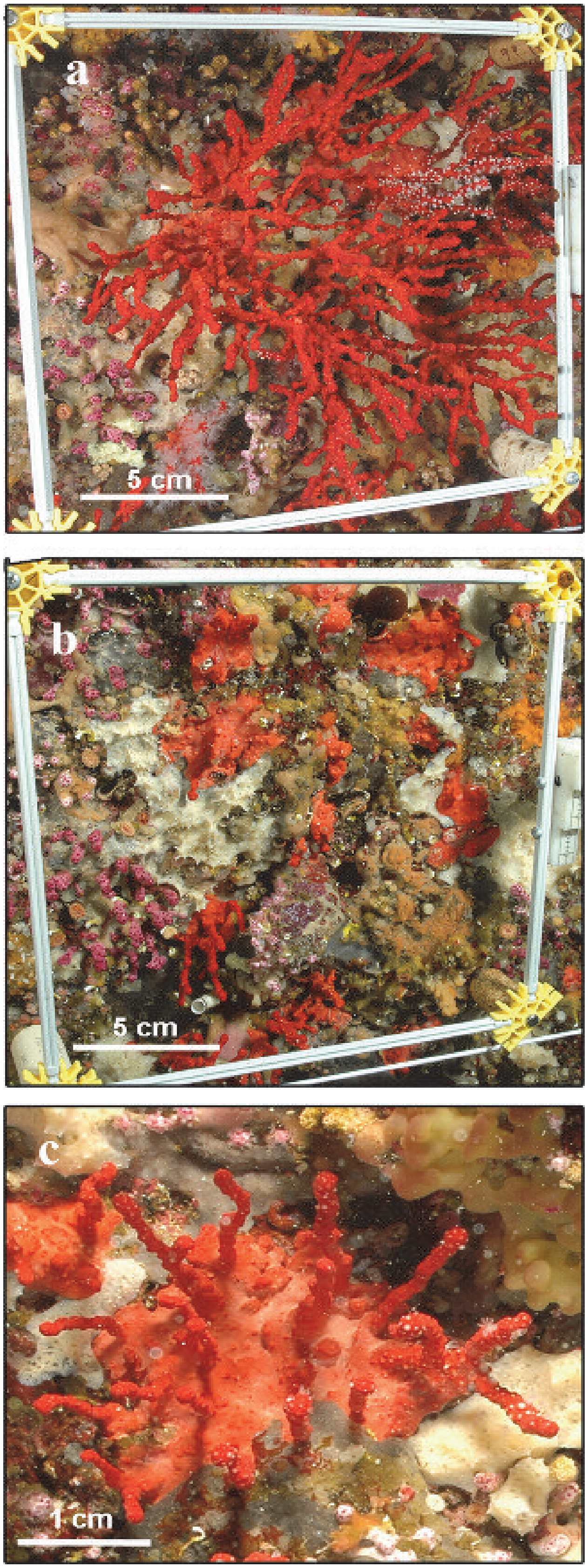

a
5 cm
b
5 cm
c
1 cm

Fig 1. Harvesting effects on red coral populations. Partial mortality at Riou is shown a) before and b) after a harvesting event. c) Detail of re-growth of new branches on a partially harvested colony. Photo credit: Medrecover (www.medrecover.org).

doi:10.1371/journal.pone.0117250.g001

3 Demographic parameters

From the photographic series, the harvested and non-harvested colonies were individually identified and compared year to year to estimate mortality rates, number of branches and colony height. We also estimated adult population density (colonies number per 400 cm^2) and recruitment rates. We considered a recruit the new button like colonies observed ranging from a minimum detection size of 2 mm to 10 mm in height. Annual recruitment rates were estimated as the number of recruits appearing for the first time in a photoquadrat and post-recruitment mortality were estimated by following these recruits through the study period.

With this dataset we were able to assess:

3.1 Changes in size-structure

To assess population size-structure changes and the recovery process, we measured maximum height of all colonies and classified them into five size classes (0–30mm; 30–60mm; 60–90mm; 90–120mm, $>$120mm). Riou population was measured before harvesting (2005), right after (2006) and four years after (2009). Maire population was measured right after harvesting (2002) and seven years after (2009). Biomass variations were estimated by applying a height-weight polynomial equation to height data. The equation was previously calculated from height and weight data measured on 300 dead red coral colonies collected in previous studies in the same region [35], and from different poaching events [26]. The resulting curve was: Weight (g) = 0.001(Height, mm)^2 + 0.096(Height, mm)—4.010 ($R^2 = 0.868$, $P < 0.001$) (S1 Fig.).

3.2 Recovery mechanisms

We quantified the cumulative survival probability of non-harvested adults, harvested adults, and new recruits based on annual mortality rates, calculated as follows:

$$m = \frac{\left(1 - \frac{N_t}{N_0}\right)}{\Delta_t} \tag{1}$$

where m is the annual mortality rate of *C. rubrum* colonies, N is the total number of colonies, and Δt is the duration of the study period. In addition we assessed the degree of recovery of affected colonies by quantifying the frequency of colonies showing new branches and the number of branches per colony during the study period.

4 Simulations of recovery process under different harvesting practices

To analyze whether recovery rates depend on harvesting practices in the long-term, we developed a set of basic stochastic demographic models under two different scenarios with contrasting levels of total (TM) and partial mortality (PM): a) removal of almost all colonies causing 90% TM and 10% PM; b) leaving the basal section in almost all colonies causing 10% TM and 90% PM. The second scenario was based on the observed mortality values at Riou (see results). The two scenarios were calculated by setting initial population densities according to the corresponding levels of total mortality. To run the model we used demographic parameters (adult density, annual recruitment rates, adult and post-recruitment mortality, and biomass increase rates per colony) obtained from the two monitored populations during the study period. The two harvesting scenarios were projected by running 100 stochastic simulations during 30 years according to the following steps:

First we estimated the changes in the number of colonies following the next formulation:

$$\begin{aligned} \mathrm{N}_{\mathrm{T(t)}} &= \mathrm{N}_{\mathrm{R(t)}} + \mathrm{N}_{\mathrm{A(t)}} \\ \mathrm{N}_{\mathrm{R(t)}} &= \mathrm{N}_{\mathrm{R(t-1)}}(1-g)(1-m_g) + r \\ \mathrm{N}_{\mathrm{A(t)}} &= \mathrm{N}_{\mathrm{A(t-1)}}(1-m_A) + \mathrm{N}_{\mathrm{R(t-1)}}g(1-m_R) \end{aligned} \tag{2}$$

where N_T is total population, N_R is total number of recruits, N_A is the total number of adults, m_R and m_A are annual mortality rate of recruits and adults respectively, r is the annual recruitment rate and g is the proportion of recruits growing to the adult stage:

$$g = \frac{G}{h_{\max} - h_{\min}} \tag{3}$$

where G is the recruit growth rate (2.5 mm · yr^{-1} in height, from reference [34]), $h_{\min}$ and $h_{\max}$ are the lower and upper height intervals for recruits.

Secondly, we estimated the evolution of biomass recovery using the biomass increases (ΔB) per colony and abundance values from the demographic models previously described. Mean (SD) biomass increases were estimated according to the next equations applied to colonies suffering partial mortality at Riou (n = 57) and Maire (n = 67) right after harvesting and 4 and 7 years after respectively:

$$\Delta B = \frac{1}{N}\sum_{i=1}^{N}\left(\frac{B_f - B_0}{\Delta_t}\right)_i \tag{4}$$

$$\mathrm{B}_{(\mathrm{t})} = \mathrm{NT}_{(\mathrm{t})}.\Delta B \tag{5}$$

where B_0 is the colony biomass right after harvesting, $\mathrm{B_f}$ is the total biomass at the end of the study period, Δt is the number of years, and NT is the total number of colonies in each population.

Results

1 Harvesting effects

Harvesting affected 30.1% of the colonies at Riou (n = 209) and 49.6% of the colonies at Maire (n = 139). At Riou, total mortality was around 9.5% and partial mortality was 90.5%, causing a large biomass loss with a 98.5% of reduction in total dry weight (Fig. 2). Harvesting targeted mainly medium and large colonies, triggering a dramatic size-distribution shift toward populations characterized by a large proportion of small colonies (Figs. 1 and 3A). At Maire, because the monitoring started after the harvesting event, we could not determine the loss of biomass nor the size-class distribution shift. Nonetheless, the same size-distribution pattern was observed after the harvesting event with no large colonies present and a great proportion of small-size colonies (Fig. 3B).

2 Temporal trends

Demographic parameters did not show large differences among sites. Mean annual density was 12.26 ± 0.80 colonies · 400 cm^{-2} at Riou (n = 30) and 11.36 ± 0.52 colonies · 400 cm^{-2} at Maire (n = 30). Densities were quite stable during the study period (S2 Fig.), and recruitment rates were low at both sites: 0.98 ± 1.40 (SD) colonies · 400 cm^{-2} at Maire and 0.21± 0.53 (SD) colonies · 400 cm^{-2} · yr^{-1} at Riou. Harvested colonies suffering from severe partial mortality did not show a differential "post affection" survival as they showed similar high values than unaffected

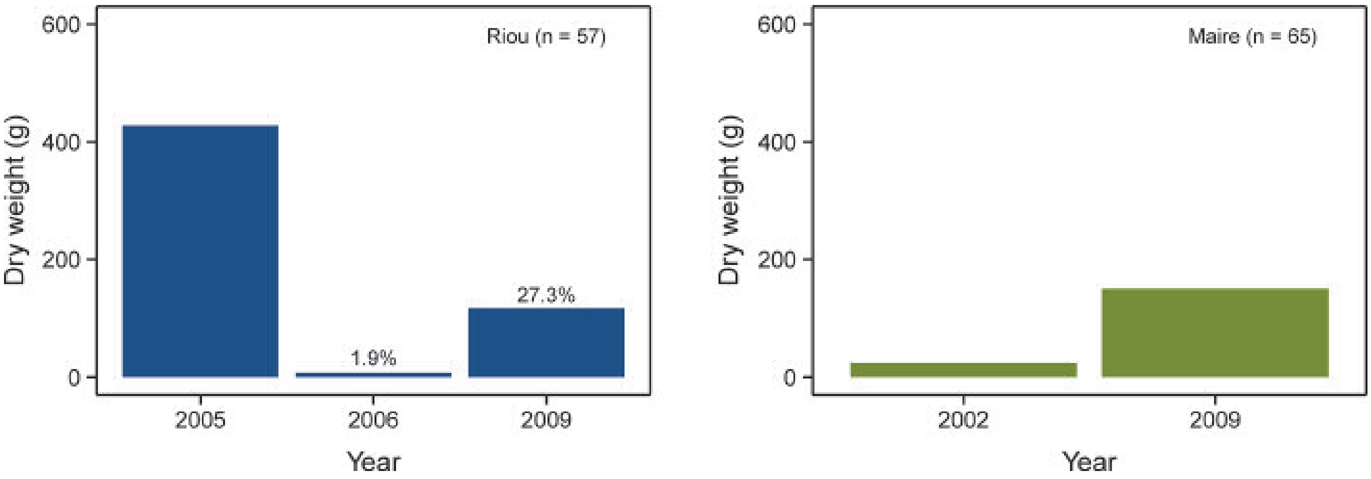


Fig 2. Biomass changes during the study period at (a) Riou and (b) Maire.

doi:10.1371/journal.pone.0117250.g002

colonies (Fig. 4A, 4B). This could explain the observed stability in adult density in both populations throughout the study period (S2 Fig.). Conversely, survival of recruits was very low and decreased rapidly at both populations (Fig. 4A and 4B).

3 Rate of recovery

The two studied red coral populations demonstrated very low rate of recovery. A small increase of biomass was observed at Riou after four years, representing 22% of the initial biomass recorded prior to the harvesting event (Fig. 2). A slight recovery was also observed by comparing size-class distribution from Riou and Maire populations after four and seven years respectively (Fig. 3). Despite a general increase in the proportion of medium size-classes, there was no recovery of the largest sizes (>100mm) and very little of colonies >80mm at Riou. At the end of the study, small colonies (0–60 mm) still represented a large proportion of the whole population (92% at Riou and 89% at Maire). Re-growth was observed in more than 75% of the harvested colonies after two years at Riou and four years at Maire (Fig. 4C). Mean number of branches in harvested colonies also increased quickly in both populations (Fig. 4D).

4 Recovery process simulations

Biomass simulations based on demographic projections showed that harvesting practices strongly influence the recovery process of *C. rubrum* populations. Harvesting practices in which the colony basis remains attached showed recovery times from 15 to 25 yr, whereas events causing total mortality (eradicating the whole colony) slowed down the recovery process, preventing the populations from recovering to initial conditions even 30 years after being harvested (Fig. 5). Riou population showed a slightly higher recovery rate than Maire population. However the influence of harvesting practices at slowing down the recovery rate when increasing total mortality was consistent for both populations (Fig. 5).

Discussion

This study provides new insights into the recovery mechanisms of a heavily exploited precious coral and illustrates how different harvesting practices can strongly modulate the recovery of affected populations. Our results also highlighted the detrimental effects of harvesting and the low rate of recovery displayed by these long-lived invertebrates.

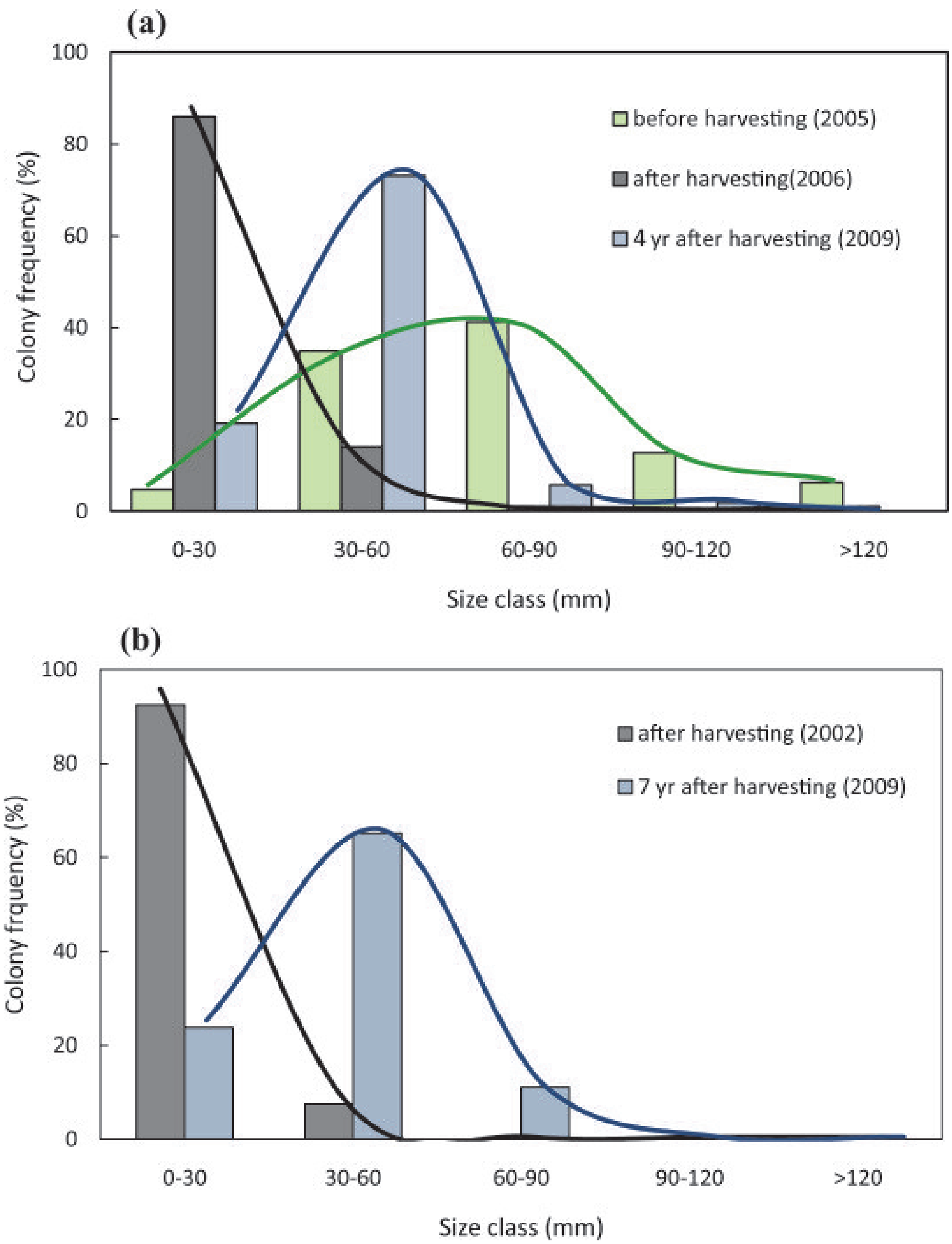


Fig 3. Size-distribution changes on harvested red coral populations. a) Size-distribution at Riou before harvesting, after harvesting, and four years after harvesting. b) Size-distribution at Maire after harvesting and seven years after harvesting.

doi:10.1371/journal.pone.0117250.g003

Harvesting heavily impacted red coral populations has led to drastic reductions of biomass and size-structure shifts towards populations dominated by small colonies. Although both populations still persisted at the end of the study period (after 4 and 7 years), they were far from initial conditions in terms of biomass and sizes. The slow recovery processes reported here confirms the long-lasting negative consequences of harvesting on slow-growing sessile organisms

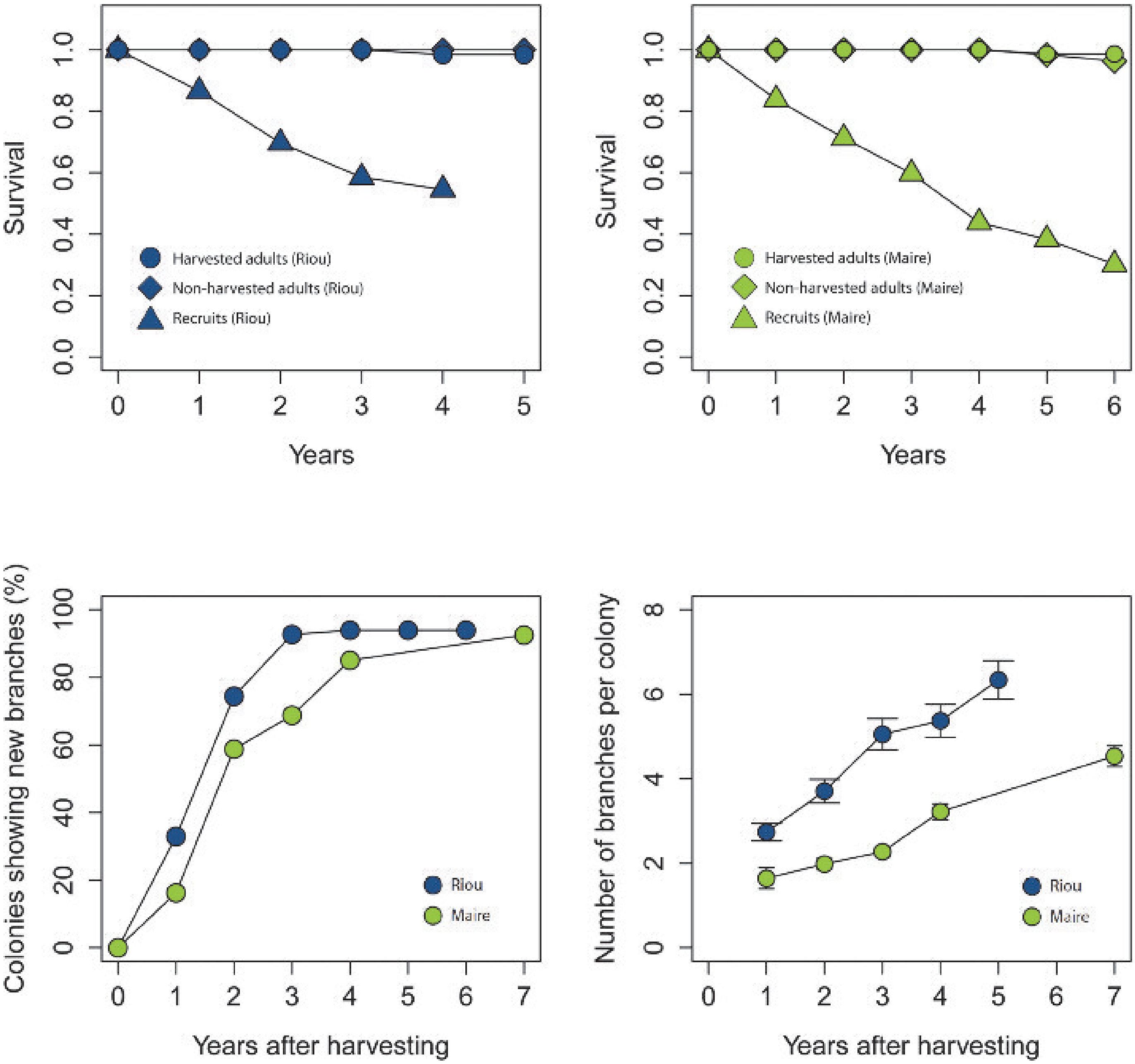


Fig 4. Demographic parameters estimated during the study period at Maire and Riou populations. Cumulative survival probability estimated at Riou (a) and Maire (b) for non-harvested colonies, harvested colonies, and recruits. (c) Temporal variation on the proportion of colonies showing new branches after fishing. (d) Temporal variation of mean (± SD) number of branches after harvesting.

doi:10.1371/journal.pone.0117250.g004

and indicates that extractive practices under the current legal framework are not sustainable from a long-term perspective [5].

We investigated the relative contribution of reproduction and re-growth of harvested colonies as drivers of recovery of red coral populations. The high survival of harvested colonies suffering partial mortality and fast growth of new branches demonstrated that re-growth plays a key role in recovery and persistence of *C. rubrum* (Fig. 4C, 4D). Similar to previous long-term studies conducted in French and Spanish localities [13], [26], the observed low recruitment rates and very low survival probability of new recruits suggest that recovery through reproduction is very limited (Fig. 4A, 4B). This demographic strategy is shared by other temperate gorgonian [36], and is concordant with life-history theory, which states that adult survival is inversely proportional to reproductive success [37]. Indeed, biomass simulations developed to compare different harvesting practices showed that when the whole colony is removed and thus reproduction is the main recovery mechanism, the process is much slower and it can take much more than 30 years to return to initial conditions pervious to harvesting. Conversely, when fishermen leave the basal section of the colonies recovery is enhanced through re-growth of new branches (Fig. 5). The biological reference point used in this study (size-class distributions at Riou prior to harvesting) does not represent an undisturbed population; therefore, recovery leading to pristine conditions would take longer periods than those reported here. Further, we must note that the models used here do not completely account for the complexity of demographic processes in long lived species. *C. rubrum* is characterized by a low dispersal that leads its populations to be generally self-seeding [27], [38], and breeding units seem also to be restricted in space, suggesting that density may play an important role in the reproduction of this species [28]. Thus, events causing total mortality on adult colonies could lower the potential for recovery even more through reproduction [40]. Alternatively, negative density-dependent processes affecting recruitment and post-recruitment survival were also reported in corals due to intra-specific competition and resources limitation (i. e. availability of suitable substrate to settle) [39]. Further research should therefore address these questions by applying more complex modeling techniques to long-term experimental data. However, the observed large and consistent differences on population trajectories depending on harvesting procedures revealed by our study represent an important first step in the characterization of the ecological consequences of different harvesting practices on *C. rubrum* populations.

Reported recent declines on the Mediterranean yields sparked a wide debate about the conservation status of *C. rubrum*. This discussion raised questions about the sustainability of this fishery and if this species should be categorized as threatened [7], [19], [20], [21], [41]. Our results show that populations demonstrate a high degree of persistence in terms of density due to high survival of affected colonies. This may explain the existence of red coral populations despite intensive harvesting during the past few centuries. Nevertheless, we emphasize the large reduction of biomass and the size-distribution shifts toward populations dominated by small colonies likely hindered their structural function. A general simplification of benthic communities may also have negative consequences for multiple trophic levels that use these habitats as shelter during early life-stages [10], [42]. This finding should be especially relevant for policy-makers. Indeed, abundance is a parameter commonly used by international organizations such as IUCN or CITES to categorize vulnerability levels in commercial species [7], [43]. However, our results challenge the suitability of abundance-based metrics to assess the conservation status of clonal (modular) organisms by showing that large declines in biomass due to partial mortality of colonies can remain masked. Furthermore, abundance measures do not reflect the reduction in reproductive potential caused by harvesting colonial organisms, which exhibit a size-based exponential increase in reproductive output [44]. The development of a new metric focused on size and biomass parameters is crucial to assess the conservation status of precious corals and to develop sustainable fisheries management plans.

On the other hand, benthic communities are currently facing multiple perturbations derived from the ongoing global change such as warming and ocean acidification [16], [17], [18], [45]. The precautionary principle accounting for potential synergistic effects of fishing and climate warming should thus be considered in these new regulations [15], [16], [46]. While climatic perturbations are generally diffuse and difficult to minimize, fishing restrictions on no-take areas can be useful tools at a local scale to enhance the resilience of sessile invertebrates through

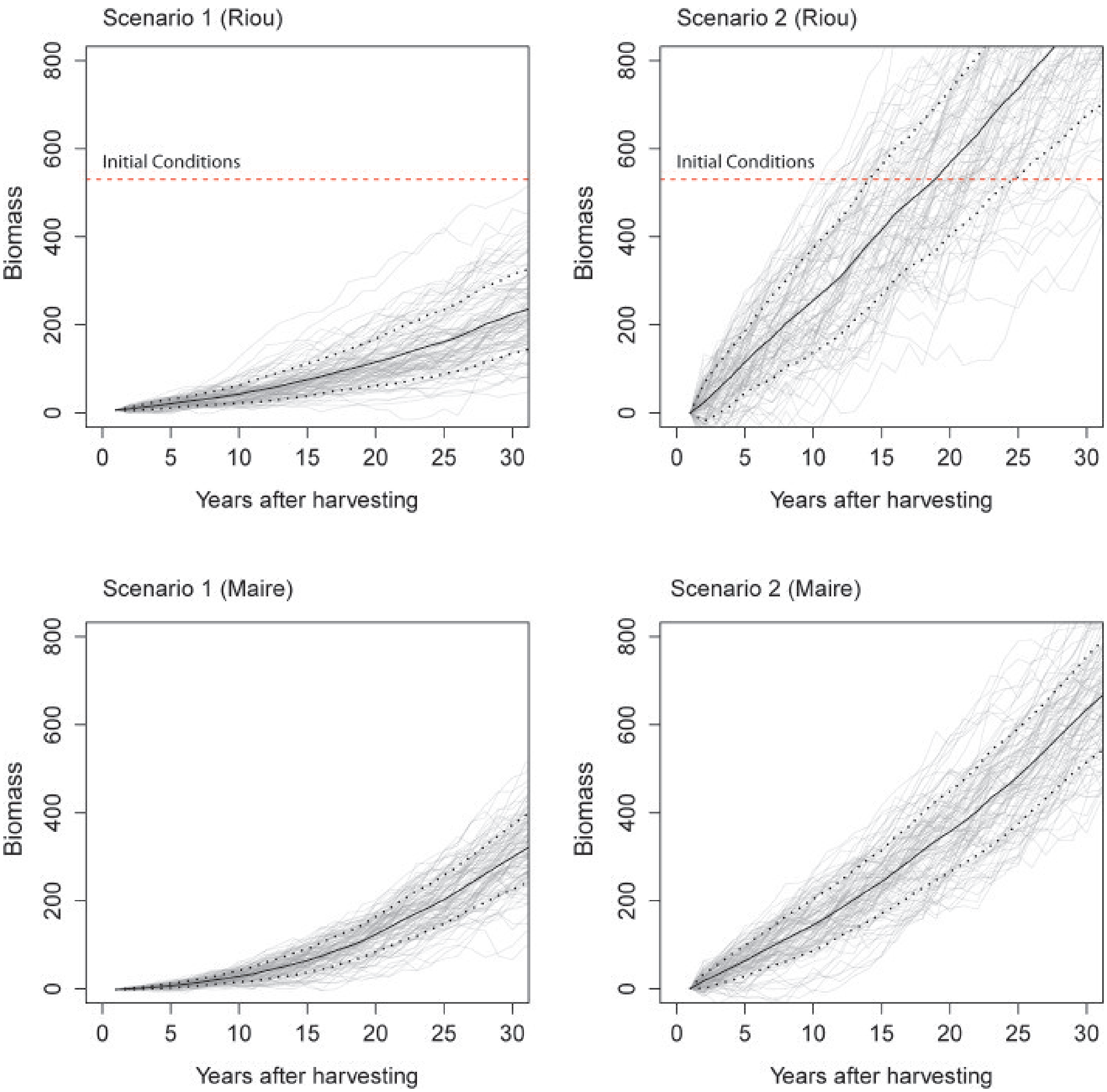


Fig 5. Biomass projections of red coral populations to compare different harvesting scenarios. Scenario 1) 90% total mortality and 10% partial mortality. Scenario 2) 10% total mortality and 90% partial mortality. Horizontal broken lines show initial conditions at Riou. Black lines represent the mean trend and dot lines the standard deviation (n = 100).

doi:10.1371/journal.pone.0117250.g005

increased larval production of large individuals [47]. MPAs also enhance the recovery of exploited populations in terms of biomass and size-structure [14], [26]. However given the low recruitment rates and limited dispersal of gorgonian larvae [27], it is unlikely that protected populations act as a source to exploited populations ensuring their long-term persistence [28]. Further, poaching and diving activities hinder the enhancement of coral populations' recovery within MPAs when regulations are not enforced [27]. Therefore, we should not just consider improving the actual network of MPAs but also moving towards a more restrictive legal framework outside of the protected areas. Several new regulations have been proposed during the last decades to improve *C. rubrum* fisheries, including the establishment of annual quotas and minimum harvesting sizes and the ban on using dredges. However, these current guidelines are still largely based on untested assumptions and have failed to improve the sustainability of coral fisheries [20]. For instance, a significant step was the recent recommendation on total ban on harvesting of *C. rubrum* populations under 50m depth [22], although poaching in shallow waters is still widespread and individual countries may avoid this prohibition by developing specific management plans. Rotating systems were also proposed for precious corals fisheries in the Pacific and the Mediterranean though there still is a large uncertainty around the recovery periods of affected populations [20]. Here, we show how red coral populations may take much more than three decades to recover and that total removal of colonies can significantly slow down this process further. Our approximations are consistent with previous studies conducted within French and Spanish MPAs where populations showed only partial recovery after 20 to 30 yrs of protection [11], [14], [26]. Additionally, there has been a recent development of new jewelry manufacturing processes that allow using small pieces of coral that can be ground to powder and mixed with epoxy or other substances [22]. This development worsens the effects of harvesting by targeting whole size ranges and including entire colonies. Recovery of populations affected by these new practices might be even more jeopardized since re-growth mechanisms are dramatically limited. Finally, this study highlights the importance of long-term ecological monitoring programs because they provide reliable data on key ecological processes such as the recovery patterns of natural populations after human-induced disturbances and enable the improvement of conservation strategies.

Supporting Information

S1 Fig. Height – weight relationship obtained from death corals (n = 300).
(TIF)

S2 Fig. Annual adult densities at the study sites.
(TIF)

Acknowledgments

We acknowledge the support of all the people that helped us with the photographic surveys during all the years. The authors are part of the Marine Conservation Research Group (2009 SGR 1174) from the Generalitat de Catalunya.

Author Contributions

Conceived and designed the experiments: CL JG. Performed the experiments: CL JG JBL FZ. Analyzed the data: IMS MG FP MFV DM PD CL JG. Contributed reagents/materials/analysis tools: IMS CL PD JG. Wrote the paper: IMS CL JBL JG.

References

1. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1988) Fishing down marine food webs. Science 279: 860–863
2. Jackson JBC, Kirby MX, Beger WH, Bjorndal KA, Botsford LW, et al. (2001) Historical Overfishing and the recent collapse of coastal ecosystems. Science 293: 629–637 PMID: 11474098

3. Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551 PMID: 17801530
4. Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, et al. (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933 PMID: 12920289
5. Lotze HK, Coll M, Margera AM, Ward-Paige C, Airoldi L (2011) Recovery of marine animal populations and ecosystems. Trends in Ecology and Evolution 26(11): 595–605 doi: 10.1016/j.tree.2011.07.008 PMID: 21852017
6. Grigg RW (2008) Resource Management of Precious Corals: A Review and Application to Shallow Water Reef Building Corals. Marine Ecology 5(1), 57–74
7. Brukner AW (2009) Rate and extent of decline in Corallium (pink and red coral) populations: existing data meet the requirements for a CITES Appendix II listing. Marine Ecology Progress Series 397: 319–332
8. Tsounis G, Rossi S, Grigg RW, Santangelo G, Bramanti L, et al. (2010) The Exploitation and Conservation of Precious Corals. Oceanography and Marine Biology: An Annual Review 48: 161–212
9. Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends in Ecology and Evolution 13: 316–321 PMID: 21238320
10. Husebø A, Nøttestad L, Fosså JH, Furevik DM, Jørgensen SB (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471: 91–99
11. Tsounis G, Rossi S, Gili JM, Arntz WE (2007) Red coral fishery at the Costa Brava (NW Mediterranean): Case study of an overharvested precious coral. Ecosystems 10: 975–986
12. Santangelo G, Abbiati M, Giannini F, Cicogna F (1993) Red coral fishing trends in the western Mediterranean Sea. Scientia Marina 57: 139–143
13. Garrabou J, Harmelin JG (2002) A 20-year study on life-history traits of a harvested long-lived temperate coral in the NW Mediterranean: insights into conservation and management needs. Journal of Animal Ecology 71: 966–978
14. Linares C, Bianchimani O, Torrents O, Marschal C, Drap P, et al. (2010) Marine Protected Areas and the conservation of long-lived marine invertebrates: the Mediterranean red coral. Marine Ecology Progress Series 402: 69–79
15. Garrabou J, Perez T, Sartoretto S, Harmelin JG (2001) Mass mortality event in red coral (Corallium rubrum, Cnidaria, Anthozoa, octocorallia) populations in the provence region (France NW Mediterranean). Marine Ecology Progress Series 207: 263–272
16. Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné, et al. (2009) Mass mortality events in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Global Change Biology 15(5): 1090–1103
17. Bramanti L, Movilla J, Guron M, Calvo E, Gori A, et al. (2013) Detrimental effects of ocean acidification on the economically important Mediterranean red coral (*Corallium rubrum*). Global Change Biology 19 (6): 1987–1908
18. Cerrano C, Cardini U, Bianchelli S, Corinaldesi C, Pusceddu A, et al. (2013) Red coral extinction risk enhanced by ocean acidification. Scientific Reports 3: 1457 doi: 10.1038/srep01457 PMID: 23492780
19. Bruckner AW (2010) Quantifying the decline in Corallium rubrum populations: Reply to Santangelo & Bramanti (2010). Marine Ecology Progress Series 418: 299–303
20. Bruckner AW (2014) Advances in management of precious corals in the family Corallidae: are new measures adequate? Current Opinion in Environmental Sustainability 7: 1–8
21. Tsounis G, Rossi S, Bramanti L, Santangelo G (2013) Management hurdles for sustainable harvesting of Corallium rubrum. Marine Policy 39: 361–364
22. Cau A, Cannas R, Sacco F, Follesca MC (2013) Adaptive management plan for red coral (*Corallium rubrum*) in the GFCM competence area. FAO, Rome doi: 10.1016/j.jfo.2013.06.003 PMID: 25632406
23. García-Rodriguez M, Massò C (1986) Estudio biomètrico de poblaciones del coral rojo (Corallium rubrum L.) del litoral de Gerona (NE de Espana). Bolletin del Instuto Español de Oceanografía 3: 61–64
24. Abbiati M, Buffoni G, Caforio G, Di Cola G, Santangelo G (1992) Harvesting, predation and competition effects on a red coral population. Netherlands Journal of Sea Research 30: 219–228
25. Bavestrello G, Bo M, Bertolino M, Betti F, Cattaneo-Vietti R (2014) Long-term comparison of structure and dynamics of the red coral metapopulaion of the Portofino Promontory (Ligurian Sea): a case study for a Marine Protected Area in the Mediterranean Sea. Marine Ecology doi: 10.1111/maec.12235
26. Linares C, Garrabou J, Hereu B, Diaz D, Marschal C, et al. (2012) Assessing the effectiveness of marine reserves on unsustainably harvested long-lived sessile invertebrates. Conservation Biology 26: 88–96 doi: 10.1111/j.1523-1739.2011.01795.x PMID: 22098377

27. Ledoux J- B, Garrabou J, Bianchimani O, Drap P, Feral JP, et al. (2010) Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, Corallium rubrum. Molecular Ecology 19: 4204–4216 doi: 10.1111/j.1365-294X.2010.04814.x PMID: 20854271

28. Ledoux J-B, Mohktar-Jamai K, Robi C, Peral J-P, Garrabou J, et al. (2010). Genetic survey of shallow populations of the Mediterranean red coral [*Corallium rubrum* (Linnaeus, 1758)]: new insights into evolutionary processes shaping nuclear diversity and implications for conservation. Molecular Ecology, 19, 675–690 doi: 10.1111/j.1365-294X.2009.04516.x PMID: 20074314

29. Torrents O, Garrabou J, Marschal C, Harmelin JG (2005) Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) in the Marseilles area (France, NW Mediterranean). Biological Conservation 121: 391–397

30. Gallmetzer I, Haselmair A, Velimirov B (2010) Slow growth and early sexual maturity: Bane and boom for the red coral *Corallium rubrum*. Estuarine, Coastal and Shelf Science. 90: 1–10

31. Hereu B, Linares C, Zabala M (1999). Avaluació de l'impacte de l'episodi de corall vermell (*Corallium rubrum*) de la zona protegida de les Illes Medes detectat durant l'hivern del 2000. In: Seguiment temporal de les Illes Medes (1999) Informe técnic per al Departament de Medi Ambient, Generalitat de Catalunya

32. Bensoussan N, Romano JC, Harmelin JG, Garrabou J (2010) High resolution characterization of northwest Mediterranean coastal waters thermal regimes: to better understand responses of benthic communities to climate change. Estuarine, Coastal and Shelf Science 87:431–441

33. Drap P, Merad D, Mahiddine A, Seinturier J, Gerenton P, et al. (2013) Automating The Measurement Of Red Coral In Situ Using Underwater Photogrammetry And Coded Targets. Paper presented at the XXIV International CIPA Symposium, Strasbourg, France. Pierre Grussenmeyer (Ed.), Vol.:XL-5/W2, pp.231–236

34. Bramanti L, Magagnini G, De Maio L, Santangelo G (2005) Recruitment, early survival and growth of the Mediterranean red coral *Corallium rubrum* (L 1758), a 4-year study. Journal of Experimental Marine Biology and Ecology 314: 69–78

35. Torrents O (2007) Biologie des populations du corail rouge *Corallium rubrum* (L. 1758) de Méditerranée nord–occidentale. PhD Thesis. Université de la Méditerraneé Aix-Marseille II

36. Linares C, Doak D, Coma R, Diaz D, Zabala M (2007) Life history and viability of a long-lived marine invertebrate: the octocoral *Paramunicea clavata*. Ecology 88: 918–928 PMID: 17536708

37. Heppell SS, Caswell H, Crowder LB (2000) Life histories and elasticities patterns: perturbation analysis for species with minimal demographic data. Ecology 81: 654–665

38. Costantini F, Fauvelot C, Abbiati M (2007) Fine-scale genetic structuring in *Corallium rubrum* (l): evidences of inbreeding and limited effective larval dispersal. Marine Ecology Progress Series 340: 109–119

39. Vermeij MJA, Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population ecology. Ecology. 89(7): 1994–2004 PMID: 18705385

40. Lasker HR (2013) Recruitment and Resilience of a Harvested Caribbean Octocoral. PLoS ONE 8(9): e74587 doi: 10.1371/journal.pone.0074587 PMID: 24040291

41. Santangelo G, Bramanti L (2010) Quantifying the decline in *Corallium rubrum* populations. Marine Ecology Progress Series 418: 295–297

42. Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69: 373–386

43. IUCN (2014) IUCN Red list of threatened species. Version 2013.2. Available: http://www.iucnredlist.org/ Accessed February 2014

44. Santangelo G, Carletti E, Maggi E, Bramanti L (2003) Reproduction and population sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. Marine Ecology Progress Series 248: 99–108

45. Coma R, Ribes M, Serrano E, Jiménez E, Salat J, et al. (2009) Global warming-enhanced stratification and mass mortality events in the Mediterranean Proceedings of the National Academy of Sciences USA 106(15): 6176–6181 doi: 10.1073/pnas.0805801106 PMID: 19332777

46. Torrents O, Tambutte E, Caminiti N, Garrabou J (2008) Upper thermal thresholds of shallow vs. deep populations of the precious Mediterranean red coral *Corallium rubrum* (L.): assessing the potential effects of warming in the NW Mediterranean. Journal of Experimental Marine Biology and Ecology 357: 7–19

47. Micheli F, Saenz-Arroyo A, Greenley A, Vazquez L, Espinoza-Montes JA, et al. (2012) Evidence That Marine Reserves Enhance Resilience to Climatic Impacts. PLoS ONE 7(7): e40832 doi: 10.1371/journal.pone.0040832 PMID: 22855690

Conservation Letters
A journal of the Society for Conservation Biology
Open Access

LETTER

Accounting for Life-History Strategies and Timescales in Marine Restoration

Ignasi Montero-Serra[1], Joaquim Garrabou[2,3], Daniel F. Doak[4], Laura Figuerola[1], Bernat Hereu[1], Jean-Baptiste Ledoux[2,5], & Cristina Linares[1]

[1] Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Avda. Diagonal 643, 08028 Barcelona, Spain
[2] Institut de Ciències del Mar, CSIC, Passeig Marítim de la Barceloneta 37–49, 08003 Barcelona, Spain
[3] Mediterranean Institute of Oceanography (MIO), UM 110 CNRS/IRD, Aix Marseille Universite, Universite de Toulon, Campus de Luminy-Oceanomed, Batiment Mediterranee, 13288 Marseille, Cedex 09, France
[4] Environmental Studies Program, University of Colorado at Boulder, Boulder, CO, 80309, USA
[5] CIIMAR/CIMAR, Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Rua dos Bragas 177, 4050–123 Porto, Portugal

Keywords
Comparative demography; coral reefs; *Corallium rubrum*; integral projection models; life-history tradeoffs; octocorals; restoration; Mediterranean sea; transplants.

Correspondence
Ignasi Montero-Serra, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Avda. Diagonal 643, 08028 Barcelona, Spain.
E-mail: monteroserra@gmail.com

Received
29 March 2016
Revised
20 December 2016
Accepted
28 December 2016

doi: 10.1111/conl.12341

Abstract

Understanding the drivers of restoration success is a central issue for marine conservation. Here, we explore the role of life-history strategies of sessile marine species in shaping restoration outcomes and their associated timescales. A transplantation experiment for the extremely slow-growing and threatened octocoral *Corallium rubrum* was highly successful over a relatively short term due to high survival and reproductive potential of the transplanted colonies. However, demographic projections predict that from 30 to 40 years may be required for fully functional *C. rubrum* populations to develop. More broadly, a comprehensive meta-analysis revealed a negative correlation between survival after transplanting and growth rates among sessile species. As a result, simulated dynamics for a range of marine sessile invertebrates predict that longer recovery times are positively associated with survival rates. These results demonstrate a tradeoff between initial transplantation efforts and the speed of recovery. Transplantation of slow-growing species will tend to require lower initial effort due to higher survival after transplanting, but the period required to fully recover habitat complexity will tend to be far longer. This study highlights the important role of life history as a driver of marine restoration outcomes and shows how demographic knowledge and modeling tools can help managers to anticipate the dynamics and timescales of restored populations.

Introduction

Marine coastal ecosystems host high levels of biodiversity and provide goods and services to a large proportion of the world’s human population (Palumbi *et al.* 2008). The cumulative effects of multiple stressors such as overfishing, habitat destruction, and pollution together with new global threats (i.e., climate change and biological invasions) have driven compositional changes, local extinctions, and wholesale destruction of many benthic communities (Jackson *et al.* 2001; Airoldi & Beck 2007). To face this challenge, actions at both global (i.e., reduction of greenhouse gas emissions) and local levels are urgently needed (Kennedy *et al.* 2013). At local scales, fishery regulations and marine protected areas can help to reduce or remove threats (Edgar *et al.* 2014). Even so, when the resilience of natural systems has been seriously diminished, active restoration may be necessary as a complementary tool to restore damaged populations and communities (Possingham *et al.* 2015).

Over the last few decades, the success of ecological restoration efforts in terrestrial landscapes has improved dramatically, with successful examples of enhancing ecosystem structure and function, and the provision of ecosystem services (Benayas *et al.* 2009; Perrings *et al.* 2015). In the marine realm, however, restoration approaches have generally been successful only at very small spatial scales and continue to present many challenges (Edwards & Gomez 2007; Rinkevich 2015). Strikingly, the degree of success in marine restoration actions is not generally related to the underlying costs of the project (Bayraktarov *et al.* 2016). This is partly due to the high methodological constraints, but also due to relatively poor understanding of the drivers underlying successful actions.

Habitat-forming species such as corals and seagrasses have been the primary targets of marine restoration activities, and transplanting asexually produced units (i.e., coral fragments or seagrass shoots) has been proposed as the tool of choice for recovering habitats by bypassing sensitive early life stages (Edwards & Clark 1998). Recently, research has shown that corals display high survival rates after transplanting when compared to the dominant organisms found in seagrass beds, oyster reefs, or saltmarsh ecosystems (Bayraktarov *et al.* 2016). However, this generalization ignores the high diversity in life-history strategies of the dominant species in these benthic communities (Darling *et al.* 2012; Madin *et al.* 2014). Indeed, life-history tradeoffs between demographic rates have been observed in hard coral species, suggesting potential effects on short-term and long-term restoration success (Edwards & Clark 1998; Dizon & Yap 2006; Glassom & Chadwick 2006). Yet, quantitative evidence of how the life history of target species shapes restoration outcomes is lacking in the scientific literature. To advance the theoretical framework of marine restoration and provide tools to enhance the effectiveness of transplantation efforts, we need to go beyond habitat type toward a fuller quantitative analysis of how life-history patterns determine the best strategies or allow better prediction of the speed and eventual success of restoration efforts.

To date, most studies of transplant success in marine systems have focused on survival rates of transplanted individuals over relatively short monitoring periods (usually less than 2 years) (Bayraktarov *et al.* 2016). However, a broad goal of restoration efforts is to recover structural complexity that can provide ecosystem services at rates similar to natural ones. Thus, when planning restoration actions, managers should consider the factors affecting the time required from any transplantation action to reach the restoration goals for the target species and habitat. Long-term monitoring programs can provide suitable data to inform this issue, but funding often constrains the duration of monitoring after restoration actions and experiments (Precht & Robbart 2006; Lindenmayer & Likens 2009). Demographic modeling methods such as matrix and integral projection models (IPMs) (Morris & Doak 2002; Ellner & Rees 2006) can be used to synthesize individual data into predictions of the longer term development of transplanted populations (Linares *et al.* 2008).

In the present study, we combined demographic monitoring of transplanted and natural colonies of a temperate coral species, a comprehensive literature review of tradeoffs in the life histories of sessile marine species, and the use of population projection models to explore the dynamics of transplant efforts targeting species with different life histories. Our results support the utility of explicitly linking life-history theory to marine restoration and provide an illustrative example of anticipating the expected dynamics and timescales of restored ecosystems.

Methods

Study system

The precious red coral *Corallium rubrum* is a structural octocoral of a highly diverse coralligenous assemblage of the Mediterranean Sea and also possesses important cultural and economic value. Due to historical overexploitation, most shallow populations of *C. rubrum* can be considered functionally impaired and many are ecologically extinct (Bruckner 2009; Tsounis *et al.* 2010). To reverse this situation, an international agreement urged Mediterranean countries to strengthen their *C. rubrum* fishery regulations during the last decade (Cau *et al.* 2013). Unfortunately, the lack of enforcement of regulations on coral harvesting along with poaching is widespread across the Mediterranean basin and represents a major problem for the management of the species, hindering the effectiveness of its conservation (Linares *et al.* 2012).

Study area and transplant experiment

In 2011, the Catalan authorities intercepted 14.5 kg of illegally harvested *C. rubrum* along the Montgrí Coast (Catalonia, Spain). About 300 red coral colonies, a small portion of the intercepted colonies, were selected for a transplant experiment. These colonies were initially kept at 16 °C and fed in aquarium facilities at the Institute of Marine Sciences in Barcelona (Spain). After 1 week, the colonies were transported in coolers to the Parc Natural del Montgrí, Illes Medes i Baix Ter in the NW Mediterranean and transplanted onto a rocky wall ranging from 15 to 17 m depth using a two-component epoxy putty as glue. The site was chosen because some sparse red coral colonies were found in the vicinity, indicating its suitability for the species (Figure 1).

Demographic traits

Four transects were established within the transplanted population and surveyed through photographic sampling after transplantation, in May 2011, and again in

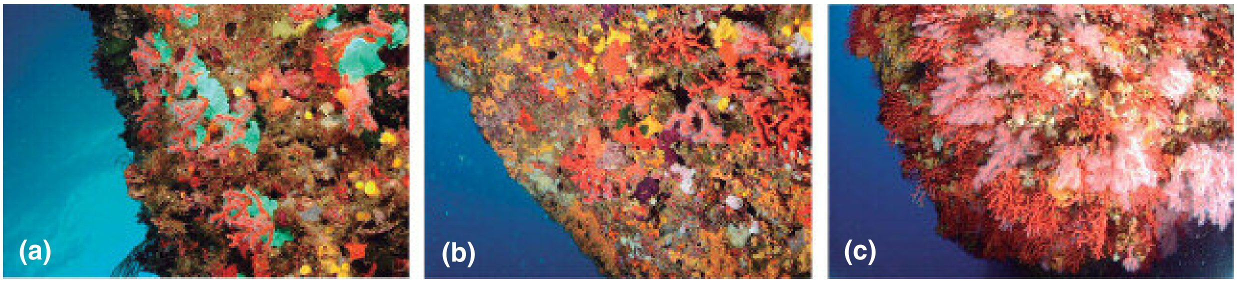


Figure 1 Restoration of *Corallium rubrum* populations. (a) A new population was transplanted in 2011; (b) most transplanted colonies survived in 2015, after 4 years of transplantation; and (c) natural well-protected *C. rubrum* populations with large colonies were used as a baseline to assess the time periods required for restoration actions. Images: J. Garrabou.

May 2015 (Figure 1). Survival rates of the transplanted colonies were quantified by individually identifying coral colonies from the photographic series from 2011 and 2015. Natural survival rates of *C. rubrum* colonies were calculated from long-term data on eight natural populations. (See Supplementary Methods for a complete description of surveys.) Reproductive potential of colonies was estimated for a sample of transplanted colonies ($n = 35$) outside the monitored transects and from a natural adjacent population ($n = 35$) in late June of 2015 by counting *C. rubrum* larvae found inside the polyps of the fertile female colonies (Tsounis *et al.* 2006). Samples were collected by SCUBA diving and fixed in 4% fromaldehyde. At the laboratory, 15 polyps per sample were dissected and larvae found inside the polyps were counted.

Literature review

We explored life-history tradeoffs in marine restoration experiments following two steps. First, we systematically reviewed all transplantation experiments of marine sessile species that we could identify in a search of the literature up to November 2015. Using *Google Scholar*, we searched for a combination of the terms "restoration," "transplantation," or "rehabilitation" with a second term related to marine sessile taxa: "coral," "gorgonian," "sponge," "macroalga," or "seagrass." We then selected those studies that conducted experimental transplants as a restoration technique and reported survival rates at least 1 year after transplanting.

We also compiled data on growth rates of sessile marine species since this vital, or demographic, rate is highly correlated to overall life history (Darling *et al.* 2012). We searched available studies reporting standard data on linear extension rates to approximate average species-specific growth rates for corals (Madin *et al.* 2016). In seagrasses, mean horizontal rhizome elongation rates were used as an indicator of the species growth rate (see Marbà & Duarte 1998); thus, seagrass and sessile invertebrates were analyzed separately.

Demographic projections

Red coral

To synthesize data on growth, survival, and reproduction into predictions of population growth and increasing sizes within populations, we used IPMs parameterized with long-term demographic data from several natural red coral populations. Full description of data analysis and model construction are given in the Supplementary Material S1. Based on annual IPMs, we computed 1,000 stochastic projections assuming that all annual models can occur with equal probability at each time-step. Maximum height of transplanted colonies was measured in 2015 using photogrammetric techniques (Drap *et al.* 2013) and the distribution of heights was used to establish the starting population vector for the projections.

Linares *et al.* (2010) argue that the structural complexity of *C. rubrum* populations can assessed by quantifying the proportion of large colonies (>100 mm), since these larger colonies provide structural complexity. Based on this parameter, we compared the outputs from our population projections to the proportion of large colonies in three relatively unimpacted *C. rubrum* populations that are located within old and well-enforced Mediterranean marine protected areas (Figure 1 & S1, Linares *et al.* 2010).

Comparative analyses

We also searched the literature for published matrix population models of other marine sessile species. We then used these models to perform deterministic population projections of 100 individuals starting at the smallest size class and computing time periods until the population reached a proportion of large individuals (largest size

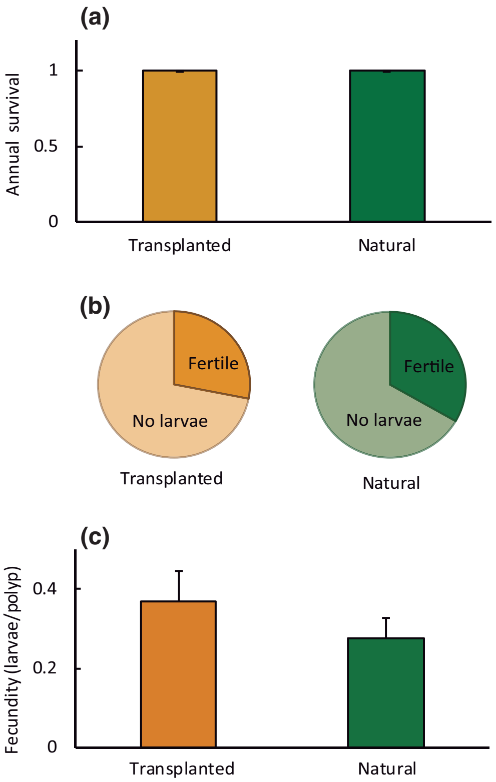


Figure 2 Demographic traits in transplanted and natural *C. rubrum* populations. (a) Mean annual survival rates; (b) proportion of fertile colonies; and (c) mean polyp fecundity, calculated as the frequency of larvae found per polyp within fertile colonies.

class) equivalent to the 20% and 80% of the expected proportion when reaching the stable stage distribution.

Results

Demographic traits of *C. rubrum* transplanted colonies

After 4 years, 99.1% of transplanted *C. rubrum* colonies were still alive. Annual survival rates of transplanted colonies did not show significant differences from control populations (Figure 2a). Transplanted colonies also had similar reproductive potential to colonies in natural populations, considering both the proportion of fertile colonies and the frequency of larvae per polyp (Figure 2b & c).

Comparative survival and growth in transplant experiments/actions

We found 50 studies that allow calculation of mean annual survival rates after at least 1 year following transplanting for a total of 59 marine structural species (Figure 3a). These included 40 species of hexacorals, which have a mean annual survival of 60.8% (range of 6.8–98.6%); five species of gorgonians, including the present study, with mean annual survival of 48.1 (range of 30.0–99.1%); one species of sponge, with mean annual survival of 85.7%; 11 species of seagrasses, with mean annual survival of 42.5% (range of 28.9–69.2%), and two seaweeds, with mean annual survival of 43.1% (range of 25.1–80.0%). We observed a significant negative correlation between survival after transplantation and the species mean growth rates measured under natural conditions in marine sessile invertebrates (Figure 3b; $n = 35$; Pearson's $r = 0.47$, $P = 0.005$; Spearman rho = 0.37, $P = 0.046$). Seagrass species revealed a parallel pattern (Figure 3c; $n = 8$; Spearman rho = 0.81, $P = 0.022$), although the relationship was only marginally significant according to Pearson's correlation (Pearson's $r = -0.69$; $P = 0.059$). Growth data measured in natural and transplanted colonies for coral species were also highly correlated (Figure S3, $n = 17$; Pearson's $r = 0.85$; $P < 0.001$).

Demographic projections and recovery periods

Red coral

The transplanted population in 2015 was dominated by small individuals (most red coral colonies were < 35 mm in height, Figure 1 & S1), while natural red coral colonies had extremely low growth rates (Figure S2). The stochastic IPMs incorporating these traits showed that a period ranging from 30 to 40 years after transplanting is needed for populations to have a proportion of large colonies comparable to that seen in the well-preserved *C. rubrum* populations used as an ecological reference (Figure 4).

Comparative analyses

The simulated recovery periods for 41 marine sessile species were highly variable in length, ranging from years to several decades (Figure 5 & Table S3). The expected recovery length was strongly and positive associated with the species' mean survival rate regardless of the conservation goal ($n = 41$; 20% threshold: $R^2 = 0.419$; $P < 0.001$; 80% threshold: $R^2 = 0.495$; $P < 0.001$). After accounting for potential artifacts due to different matrix dimensions, mean survival rates were still a strong predictor of the expected recovery periods (Table S1).

Discussion

Marine restoration is a relatively young discipline with most efforts only operating at very small spatial scales (Bayraktarov *et al.* 2016). Filling knowledge gaps on the processes underlying restoration success is therefore

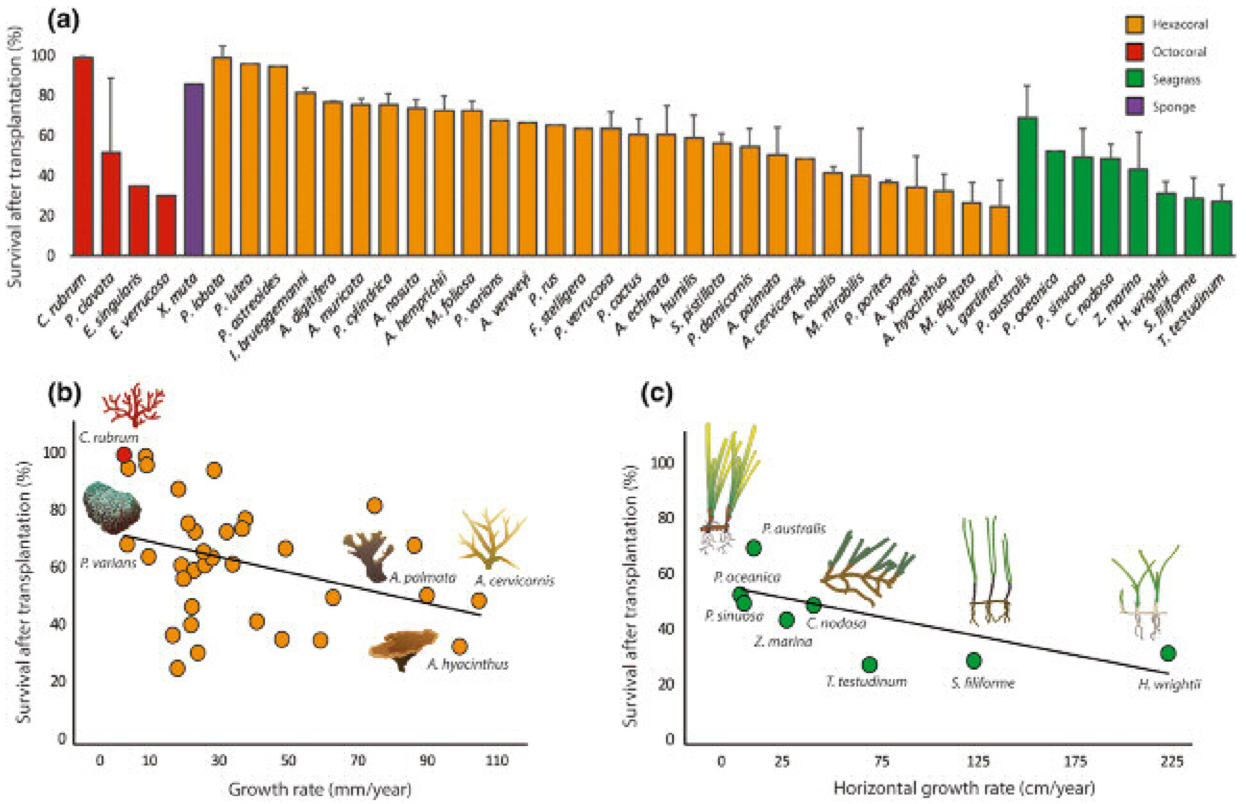


Figure 3 Survival rates of marine sessile species in transplant experiments. (a) Mean annual survival rates (Mean ± SE). (b) Life-history tradeoff between survival after transplantation and growth rates in 35 marine sessile invertebrate species and (c) life-history tradeoff between survival after transplantation and growth rates in eight seagrass species. Each dot represents a species for which mean annual survival after transplantation and mean growth rate could be calculated from a range of published studies (see Table S1). In seagrass species, growth represents mean horizontal rhizome elongation rate (see Marbà & Duarte 1998). Images: Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

crucial to help further develop this field and ensure meaningful planning and success over larger spatial and temporal scales. In this study, we quantify the role of life history in shaping restoration outcomes and demonstrate a consistent tradeoff between survival and growth across different taxa with contrasting life history and functional traits, which in turn drives a tradeoff between required minimal transplantation effort at the start of a project and the minimum possible speed of ecosystem recovery.

Anticipating mortality patterns after transplantation is central to the design of any restoration action since it may determine the initial attaching effort required to achieve specific conservation goals. Here, a systematic review of transplantation experiments from tropical and temperate habitat-forming species revealed a negative tradeoff between growth and survival after transplantation that was supported in spite of differences in experimental techniques and physical properties of the environment that were not explored (Figure 3b). Slow growing massive hard corals such as *Porites astreoides* and *P. lutea* and the sponge *Xestospongia muta* showed the highest survival after transplantation, with rates ranging from 86% to 98%. On the contrary, fast-growing corals such as *Acropora cervicornis*, *A. yongei*, and *A. palmata* had survival rates that ranged from 35% to 44%. These results were consistent with previous transplant experiments in tropical coral species with contrasting life histories (Edwards & Clark 1989; Dizon & Yap 2006). Similarly, among seagrasses, the three slow-growing *Posidonia* species showed higher shoot survival after transplantation (from 49% to 69%) compared to faster growing *Syringodium filiforme* (29%) and *Halodule wrightii* (27%) (Figure 3c). Our findings are in agreement with allocation theory, which predicts that tradeoffs between vital rates such as growth, reproduction, and survival may arise from energetic constraints acting at physiological levels (Stearns 1989). Further, branching morphologies associated with faster life histories may increase exposure to physical damage and result in higher mortality rates (Madin *et al.* 2014).

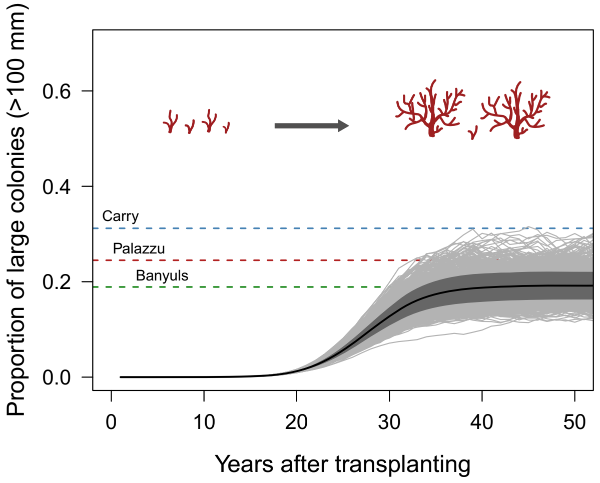


Figure 4 (a) Predicted temporal dynamics of the *C. rubrum* population size frequency distribution. Black line represents the mean and shaded area represents the standard error of 1,000 stochastic projections. The size frequency distribution of three natural and well-protected *C. rubrum* populations (dotted lines) was used as an ecological baseline (Linares *et al.* 2010).

There are also a number of external drivers that can strongly influence restoration success such as predation and herbivory, density of transplants, and catastrophic events (Shaish *et al.* 2010; Gomez *et al.* 2014). In spite of the clear importance of these effects, our results show that species' life histories can still provide strong predictive power concerning the outcome of transplantation projects. Better understanding of both the intrinsic and extrinsic drivers of mortality patterns after transplantation would be ideal and could lead to the implementation of more successful restoration designs, since this combined approach can better define both anticipated time periods for restoration and also the relative benefits of direct transplantation effort.

There have been major international calls to ban the international trade in precious coral and to implement management regulation aimed to ensure the conservation of these species (Bruckner 2014). Yet, the feasibility of restoration actions for these emblematic species has remained uncertain and this may hinder the potential for development of future restoration plans. In the present study, we observed that the colonies of the octocoral *C. rubrum* were extremely resistant to the stress of transplantation, displaying high survival rates similar to those in natural populations (Figure 2a, Garrabou & Harmelin 2002). It is remarkable to observe this high survival rate in transplanted *C. rubrum* colonies that were subject to the stresses of being harvested, kept out of the water in the poachers' nets, transported, maintained in aquaria for 1 week, and then transplanted back into natural habitat. Yet, these transplanted *C. rubrum* colonies had a similar proportion of fertile colonies and even higher frequency of larvae per polyp after 4 years than observed for colonies in natural populations (Figure 2b & c). Assessing reproductive potential is also critical when working with most marine sessile species which, like *C. rubrum*, show limited larval dispersal and

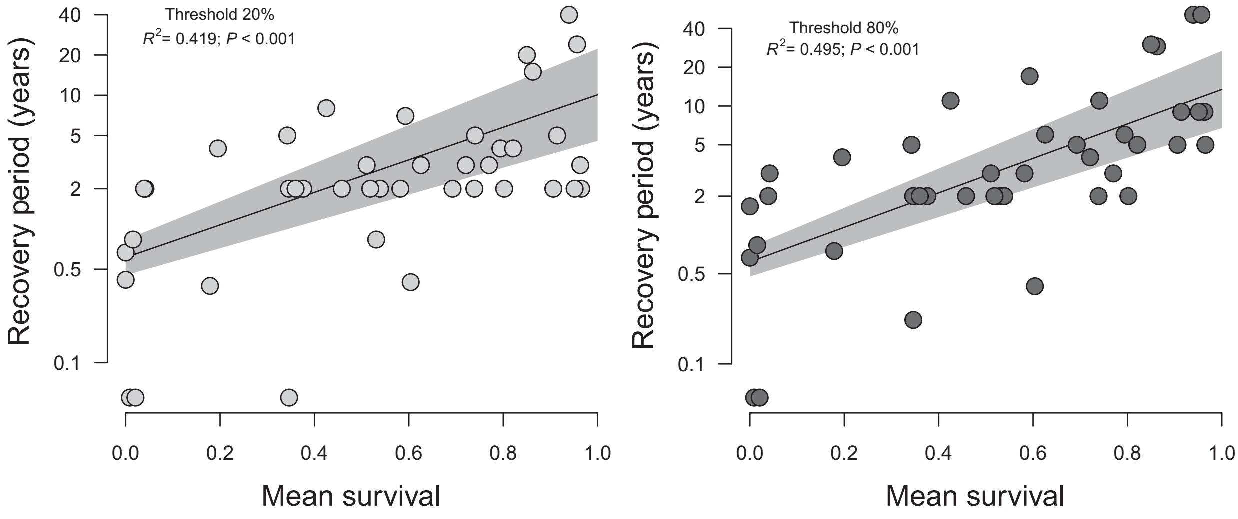


Figure 5 Projected recovery times for 41 marine sessile invertebrate species using published matrix populations models (Table S3) and setting a recovery threshold of (left) 20% and (right) 80% of the number of large colonies expected in a population at the stable stage distribution. The black lines and the shaded areas correspond to the mean and standard errors of the linear models (Table S1).

high self-recruitment rates (Ledoux *et al.* 2010). Indeed, to effectively recuperate populations through a single transplantation effort, newly restored populations must also be viable in the long term, with reproduction reaching natural rates. Here, the high survival and reproductive potential displayed by transplanted *C. rubrum* confirmed the potential success of this restoration action and strongly support the feasibility of these techniques, at least at local spatial scales, with potential applications for other long-lived precious coral species.

As important as choosing a suitable species and restoration method is considering the appropriate time scale and ecological baselines over which to evaluate restoration outcomes or to expect the restoration of ecological functions (Bull *et al.* 2014). Stochastic projections developed here revealed that periods ranging from 30 to 40 years may be necessary for newly established *C. rubrum* populations to show a colony size distribution comparable to those observed in well-preserved natural populations (Linares *et al.* 2010). These results suggest that, similar to relatively fast-growing terrestrial forest systems (Vesk *et al.* 2008), long-lived coral stands can take up to several decades to recover their functionality and to allow the development of associated organisms, such as fish and invertebrates, as may occur in tropical coral reefs (e.g., Cabaitan *et al.* 2008). More interestingly, we found that potential recovery periods can be accurately predicted by the specific mean survival, demonstrating the strong influence of the species' life histories on the temporal scales associated with restoration actions (Figure 5).

Overall, this study demonstrates a tradeoff between initial transplantation effort needed to achieve a target density of individuals and the speed of recover that may be achieved in a restoration action. For instance, targeting fast-growing species such as *A. cervicornis or A. hyacinthus* (with survival rates ranging from 40% to 50%) will require a twofold to threefold initial amount of attached colonies to obtain the same density of survivors compared to actions targeting slow-growing-resistant species such as the red coral *C. rubrum* or the massive coral *P. lutea*. On the other hand, life histories of the target species will also have a strong effect on the expected recovery periods that may vary as much as 20–30 years (Figure 5). Finally, because life history and functional traits are highly correlated (Adler *et al.* 2014), favoring specific strategies can have long-term consequences for habitat complexity and ecosystem responses to global change (Ortiz *et al.* 2014).

Acknowledgments

The authors thank the Agents Rurals de Catalunya for their invaluable work against red coral poaching. We are indebted to A Lorente for his support. We thank E Aspillaga and L Navarro for field assistance. P Capdevila, A Gori, K Kaplan, A Medrano, and two anonymous reviewers provided valuable comments on the manuscript. Funding was provided by the Spanish MINECO (CTM2009-08045 and CGL2012-32194), the Oak Foundation, the TOTAL Foundation Perfect Project, and the European Union's Horizon 2020 research and innovation programme under grant agreement No 689518 (MERCES). This output reflects only the author's view and the European Union cannot be held responsible for any use that may be made of the information contained therein. IMS was supported by a FPI grant (BES-2013-066150), CL by a Ramon y Cajal (RyC-2011-08134), and JBL by a Postdoctoral grant (SFRH/BPD/74400/2010). Authors are part of the Medrecover group (2014SGR1297).

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Population size frequency distribution of the transplanted colonies represented by the brown bars and the brown line.

Figure S2. Size-dependent growth of *C. rubrum* colonies based on data from two natural populations.

Figure S3. Growth rates in natural versus transplanted coral colonies (log-scale) for 17 coral species.

Table S1. Summary statistics for the linear model fitted to the expected recovery periods.

Table S2. Source data of survival in transplant experiments and growth references of the marine sessile species included in the comparative analysis.

Table S3. Source data of population matrix models used to project potential recovery periods.

References

Adler, P.B., Salguero-Gómez, R., Compagnoni, A. *et al.* (2014). Functional traits explain variation in plant life history strategies. *Proc. Natl. Acad. Sci. U. S. A.*, **111**(2), 740-745.

Airoldi, L. & Beck, M.W. (2007). Loss, status and trends for coastal marine habitats of Europe. *Oceanogr. Mar. Biol. Annu. Rev.*, **45**, 345-405.

Bayraktarov, E., Saunders, M.I., Abdullah, S. *et al.* (2016). The cost and feasibility of marine coastal restoration. *Ecol. App.*, **26**(4), 1055-1074.

Benayas, J.M.R., Newton, A.C., Diaz, A. & Bullock, J.M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science*, **325**(5944), 1121-1124.

Bruckner, A.W. (2009). Rate and extent of decline in *Corallium* (pink and red coral) populations: existing data meet the requirements for a CITES Appendix II listing. *Mar. Ecol. Prog. Ser.*, **397**, 319-332.

Bruckner, A.W. (2014). Advances in management of precious corals in the family Corallidae: are new measures adequate? *Curr. Opin. Environ. Sustain.*, **7**, 1-8.

Bull, J.W., Gordon, A., Law, E.A. *et al.* (2014). Importance of baseline specification in evaluating conservation interventions and achieving no net loss of biodiversity. *Conserv. Biol.*, **28**, 799-809.

Cabaitan, P.C., Gomez, E.D. & Aliño, P.M. (2008). Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. *J. Exp. Mar. Biol. Ecol.*, **357**(1), 85-98.

Cau, A., Cannas, R., Sacco, F. & Follesa, M.C. (2013). *Adaptive management plan for red coral (Corallium rubrum) in the GFCM competence area*. FAO, Rome.

Darling, E.S., Alvarez-Filip, L., Oliver, T.A. *et al.* (2012). Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.*, **15**, 1378-1386.

Dizon, R. & Yap, H. (2006). Effects of coral transplantation in sites of varying distances and environmental conditions. *Mar. Biol.*, **148**, 933-943.

Drap, P., Merad, D., Mahiddine, A. *et al.* (2013). Automating the measurement of red coral in situ using underwater photogrammetry and coded targets. *XXIV International CIPA Symposium*. Strasbourg, France. Vol.:XL-5/W2, pp. 231-236.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J. *et al.* (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, **506**(7487), 216-220.

Edwards, A.J. & Clark, S. (1998). Coral transplantation: a useful management tool or misguided meddling? *Mar. Pollut. Bull.*, **37**, 474-448.

Edwards, A.J. & Gomez, E.D. (2007). Reef restoration concepts and guidelines: making sensible management choices in the face of uncertainty. *Coral Reef Targeted Research & Capacity Building for Management Programme*. St Lucia, Australia. 38 pp.

Ellner, S.P. & Rees, M. (2006). Integral projection models for species with complex demography. *Am. Nat.*, **167**(3), 410-428.

Garrabou, J. & Harmelin, J.G. (2002). A 20-year study on life-history traits of a harvested long-lived temperate coral in the NW Mediterranean: insights into conservation and management needs. *J. Anim. Ecol.*, **71**, 966-971.

Glassom, D. & Chadwick, N.E. (2006). Recruitment, growth and mortality of juvenile corals at Eilat, northern Red Sea. *Mar. Ecol. Prog. Ser.*, **318**, 111-122.

Gomez, E.D., Cabaitan, P.C., Yap, H.T. & Dizon, R.M. (2014). Can coral cover be restored in the absence of natural recruitment and reef recovery? *Rest. Ecol.*, **22**(2), 142-150.

Jackson, J.B.C., Kirby, M.X., Beger, W.H. *et al.* (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629-637.

Kennedy, E.V., Perry, C.T., Halloran, P.R. *et al.* (2013). Avoiding coral reef functional collapse requires local and global action. *Curr. Biol.*, **23**(10), 912-918.

Ledoux, J.-B., Garrabou, J., Bianchimani, O. *et al.* (2010). Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, *Corallium rubrum. Mol. Ecol.*, **19**, 4204-4216.

Linares, C., Bianchimani, O., Torrents, O. *et al.* (2010). Marine protected areas and the conservation of long-lived marine invertebrates: the Mediterranean red coral. *Mar. Ecol. Prog. Ser.*, **402**, 69-79.

Linares, C., Coma, R. & Zabala, M. (2008). Restoration of threatened red gorgonian populations: an experimental and modelling approach. *Biol. Conserv.*, **141**, 427-437.

Linares, C., Garrabou, J., Hereu, B. *et al.* (2012). Assessing the effectiveness of marine reserves on unsustainably harvested long-lived sessile invertebrates. *Conserv. Biol.*, **26**, 88-96.

Lindenmayer, D.B. & Likens, G.E. (2009). Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends Ecol. Evol.*, **2**, 482-486.

Madin, J.S., Anderson, K.D., Andreasen, M.H. *et al.* (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Sci. Data*, **3**, Article number: 160017.

Madin, J.S., Baird, A.H., Dornelas, N. *et al.* (2014). Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecol. Lett.*, **17**, 1008-1015.

Marbà, N. & Duarte, C. (1998). Rhizome elongation and seagrass clonal growth. *Mar. Ecol. Prog. Ser.*, **174**, 269-280.

Morris, W.F. & Doak, D.F. (2002). *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

Ortiz, J.C., Bozec, Y.M., Wolff, N.H. *et al.* (2014). Global disparity in the ecological benefits of reducing carbon emissions for coral reefs. *Nat. Clim. Change*, **4**(12), 1090-1094.

Palumbi, S.R., Sandifer, P.A., Allan, J.D. *et al.* (2008). Managing for ocean biodiversity to sustain marine ecosystem services. *Front. Ecol. Environ.*, **7**, 204-211.

Perrings, M.P., Sandish, R.J., Price, J.N. *et al.* (2015). Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere*, **6**(8), 1-25.

Possingham, H.P., Bode, M. & Klein, C.J. (2015). Optimal conservation outcomes require both restoration and protection. *PLoS Biol.*, **13**(1), e1002052.

Precht, W. F., & Robbart, M. (2006). Coral reef restoration: the rehabilitation of an ecosystem under siege. Coral reef restoration handbook. Taylor and Francis, Boca Raton, 1–24.

Rinkevich, B. (2015). Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? *Curr. Opin. Environ. Sustain.*, **7**, 28-36.

Shaish, L., Levy, G., Katzir, G. & Rinkevich, B. (2010). Employing a highly fragmented, weedy coral species in reef restoration. *Ecol. Eng.*, **36**(10), 1424-1432.

Stearns, S.C. (1989). Trade-offs in life-history evolution. *Funct. Ecol.*, **3**, 259-268.

Tsounis, G., Rossi, S., Aranguren, M. *et al*. (2006). Effects of spatial variability and colony size on the reproductive output and gonadal development cycle of the Mediterranean red coral (*Corallium rubrum* L.). *Mar. Biol.*, **148**(3), 513-527.

Tsounis, G., Rossi, S., Grigg, R. *et al*. (2010). The exploitation and conservation of precious corals. *Oceanogr. Mar. Biol. Annu. Rev.*, **48**, 161-212.

Vesk, A.P., Nolan, R., Thomson, J.R. *et al*. (2008). Time lags in provision of habitat resources through revegetation. *Biol. Conserv.*, **141**(1), 174-186.