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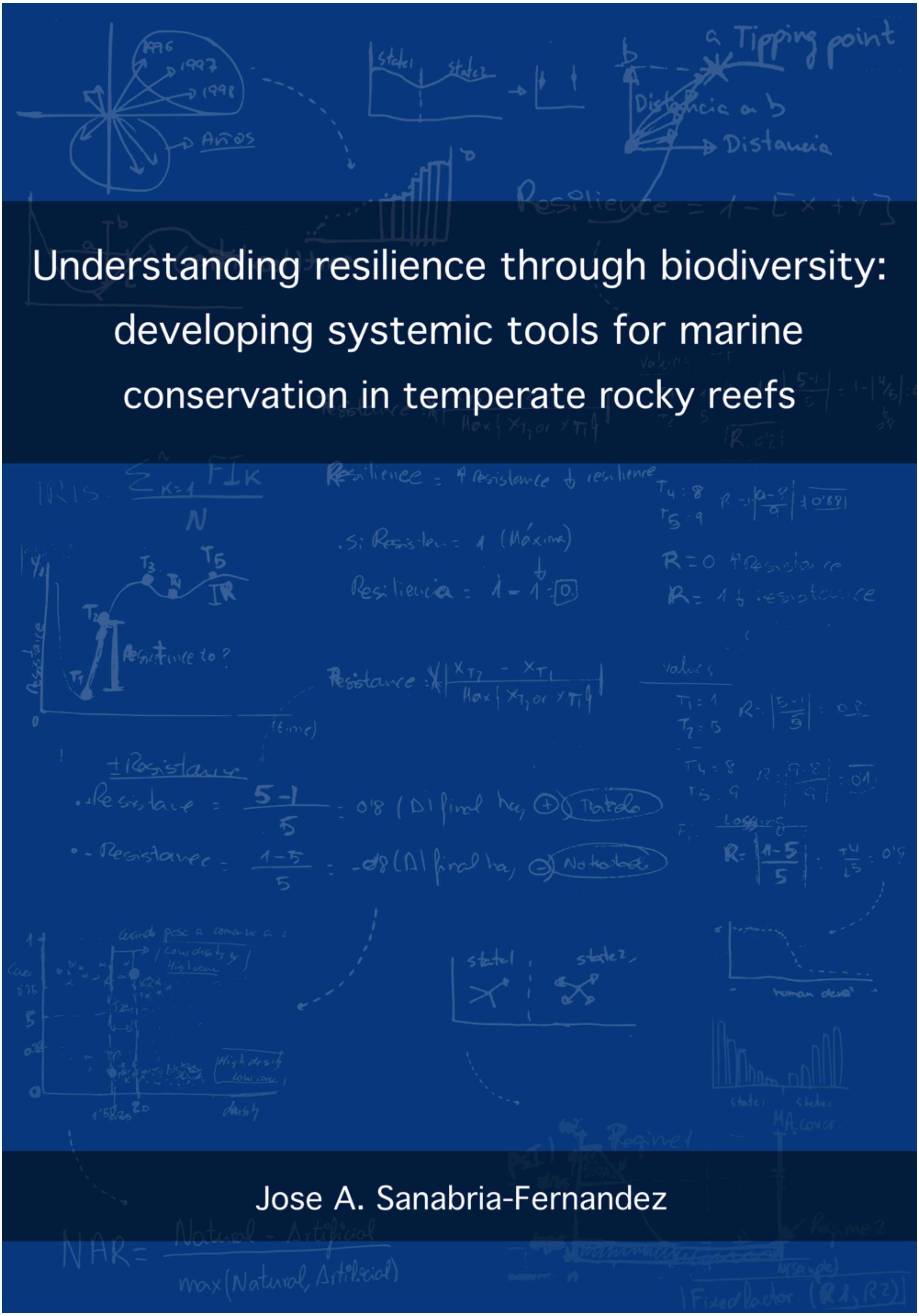
Understanding resilience through biodiversity: developing systemic tools for marine conservation in temperate rocky reefs

José Antonio Sanabria Fernández



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Sanabria-Fernandez, J.A., 2021. Understanding resilience through biodiversity: developing systemic tools for marine conservation in temperate rocky reefs. Doctoral thesis. Universidad de Barcelona. 234 pp.

Cover design by Jose A. Sanabria-Fernandez. Cover and back cover created from research notes taken throughout the thesis.

UNIVERSITAT DE BARCELONA

Facultad de Biología
Departamento de Biología Evolutiva, Ecología y Ciencias Ambientales
Programa de doctorado en Biodiversidad (HDK04)
Conservación y Gestión de la Biodiversidad

Understanding resilience through biodiversity: developing systemic tools for marine conservation in temperate rocky reefs

Entendiendo la resiliencia a través de la biodiversidad: desarrollando herramientas sistémicas para la conservación marina de los arrecifes rocosos templados

Memoria presentada por Jose A. Sanabria-Fernandez para optar al grado de doctor por la Universidad de Barcelona

Jose A. Sanabria-Fernandez
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Blanes, septiembre 2020

El tutor de la tesis,

Mikel Becerro
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La tutora de la tesis,

Creu Palacín Cabañas
Universidad de Barcelona

A las tres mujeres de mi vida,
madre, hermana y compañera de vida

Agradecimientos

Hace escasos días tuve la suerte de leer en los agradecimientos de cierto trabajo final de master que La gratitud en silencio no sirve a nadie, compartiendo totalmente esa opinión comezaré a escribir el útimo y más difícil apartado de la tesis, los agradecimientos.

Indiscutiblemente gracias a la persona que me ha enseñado los valores más humanos y me ha convertido en lo que hoy en día soy. Me has enseñado a poner toda la fuerza, voluntad y esmero en todo aquello que hago. A combatir contra una y mil adversidades únicamente con mis manos. A perseverar y sacar lo mejor de mi en el más arduo de los escenarios, superándome día tras día. Y, me has enseñado que a la vez que se te cierra una puerta, tu puedes abrir ventanas. Y todo ello me lo has ido enseñando en los felices y también difíciles escenarios vividos a lo largo de los años. Gracias por tu titánico esfuerzo y por elaborar con tus propias manos la oportunidad de mis estudios universitarios. Gracias mamá, eres la persona más fuerte que jamás he conocido, además de ser un ejemplo a seguir. Me has enseñado todo aquello que no se puede aprender. Por todo ello me siento infinitamente afortunado y orgulloso de ser tu hijo.

A mi hermana, siempre dispuesta a dar la opinión más realista y como bien dice ella, sin anestesia sobre la realidad. Gracias, por que sé que siempre estás ahí o allí, pero estás. Porque a veces he estado presente pero a la vez ausente. Eres un ejemplo de valentía por la lucha de tu sueño. Te he animado, te animo y te animaré a que continues perseverando, porque antes de lo que crees, lo conseguirás! Pero recuerda, al tfm le queda en último empujón!

También quiero alzar la mirada hacía las dos estrellas que más brillan del filmamento y hacerles saber que este logro, también, es de ellos, a mi abuela Glória y mi abuelo Antonio.

A la persona que pone cordura a mis locuras (aunque se te escape alguna :-P). Compañera de este viaje llamado vida, tengo la suerte de compartir contigo este maravilloso camino. Hemos atravesado juntos la etapa de la tesis, prácticamente 5 añitos, en los cuales hemos perseverado por conseguir nuestro sueño. También, me has ayudado a crecer en el aspecto crítico, gracias a tus key questions, que son capaces de desmontar *(casi) cualquier idea jajaja. Además, ha sido una etapa sumamente bonita en la cual hemos disfrutado y crecido como pareja, además de compartir burbujas en cada uno de los rincones del globo visitados. Prácticamente, en estos años, hemos vivido en siete ciudades de tres países, no esta nada mal, pero creo que el futuro viene aún mejor ☺. Gracias por esa visión pragmática y crítica que busca llegar al máximo en todo lo que haces, sin olvidarte del proyecto que mantenemos día a día, codo a codo y, sonrisa a sonrisa. También, agradecer a la familia política (incluyendo los residentes en Argentina), el apoyo y ánimos constantes!. En definitiva, gracias por soportar innumerables conversaciones sobre la bolita de la resiliencia y enhorabuena por esa pedazo de tesis que te has marcado, olé!*

Pepito, hace años me enseñaste una de las lecciones más importantes que he aprendido nunca y es que la familia no siempre lleva la misma sangre. Eres un ejemplo de perseguir y conseguir tu sueño. Para aquellos que no tengan el placer de conocer a Pepe, le dedicaré unas breves palabras. Es una persona que en la mismísima Legión Española te apodaron Hulk (básicamente porque estas más fuerte que un limón y eres más grande que un ropero de cuatro puertas), lamentablemente, amigo, te dire que por muy grande que te pongas, nunca, tendrás cabida para albergar el enorme corazón que tienes.

Indudablemente, gracias a tod@s aquellos amig@s que me han acompañado en estos años, Isi, Enrique, Alberto, López (y familia), Marquez (y familia), Romero (y familia), Pija (y familia), Alejandra, Maria José, Borja (esto se acaba ya!), Lidia, Cubetita.

También agradecer a Mikel el tiempo cedido, conocimiento compartido y las conversaciones telefónicas, que en su mayoría acababan con la síntesis de que debíamos randomizar los datos. Además, aprendí que en R se puede hacer todo, aunque la puesta en escena fuese "compleja". Gracias por todos estos años que culminan con esta tesis. También en Blanes, tuve la oportunidad de trabajar con Laurita de Úbeda (recuerda que al agua siempre hay que ir temprano) y María (¿un photoquadrat más?), que compartimos, junto con Natali, buenos momentos ☺. En Blanes residen Rafa y Ana, ambos siempre dispuestos a ayudarnos, en todo lo que hiciese falta sin dudarlo. En relación al CEAB, gracias al Patrón (Ferrán), porque siempre has estado dispuesto a hacer fácil lo difícil, además de apoyarnos en las campañas que hemos realizado. Al mejor informático, Ramón, la persona con más don para los ordenadores, siempre resuelve el problema. También *gracias a Ángel, por la disposición y ayuda prestada en la elaboración de estructuras experimentales. Y por supuesto, muchísimas gracias a Emma, Carmela, Marta, Margarita, Concha, Kenny, Maribel y Roger.*

A lo largo de la tesis tuve la fortuna de formar parte del Departamento de Química-Física de la Universidad de Cádiz, bajo la dirección del Dr. Jesús Forja. En aquel departamento me enseñaron desde el primer día un aspecto desconocido para mi en ciencia "la calidad humana del equipo", algo que no se puede aprender de ningún paper. Sin duda, mi paso por Cádiz, fue un punto de inflexión (positivo) en mi formación, quiero agradecer a todo el equipo, la paciencia por tener a un biólogo en el lab. Especialmente gracias a Jesús, Dori (siempre con una sonrisa y dispuesta a ayudar), Lalo, Rocío, Vivian (Sheriff, gracias por tus ánimos y consejos), también gracias a Valentina, Lola, Ana, Sandra, Bea y Jairo. Recuerdo con una gran sonrisa las campañas oceanográficas en la Bahía de Cádiz, Gualdalquivir, Guadalete, Guadiana y Tinto y Odiel. Hábeis conseguido que un sevillano logre entender la diferencia entre Gadita y Beduino!

En Cádiz también tuve el placer de conocer al Dr. González-Duarte, (hereafter, Manué), gracias por aportar esa visión ecológica al INMAR (las reuniones de pasillo alegraban el día). También, agradezco todos los consejos, sugerencias y ánimos durante estos años y por muchos años más!

Rodri, gracias, por los infinitos ánimos y consejos que durante estos años me has ido transmitiendo. Parece que era ayer cuando me dejabas el coche para que fuese a muestrear! (2013, Tenerife). Y como siempre, a seguir.

Gracias por la fuerza y honestidad transmitida Berta, quizás, sin ser consciente me has ayudado a perseverar en el camino.

Por supuesto, muchísimas gracias a Creu Palacín (tutora), por todas las facilidades proporcionadas y a Dolors Vinyoles, por las sugerencias, ánimos y ayuda prestada.

Muchísimas gracias al Club Ánfora de Actividades Subacáticas de Melilla, por apostar y confiar en los proyectos que se han realizado (INBIOMAR), el que se está realizando (INBIOMAR II) y, por lo que vendrán en el futuro.

También agradecer, al equipo profesional y humano de los proyectos INBIOMAR e INBIOMAR II, por su esfuerzo y voluntad de superación, *especialmente al Presi (Ángel, por las clases de astronomía), Alberto (recuerda el Symphodus doderleini tiene una línea de color argentado), Domingo, Manué, Juanjo, Paco, Laurita de Úbeda, y todos aquellos que han pasado horas y horas cargando botellas o han sido nuestros patrones mientras nosotros estábamos muestreando ¡¡¡GRACIAS!!!.*

También en el norte de África, pero esta vez en Ceuta conocí una de las personas más comprometidas con la conservación del medio marino, Javi propieratio del Centro de buceo Burbujas. Gracias por facilitarnos nuestras fugazes pero intensas visitas, y por ayudarnos, siempre, en todo lo posible. Sin duda, continuaremos disfrutando de los magníficos fondos marinos y de la buena gente de Ceuta.

Infinitas gracias al Club de buceo Oxígeno de Fuerteventura, especialmente a Araceli, Emilio y Dani, por demostrarnos que se puede bucear los 365 días del año (incluso con alguna doble). También agradecer la confianza depositada en las ideas para estudiar sus fondos. Y como no puede ser de otra forma, por tener la zodiac en el agua cada vez que vamos a muestrear! ☺

Gracias al estudiante que depositó su confianza para realizar cierto trabajo de final de máster. Me has brindado la oportunidad de continuar aprendiendo desde otra perspectiva, eres un ejemplo de perseverancia, enhorabuena.

Also, thanks to the Reef Life Survey team for supporting and facilitating the work at a distance. Special thanks to Graham, Rick, and Toni.

Durante la tesis, tuve la suerte de conocer a personas maravillosas, que hicieron las estancias internacionales más acogedoras. En Chile, gracias Antonio, Claudia (y su familia), Don Iván por esas recetas y buenas tardes que pasamos. También gracias a Alex por aquellas clases teóricas sobre resiliencia y regímenes. Indudablemente, gracias a Sergio y Alejandro por la oportunidad de conocer otra aproximación a la investigación. Y a dos personas que tuve la oportunidad de conocer y traerme su amistad, a Clarita y Monique, que serán doctoras en los próximos meses!!! En Francia, infinitas gracias al Institut d'écologie et des sciences de l'environnement de Paris por su calurosa acogida y hacerlo todo fácil. Por supuesto a Vasilis, por la disposición, conocimiento y tiempo compartido.
Muchísimas gracias a tod@s, esta tesis tiene un pedacito de tod@s vosotros.

Financial Support

This thesis has been partially financed with the following research grants projects MARINERES [CGL2013- 49122-C3-1-R] of the Spanish Ministry of Economy and Competitiveness. DIVERSAT [RTI2018-098970-B-100] of the Spanish Ministry of Science, Innovation, and Universities. And INBIOMAR [PRCV00676], which count with the support of the Biodiversity Foundation of the Ministry for the Ecological Transition and the Demographic Challenge. Also, the Montcelimar Foundation trough research training grants.

Summary

The degradation of natural diversity results in the erosion of key systemic properties such as resilience, or the capacity to recover from disturbances. Resilience loss leads to an increase in the fragility and vulnerability of natural communities, fearfully approaching, if not surpassing, the tipping point that turns them into degraded communities with fewer ecosystem services. A potential pathway to avoid the continuous decline of resilience is to generate biodiversity-inclusive resilience metrics that can be broadly applied, monitored, and taken into consideration before conservation decision making. It is hard to manage what cannot be measured.

This thesis contributed to our understanding of the resilience of marine temperate rocky reefs, integrating biodiversity metrics with environmental variables and management actions. To do so, this thesis put forward multiple community metrics that allowed a global and integrative vision of the actual situation of the temperate rocky reefs of the Iberian Peninsula, the Spanish territories in Northern Africa, the Balearic Islands, and the Canary Islands. In particular, the thesis investigated the impact of artificial substrates on diversity, quantified the resistance of marine communities to recover a more pristine stage, analyzed the efficiency of marine protection on fish communities, and developed a new integrative tool that allowed the quantification of marine resilience by harmonizing numerous biological, environmental, and management factors that regulate the resilience of temperate marine systems.

The results obtained in this thesis showed the negative impact of artificial substrates on diversity, mainly in sessile organisms or species with reduced mobility. This thesis provided evidence that unprotected marine areas were more resistant than partially protected areas to recover their diversity. Furthermore, marine protection had greater benefits on the biomass than on the diversity of the marine fish community. This thesis also laid the foundations to quantify resilience and to detect priority areas to preserve, reflecting the importance of adequate marine management.

This thesis is, therefore, a compendium of studies that reflects my commitment to advance our understanding of marine biodiversity. The research carried out in this thesis evaluated the current status of our littoral rocky reefs and promoted its conservation using emerging ecological concepts with strong implications for management. In particular, my thesis set the basis for an improved understanding of the resilience of temperate rocky reefs providing widely-spread, georeferenced empirical estimates of resilience, a particularly elusive topic in the scientific literature to date. Overall, this thesis actively sought to promote a healthier, more diverse marine environment through the study of biodiversity-based resilience and its potential to improve management.

Resumen

La acentuada degradación que están sufriendo los ecosistemas naturales promueve la erosión de propiedades comunitarias vitales como la resiliencia, o la capacidad de recuperación. La pérdida de resiliencia conlleva un aumento de la fragilidad y vulnerabilidad de las comunidades naturales, haciendo que estas comunidades naturales se aproximen temerosamente al punto de inflexión que las conduce a convertirse en comunidades degradadas, disminuyendo los servicios ecosistémicos proporcionados. Una potencial vía para evitar la continua degradación de resiliencia es estudiar esta métrica a través de la diversidad biológica, de tal forma que se puedan aplicar, supervisar y, considerar esta información antes de la toma de decisiones en conservación. Es difícil gestionar lo que no se puede medir.

La presente tesis contribuye a conocer el estado de la diversidad y resiliencia marina en diferentes contextos de los arrecifes rocosos templados marinos. Para ello, la tesis elaboró métricas comunitarias que permitieron crear una visión global e integradora de la situación real de los arrecifes rocosos de la Península Ibérica, archipiélago Canario y Balear y, el norte de África. En concreto, la tesis investigó el impacto que tienen los substratos artificiales sobre la diversidad, cuantificó la resistencia de las comunidades marinas a recuperar un estado más prístino, estudió la eficiencia que tienen las figuras de protección sobre la comunidad de peces marinos. Y, desarrolló una nueva herramienta integradora que permitió cuantificar la resiliencia marina mediante la armonización de numerosos factores biológicos, ambientales y de gestión que regulan la resiliencia de los sistemas marinos de las zonas templadas.

Los resultados obtenidos en la tesis ponen de manifiesto el impacto negativo que tienen los substratos artificiales en la diversidad de los organismos marinos, principalmente en la comunidad sésil o con movilidad reducida. La tesis aportó pruebas de que las zonas marinas no protegidas son más resistentes que las zonas parcialmente protegidas para recuperar su diversidad. También se ha reflejado que la protección marina presenta mayores beneficios

en la biomasa que en la diversidad de la comunidad de peces marinos. Y por último, esta tesis siesta las bases para cuantificación de la resiliencia y detección de zonas prioritarias a conservar, lo que refleja la importancia de una ordenación marina adecuada.

Por todo ello, esta tesis es un compendio de estudios que reflejan mi compromiso de avanzar en nuestra comprensión de la biodiversidad marina, evaluar el estado actual de nuestros arrecifes rocosos templados y promover su conservación utilizando conceptos ecológicos emergentes con fuertes implicaciones para la ordenación. En particular, mi tesis ha sentado las bases para una mejor comprensión de la capacidad de recuperación de los arrecifes rocosos de las zonas templadas, proporcionando estimaciones empíricas de resiliencia georreferenciadas y sobre una gran área geográfica, un tema particularmente elusivo en la literatura científica hasta la fecha. En definitiva, esta tesis promueve activamente *un medio ambiente marino más saludable y más diverso mediante el estudio de la resiliencia basado en la biodiversidad y su potencial para mejorar la gestión.*

Contents

Director's report

Dr. Mikel Becerro, a tenured scientist at the Spanish National Research Council (CEAB-CSIC), as supervisor of the Ph.D. thesis entitled "*Understanding resilience through biodiversity: developing systemic tools for marine conservation in temperate rocky reefs*"

INFORMS that

the research developed by Jose A. Sanabria-Fernandez for his doctoral thesis has been organized in 8 sections including a General Introduction, General Discussion, Conclusions, and five additional chapters summarizing empirical investigations

three out of these five chapters correspond to scientific papers published in international, peer-reviewed journals that were in the first quartile of their respective research areas (Q1 journals) as classified by the Journal of Citation Reports at the time of publication. Also, below is a list of chapters, the impact factor of the journal (IF), the quartile (Q), and the current stage of publication.

Chapter I: Sanabria-Fernandez, J.A.[1,2], Lazzari, N.[1,3], Riera, R.[4,5], Becerro, M.A[1], 2018. Building up marine biodiversity loss: artificial substrates decrease the number and abundance of low occupancy benthic and sessile species. *Marine Environmental Research*, 140, 190-199. doi.org/10.1016/j.marenvres.2018.06.010. IF: 2.727; Q1; published.

Chapter II: Sanabria-Fernandez, J.A.[1], Alday, G.J.[6], Becerro, M. A [1], 2020. Measuring community recovery: unprotected marine areas have more resistance than partially protected areas to increase their diversity. To be submit to *Conservation Biology*. IF: 5.405; Q1; in preparation.

Chapter III: Sanabria-Fernandez, J.A. [1,2], Alday, J.G.[6], Lazzari, N. [1,3], Riera, R.[5], Becerro, M.A[1], 2019. Marine protected areas are more effective but less reliable in protecting fish biomass than fish diversity. *Marine Pollution Bulletin*, 143, 24–32. doi.org/10.1016/j.marpolbul.2019.04.015. IF: 4.049; Q1; published.

Chapter IV: Sanabria-Fernandez, J.A. [1,2], Lazzari, N. [1], Becerro, M.A[1], 2019. Quantifying patterns of resilience: What matters is the intensity, not the relevance, of contributing factors. *Ecological Indicators*,107:1055665.doi.org/10.1016/j.ecolind.2019.105565. IF: 4.229; Q1; published.

Chapter V: Sanabria-Fernandez, J.A.[1], Lazzari, N. [1], Becerro, M.A[1], 2020. Enhancing and preserving marine resilience trough management actions: How to identify top resilient areas and make them more resilient. To submit to *Global Change Biology*. IF: 8.555; Q1; in preparation.

CERTIFIES that

Jose A. Sanabria-Fernandez has led the research presented in his Ph.D. During all this time conducting his research, he has discussed the research concepts, the sampling strategies, the data analyses, the interpretation of results, and the structure and writing of the manuscripts

the research presented in his Ph.D. thesis has not contributed to, nor has been part of, any other national or international doctoral thesis.

Dr. Mikel Becerro

Blanes, 25 September 2020

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[6] Departament de Producció Vegetal i Ciència Forestal, Universitat de Lleida-AGROTECNIO, Av. Rovira Roure, 191, E-25198 Lleida, Spain

Additional publications

6. Edgar, G.J., Cooper, A., Baker, S.C., Barker, W., Barrett, N.S., Becerro, M.A., Bates, A., Brock, D., Ceccarelli, D., Clausius, E., Davey, M., Davis, T.R., Day, P., Green, A., Griffiths, S.R., Hicks, J., Hinojosa, I.A., Jones, B., Larkin, M.F., Lazzari, N., Ling, S.D., Mooney, P., Oh, E., Pérez-Matus, A., Pocklington, J.B., Riera, R., **Sanabria-Fernandez, J.A.**, Seroussi, Y., Shaw, I., Shields, D., Shields, J., Smith, M., Soler, G.A., Stuart-Smith, J., Turnbull, J.., Stuart-Smith, R.D. Reef Life Survey: Establishing the ecological basis for conservation of shallow marine life. Under review in *Biological Conservation*.

5. Lazzari, N., Becerro, M., **Sanabria-Fernandez, J.A.**, Martín-López, B. Assessing social-ecological vulnerability of coastal systems to fishing and tourism. Under review in *Science of the Total Environment.*

4. Lazzari, N., Martín-López, B., **Sanabria-Fernandez, J.A.**, Becerro, M.A. 2019. Alpha and beta diversity differences across coastal marine socialecological systems: a community and functional approach. *Ecological Indicators*, 109: 105786.

3. Lazzari, N., Becerro, M., **Sanabria-Fernandez, J.A.**, Martín-López, B. 2018. Spatial characterization of coastal marine social-ecological systems: insights for integrated management. *Environmental Science & Policy*, 92,56-65.

2. Riera, R., Menci, C., **Sanabria-Fernandez, J.A.**, Becerro, M.A. 2016. Do recreational activities affect coastal biodiversity? *Estuarine, Coastal and Shelf Science*, 178, 129 - 136.

1. Hummel, H., Frost, M., Juanes, J.A., **Sanabria-Fernandez, J.A.** et al. 2015. A comparison on the degree of implementation of marine biodiversity indicators by European by European countries in relation to the marine strategy framework directive MSFD. *Journal of the Marine Biological Association of the United Kingdom*, 1-13. doi:10.1017/S002531541500023.

General introduction

Picture: Underwater seascape from the Peñón de Vélez de la Gomera (Spanish territories in the African continent). In the picture you can see specimens of *Chromis chromis* and *Diplodus sargus*. Jose A. Sanabria-Fernandez took this picture during an INBIOMAR 2019 research grant sampling trip.

Simply defined, biodiversity is the variability of all living organisms on Earth. But underneath this apparent simplicity lays a concept that operates at multiple levels of organization, from genes to species, communities, ecosystems, landscapes, or biomes regardless of their marine, terrestrial, or freshwater nature (Wilson, 1992). Biodiversity broadens the classical “species” concept to embrace the functions that these multiple levels of organization play. We, human beings, are a part of the biodiversity concept, a part that is becoming increasingly influential on a global scale. Biodiversity also is our health support system (CBD, 2016) providing endless benefits that directly contribute to human well-being (Millennium Ecosystem Assessment, 2005; Díaz et al., 2006). Oxygen-deficient atmospheres below 19% cause negative effects on humans and below 10% we would die promptly (Spelce et al., 2016). Marine phytoplankton releases over ~80% oxygen to the atmosphere (Hoegh-Guldberg and Bruno, 2010), a critical contribution to our survival that often gets unnoticed. Besides oxygen, food, medicines, and other materials that we use daily are obvious services that biodiversity provides. Biodiversity also is behind physical protection from climate events and other more subtle social, emotional, spiritual, and cultural benefits (Millennium Ecosystem Assessment, 2005). We, as a society, are intrinsically linked to biodiversity (Naeem et al., 2016), our health depends on it (Chivian et al., 2010), and, yet, we are becoming its major threat (McKee et al., 2003; Lovejoy, 2019).

Humans are the main drivers of change on earth. In the age of humans, the Anthropocene, we have altered over 50% of the land's surface (Hooke et al., 2012). Current extinction rates reached a new maximum in the earth's history (Barnosky et al., 2011; Dirzo et al., 2014), exceeding 1000 times background extinction rates of the six great extinctions (Alroy 2015; De Vos et al., 2015). In mammals alone, the current extinction rate is over 50 times higher than before humans existed (Ceballos et al., 2015). Our actions also threaten global marine biodiversity. Currently, the major threats of marine biodiversity are all human-driven: pollution, overfishing, invasive species, climatic threats, and habitats fragmentation (Craig, 2012; Díaz et al., 2019). In the last 40 years, we have lost 40% of the world's ocean marine biodiversity (Loh et al., 2005; WWF, 2018), with 54% coral reefs (Berkelmans et al., 2003; Wilkinson, 2008), 45% of kelp forests, and 34% of the seabed meadows (Telesca et al., 2015) as worrisome examples. This diversity loss also degrades our relationship with nature (Millennium Ecosystem Assessment, 2005; Naeem et al., 2016). A splendid example of the degradation of nature-human relationship is the collapse of Canadian society due to the collapse of Atlantic cod fisheries (Myers et al., 1997).

Ironically, our unsustainable relationship with nature is bound to degrade the well-being we sought after in the first place (Millennium Ecosystem Assessment, 2005). This is clear in coastal areas, a highly diverse and productive area that concentrates the majority of the world's population (Neumann et al., 2015). Coastal areas are at risk for many reasons, but urban sprawl is certainly increasing worldwide, causing habitat fragmentation and transforming natural environments into artificial landscapes (Airoldi and Bulleri, 2011). The traditional "artificial reef" concept refers exclusively to artificial structures intentionally sank in shallow areas to avoid bottom trawling and to improve fisheries (Baine, 2001). Traditionally, artificial reefs are therefore a management action to improve an environmental condition. But the reality of the artificial substrates in littoral waters are much broader and, certainly, beyond environmental conservation goals. The actual ecological consequences of the broader concept of artificial reefs on marine diversity remain unclear but the implications for management loom large. It is, precisely, our capacity to manage marine environments which provides a window of opportunity for the world's biodiversity (Palumbi et al., 2009). We need effective management to halt biodiversity loss, promote sustainability, and enhance social and ecological resilience (Folke et al., 2004).

The implementation of Marine Protected Areas (MPAs) is a common management tool used to preserve biodiversity (Hilborn, 2016; Campbell et al., 2017). Currently, the enormous number of 26,984,530 km^2 is the total marine area protected globally covering 7.47% of the ocean surface (UNEP-WCMC, 2020). Although the positive trend in ocean protection is highly relevant, we still lag behind the level of terrestrial protection (Gownaris et al., 2019) and well below the conservational goals set in international treaties (Leadley et al., 2014). Inside MPAs, human activities are strongly regulated and, sometimes, prohibited (Al-Abdulrazzak and Trombulak, 2012), allowing nature to thrive in these areas with reduced anthropogenic threats. Yet, many MPAs are just paper parks with little or no effect as compared to unprotected areas (Edgar et al., 2014). MPA inefficiency has enormous economic costs and minimum ecological benefits (Balmford et al., 2004; Jantke et al., 2018). Unfortunately, inefficient MPAs are the norm (Edgar et al., 2014) and there is an urgent need to reverse this ratio if we aim to truly preserve our oceans. Studies on recovery costs have the potential to convert inefficient MPAs into efficient MPAs in the near-future. The recovery cost analysis may be approached using time as the target variable (i.e., how much time will it take to convert an inefficient MPA into an efficient one) or using other ecologically relevant variables (i.e., how many additional species will recover if we manage to convert an inefficient MPA into an efficient one). There is a vast lack of knowledge about the MPA recovery process, specifically, about the biodiversity cost associated with protection (or lack thereof). This knowledge could reformulate marine protection guidelines leading to increased MPA effectiveness and larger social and ecological profits (Marra et al., 2016; Strain et al., 2018).

Marine protection contributes to improving the state of diversity from multiple points of view (Edgar and Barrett, 1999; Barrett et al., 2007) such as fish density, invertebrate abundance, or macroalgal cover. These benefits have been studied using different approaches. Marine protection increases community-level traits such as species richness (Ciriaco et al., 1998), functional and trophic diversity (Stelzenmüller et al., 2009; Villamor and Becerro, 2012), the biomass of threatened species (Harmelin-Vivien et al., 2015), or the biomass of commercial fish (Barrett et al., 2007; Fenberg et al., 2012). Usually, each study targets a single diversity indicator, shedding light on a specific community trait (Villamor and Becerro, 2012; Harmelin-Vivien et al., 2015). A more integrative approach using multiple indicators would provide a more comprehensive view of the role of protection in diversity, but such an approach is currently missing. A potential solution to fill this integrative gap is the construction of an indicator that simultaneously gathers information about several biological traits (Claudet et al., 2006). Such an indicator would allow for a broader perspective on the benefits of protection in biodiversity, with tangible applications in management.

An important biodiversity-driven benefit of protection is to provide stability against disturbance (MacArthur, 1955; Walker, 1992; Lindegren et al., 2016). Biodiversity loss leads to a community decrease in robustness, resistance, and ecological resilience (Gunderson et al., 2009; Oliver et al., 2015), which in turn increases the fragility, vulnerability, and weakness of the community (Gunderson et al., 2009). In this sense, resilience is a key property that provides information about the status of an ecosystem and its capacity to recover from disturbance. Although resilience has multiple definitions, it is often defined as the magnitude of disturbance that can be absorbed by a system before shifting its structure (Holling, 1973). The resilience of marine systems depends on three major dimensions: the biological, anthropogenic, and environmental dimensions. An example of the biological dimension is the relationship between the abundance of top predators and the resilience of a system. A decrease in the abundance of top predators leads to a decrease in resilience, so the abundance of top predators can function as a proxy for resilience (Llope et al., 2011). From an anthropogenic perspective, fishing pressure is a resilience threat because resilience decreases as the fishing resources wane (Barnett and Baskett, 2015). Environmentally, ocean warming is a critical threat to the resilience of kelp forests (Wernberg, 2010). As noticed above for diversity, these studies provide a partial vision related to the specific indicator/trait/dimension investigated. The integration of multiple resilience dimensions into a single indicator would allow for a broader understanding of marine resilience (Maynard et al., 2010; Ladd and Collado-Vide, 2013; Gibbs and West, 2019). It would also allow suggesting proper management guidelines to safeguard marine resilience, a very desirable property particularly for those ecosystems where resilience has received little attention, such as temperate rocky reefs.

Efficient management should strengthen the resilience of marine communities (Folke et al., 2004; Levin and Lubchenco, 2008). Establishing management actions based on specific resilience factors is a mechanism that allows preventing resilience loss. For example, fishing pressure, anthropogenic pollution, or anthropogenic physical pressure threaten resilience (Jackson 2001; Llope et al., 2011; Barnett and Baskett, 2015). We could regulate, for example, fishing pressures by developing a restrictive fisheries policy (Williams et al., 2016; Bejarano et al., 2019). Management is a tool to preserve biodiversity and to increase the resilience of the seas (Folke et al., 2004). This management involves the regulation of specific management factors on an appropriate geographical scale (Gunderson et al., 2009). Additionally, knowing how much these management factors can be improved allows us to elaborate on efficient and specific management actions at the factor level. In line with this, the need to establish quantitative measures of resilience is a priority on many international panel agendas, such as the Aichi targets of the Convention of Biological Diversity (CBD), or the International Union for the Conservation of Nature (IUCN). Resilience is a critical area that would benefit from applying ecological knowledge into actual attempts to empirically measure the resilience of a site. If possible, we could then quantify resilience across multiple temporal and spatial scales to detect top resilience areas (and low resilience areas) or resilience trends as a response to our management actions (or lack thereof). Certainly, a conservational challenge of the Anthropocene (Cumming, 2016; Angeler et al., 2020).

Why this thesis?

This thesis comprises five chapters, the first three aim at assessing and learning about the impact of certain human actions on biodiversity. In particular, the first one is focused on assessing the impact of artificial substrates on marine diversity. This problem is growing by leaps and bounds on our shores, causing the fragmentation of habitats and loss of diversity. This chapter has been conducted from a community perspective based on species intrinsic characteristics such as density and mobility. To assess this impact, we developed an indicator called Natural Artificial Reefs, based on the comparison of the artificial reef and its closest natural counterpart in Tenerife island (Canary Islands, Spain).

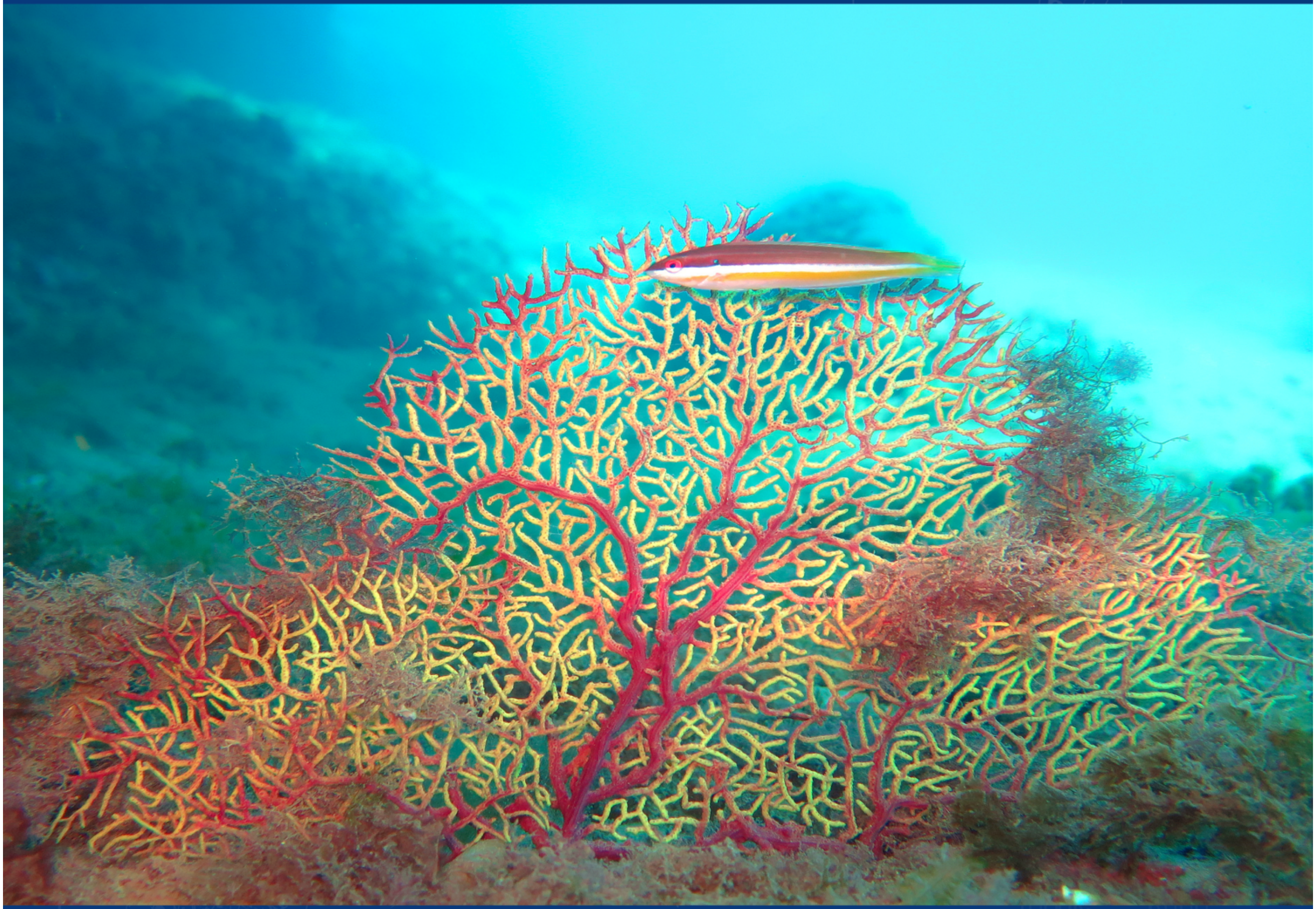
Marine protection is an essential tool to maintain and preserve the biodiversity of our seas. Unfortunately, paramount geographical areas to be preserved are still unknown in terms of the cost of recovery of the biological community. Therefore, the second chapter focuses on studying and quantifying the degradation and the cost of recovery of marine diversity. This study is community-focused and, so, we have considered fish, macroinvertebrates (mobile and sessile), and macroalgae. To quantify this phenomenon of recovery and degradation, a multivariate methodology based on the density of each species has been developed. This community perspective brings to light the recovery process from a comprehensive and solid approach. Cabo de Gata marine reserve was the chosen scenario to develop this new methodology, as it includes adjacent protected and unprotected areas.

Nowadays, there are a great number of categories of protected areas established in seas and oceans around the world (Abdulrazzak and Trombulak, 2012; Day et al., 2019). Unfortunately, there is still a large gap in knowledge about the (in)efficiency of such categories on the marine fish community. The third chapter focuses on assessing and quantifying the efficiency of marine protection over the fish community. To quantify this efficiency, we have designed the Conservation Status Index (CSI) based on the difference between protected and unprotected areas in each ecoregion studied. The CSI involves nine individual indicators grouped around biomass, diversity, and other relevant aspects of the marine fish community. This study looked at 22 marine protection categories spread over four marine ecoregions in temperate zones.

Resilience is a key property for the appropriate functioning of natural biological communities. However, there isn't much knowledge about the quantification of this property in temperate seas. Besides, the current knowledge about the factors that modulate it is extremely limited and local based. Therefore, in the fourth chapter, we have addressed this problem by developing a Resilience Indicator for temperate regions (IRIS). We designed this resilience indicator by integrating 17 resilience factors known to regulate resilience. These 17 factors included the biological, anthropogenic, and environmental dimensions of resilience. The IRIS allowed us to obtain a more comprehensive and robust vision of resilience in temperate seas than that provided by single indicators. It also lays the foundation for studying chronological trends in the ecoregion of the Alboran Sea.

Conservation and resilience management is essential to preserve healthy oceans. To stop the loss of resilience and, eventually, enhance the resilience of our oceans are major environmental goals. The last chapter is focused on detecting highly resilient areas where conservation may be a priority. Equally important is to identify resilience areas where proper management of anthropogenic factors can result in improved resilience. In this chapter, we used the IRIS indicator described in Chapter IV to assess the resilience of the five marine ecoregions of the world present in the Spanish littoral: Alboran, Atlantic, Canaries, Mediterranean, and Sahara.

Objectives



Picture: Underwater picture from Melilla, composed by *Leptogorgia sarmentosa* and *Coris julis*. Jose A. Sanabria-Fernandez took this picture during an INBIOMAR II 2020 research grant sampling trip.

Objectives

The thesis global aim is to contribute to the knowledge of resilience using marine biodiversity as a study model. To achieve this aim, the thesis developed indicators to assess the diversity and resilience status in temperate rocky reef communities. In this sense, the thesis investigated in all five chapters a variety of scenarios such as artificial and natural reefs and protected and unprotected areas with different levels of management actions.

The thesis chapters are:

Chapter I Assessing the impact of artificial reefs on marine biological diversity.

Chapter II Quantifying the resistance to recovery from unprotected to protected marine biological communities.

Chapter III Evaluating the (in)efficiency of marine protected areas to enhance diversity, biomass, and other relevant aspects of the fish community.

Chapter IV Calculating the Inclusive Resilience Indicator of a Site (IRIS) to quantify the resilience of temperate rocky reefs.

Chapter V Finding priority areas to preserve and enhance the marine resilience of temperate rocky reefs.

Chapter I

Building up marine biodiversity loss: artificial substrates decrease the number and abundance of low occupancy benthic and sessile species

This research is based on:

Sanabria-Fernandez JA, Lazzari N, Riera R, Becerro MA, 2018. Building up marine biodiversity loss: artificial substrates decrease the number and abundance of low occupancy benthic and sessile species. Marine Environmental Research, 140, 190–199.

Picture: Underwater seascape with artificial reef in Playa San Juan, Tenerife Island (Canary Islands). Jose A. Sanabria-Fernandez took this picture in 2012 during the sampling trip.

Abstract

Ocean sprawl is replacing natural substrates with artificial alternatives. We hypothesized that, after submersion, high occupancy, high mobility species colonize artificial substrates faster than low occupancy, low mobility species, a biodiversity divergence that will slowly fade out with time. Using quantitative visual census of species in 10 artificial and their adjacent natural substrates, we tested for the existence and temporal evolution of this divergence. Assigning species to one of three occupancy and one of three mobility categories, we found that artificial substrates increased the performance of high mobility, high occupancy species while decreased the performance of low mobility species with medium and low occupancy. This biodiversity divergence remained unchanged over the 50-year underwater timespan of the artificial substrates investigated. Our results suggest that proliferation of artificial substrates is building up a biodiversity loss driven by the least conspicuous and uncommon benthic and sessile species that is undermining coastal marine biodiversity.

1.1. Introduction

Coastal environments are critical components of the Earth support system. They provide us with goods and services that surpass those provided by any terrestrial ecosystem (Costanza et al., 1997). The relevance of coastal systems stems from their specific biological and environmental traits. Coastal waters up to 200 m deep are about 5-10% of the world surface, yet they account for 25% of the primary production of the oceans, 79% of marine fish species, and 90% of marine exploitation (Barnabé and Barnabé-Quet, 2000; Ray and McCormick-Ray, 2009). In short, coastal waters hold the greatest variety and abundance of marine species (Gray, 1997) but they also are among the most threatened by anthropogenic stressors (Halpern et al., 2007).

Demographic pressures on coastal ecosystems are steadily increasing as coastal zones are home to a large and growing proportion of the world's population, which could rise by more than 50% between 2000 and 2030 (Neumann et al., 2015). Human-induced changes of the coastal environment occur through a variety of activities such as overfishing, pollution, or habitat destruction. Habitat degradation, fragmentation, and loss are major threats to biodiversity (Sih et al., 2000). These are widespread phenomena in coastal areas with over 50% of the world and 86% of Europe’s coasts at moderate or high risk of degradation (Bryant et al., 1995). Given the high value of the coastal services to humans, coastal degradation may cause a great environmental burden with important implications to our society (Costanza et al., 2014). A better understanding of the effect of human alterations on the marine coastal diversity will certainly help minimize the negative consequences of coastal development and promote more efficient biodiversity conservation and management.

Ocean sprawl, the proliferation of artificial structures in the sea, is an important component of coastal degradation in marine environments (Duarte et al., 2012; Firth et al., 2016). Breakwaters, dykes, coastal defense structures, and other human-made constructions are increasingly present in coastal areas to meet the growing demand for commercial, touristic, and residential activities of the last decades (Bulleri and Chapman, 2010; Firth et al., 2016). Artificial structures are becoming a significant habitat for marine organisms in detriment of their natural counterparts (Airoldi and Beck, 2007; Dugan et al., 2011; Duarte et al., 2012; Bishop et al., 2017). Beyond some striking examples of ocean sprawl scattered over the world (e.g., Dubai or Qatar in the Persian Gulf, Penang Is or Singapore in the Malay Peninsula, Firth et al., 2016; Chee et al., 2017), the phenomenon is truly widespread and a cause of environmental concern. The Mediterranean coasts of France, Italy, and Spain have over 1,500 km of artificial structures (Airoldi and Beck, 2007), which represents about 15% of their coastline. Ocean sprawl causes loss of coastal habitats (e.g., Airoldi and Beck, 2007) and shifts in species abundance and distribution (Clynick et al., 2008; Airoldi and Bulleri, 2011; Burt et al., 2011; Heery et al., 2017). Yet, we are far to understand the ecological importance of artificial habitats and whether, given enough time, artificial substrates will have the capacity to hold communities equivalent to those on natural substrates.

Artificial habitats may add new variables and habitat types (e.g., material, rugosity, or dark sciaphilic habitats in shallow communities) with important implications in community organization and functioning (Chapman, 2003; Bulleri and Chapman, 2010; Ponti et al., 2015). High mobility species such as fish may colonize new habitats sooner than species with more limited mobility such as mobile invertebrates or sessile organisms, which may rely more strongly on reproductive traits (Kinlan and Gaines, 2003; Perkol-Finkel and Benayahu, 2007; Lin et al., 2008; Miller et al., 2009; Gothland et al., 2014). Species abundance and size of the organisms may also determine their capacity to colonize new habitats, with common (i.e., abundant) species having numerical advantage over uncommon species in terms of space occupation (MacKenzie et al., 2003; Strain et al., 2017). Similarly, widely distributed species that inhabit numerous locations (frequent, high occupancy species) are more likely to colonize artificial habitats because surrounding natural reefs may act as a “pool source” (Svane and Petersen, 2001). On the other hand, irregularly distributed species inhabiting few locations (infrequent, low occupancy species) may need longer time periods to colonize artificial habitats, underpinning a secondary successional diversity (Tilman, 1988). Colonization of artificial habitats by common and high occupancy species may create a false state of similarity with natural substrates because the less conspicuous species (uncommon and low occupancy species) are easier to overlook. Yet, the less conspicuous species are bond to represent a significant percentage of the overall biodiversity (Whittaker, 1965) and play critical roles in ecosystem functioning (Grime, 1998), so their absence in artificial habitats would tone down biodiversity severely.

It is unclear whether artificial habitats deviate significantly from natural substrates or they can function as their natural counterparts given enough time (Carr and Hixon, 1997; Glasby and Connell, 2001; Perkol-Finkel et al., 2006). We herein hypothesized that species composition and abundance in artificial habitats deviate from natural reefs. Artificial substrates will favor some species and disfavor others, resulting in significant community differences between natural and artificial habitats. These differences, however, may decrease over the long term making artificial substrates suitable environments to maintain current levels of marine biodiversity. In our study, we selected 10 artificial substrates that have been underwater from 0 to 54 years and tested whether the number and abundance of species differed with their associated natural reefs.

1.2. Material and Methods

We quantified species composition and abundance in 10 locations in Tenerife, Canary Islands (Fig. 1.1, Table 1.1). At each location, we surveyed hard bottom habitats with either artificial or natural substrates. All artificial structures in our study were breakwaters, mostly built to provide shelter for boats. None of the artificial structures investigated in our study aimed to enhance species, to restore habitats, to prevent areas from trawling or fishing, or to promote recreational fishing or diving. In this regard, all the artificial substrates investigated were located in the seaward site of the breakwaters, had similar exposure, orientation, slopes and depths, then their natural counterparts and resembled their nearby rocky reefs but with big quarry rocks or concrete boulders added to provide coastal defense (Table 1.1). The artificial boulders did provide a sciaphilic habitat mostly missing in the natural reefs of our study due to the large number of dark spaces created by the three-dimensional artificial structures. We obtained from official sources (Cabildo de Tenerife, Autoridad Portuaria de Tenerife, and City Councils) the year of construction of each artificial structure to calculate the number of years they have been underwater until we surveyed them. At each site, we ran three visual censuses that quantified fish, invertebrate, and sessile species using the Reef Life Survey methodology (Edgar and Stuart-Smith, 2014) during summer 2012 (June-September). Briefly, the first visual census quantified number and abundance of demersal fish species in an area of 50 x 10 meters. The second visual census quantified macro invertebrate and cryptic fish species in a 50 x 2 meters. Finally, to quantify sessile species, we took 25 x 25 cm photoquadrat (PQ) every 2.5 meters along the 50 meter long transect, for a total of 20 PQs. Then, for each PQ, we generated 20 random points with the software CPCe V. 4.1 (Kohler and Gill, 2006) to quantify the percent cover of sessile species. These three methods also represent degree of mobility, as the first method targets the highly mobile, swimming, demersal fish community (high mobility), the second method targets the benthic invertebrate and cryptic fish community (medium mobility), and the third method targets the fixed-to-the-substrate invertebrate and algal sessile community with highly restricted or no mobility as adults (low mobility).

Because we quantified species abundances in artificial substrates and adjacent natural reefs, we “paired” for every species in our study the abundance data in each artificial substrate to its natural counterpart using the following abundance based index:

$$\mathrm{NAR} = \frac{\mathrm{Natural} - \mathrm{Artificial}}{\max(\mathrm{Natural}, \mathrm{Artificial})}$$

where Natural is the number of specimens of a single species present in the natural substrate, Artificial is the number of specimens of the same species present in the artificial substrate, and max(Natural, Artificial) is the largest of these abundances. NAR computation for sessile species, quantified through the use of PQs, was identical except for the use of percent cover instead of abundance.

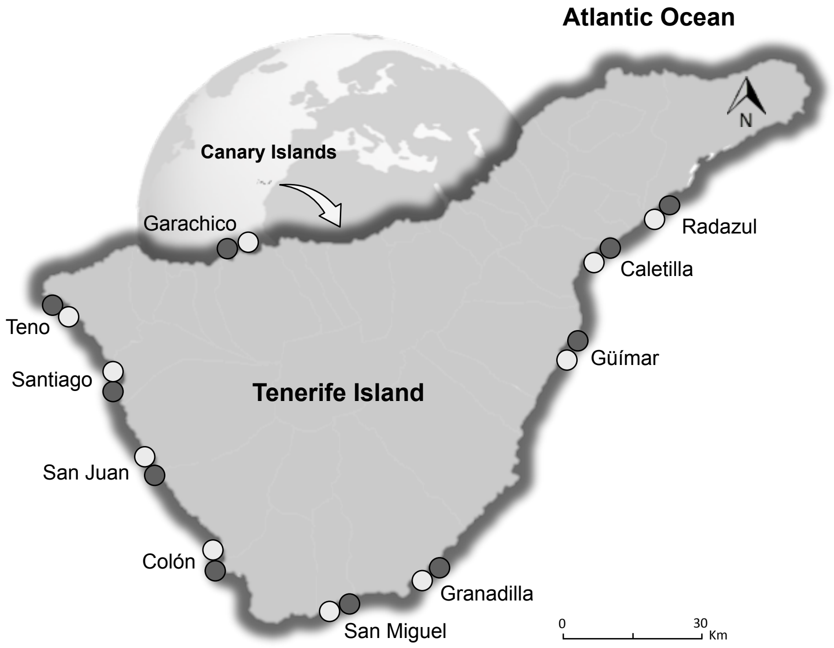


Figure 1.1. Sampled artificial substrates (dark circle) and adjacent natural reefs (light circle) scattered along the coast of Tenerife, Canary Islands. See Table 1.1 for additional site information.

Table 1.1. Sampling locations (and numbers for their identification in Figure 1.1) with average depth (m), latitude and longitude for both natural and artificial substrates, age of the artificial substrate (in years from submersion to sampling time) and type of material used for the construction of the breakwaters, i.e., material of artificial substrates.

Number	Location	Natural Substrate (NS)	Depth NS	Artificial Substrate (AS)	Depth AS	Age AS	Material AS
1	Garachico	28°22'17.38'' N 16°45'10.33'' W	5	28°22'24.13'' N 16°45'09.62'' W	2.5	0	Concrete
2	Teno	28°20'32.78'' N 16°55'06.98'' W	4.6	28°20'30.86'' N 16°55'11.27'' W	5.4	34	Concrete
3	Santiago	28°16'06.98'' N 16°51'05.11'' W	6.8	28°14'54.31'' N 16°50'34.74'' W	8.8	35	Concrete
4	San Juan	28°10'46.50'' N 16°49'10.26'' W	6.2	28°10'46.03'' N 16°48'57.61'' W	6.6	24	Concrete
5	Colón	28°06'00.46'' N 16°45'20.83'' W	7.9	28°04'47.04'' N 16°44'17.59'' W	7	27	Concrete
6	San Miguel	28°01'21.15'' N 16°36'33.25'' W	3.7	28°01'17.96'' N 16°36'36.42'' W	4.7	8	Concrete
7	Granadilla	28°05'16.07'' N 16°29'25.39'' W	6.5	28°05'14.39'' N 16°36'37.25'' W	3.3	18	Concrete
8	Güímar	28°17'42.79'' N 16°22'21.10'' W	3.8	28°17'16.32'' N 16°22'42.67'' W	3.2	4	Quarry rock
9	Caletillas	28°23'02.74'' N 16°21'11.87'' W	3.6	28°22'54.29'' N 16°21'21.81'' W	5.9	54	Concrete
10	Radazul	28°24'07.77'' N 16°19'39.77'' W	6	28°24'05.50'' N 16°19'35.72'' W	5.8	4	Quarry rock

For every species, NAR (Natural-Artificial Ratio) is the proportion of change in the number of specimens (or percent cover) found in artificial as compared to natural substrates. NAR values range between 1 and -1, with positive values when the species is more abundant in the natural substrate and negative values when the species is more abundant in the artificial substrate. Therefore, a NAR value of 0.75 represents a situation where the abundance of one species in the artificial substrate is 75% less than that in the natural reef, while the opposite is true for a NAR value of -0.75 (i.e., abundance in the natural substrate is 75% less than that in the artificial substrate). For any given species, NAR equals 0 when the number of specimens in both substrates is identical.

Finally, we also categorized species as low, medium, or high occupancy species based on the number of locations (including both substrate types) where every species was found. Out of the 10 locations we sampled, we defined low occupancy species as those that occurred in 3 or less locations, high occupancy species as those that occurred in 8 or more locations, and medium occupancy species as those that occurred in 4 to 7 locations. It is important to note that these three categories classified species independently of the actual number of specimens quantified for each species. For example, a high occupancy species may have a very small number of specimens, being considered “rare” under an abundance criterion. Similar, a low occupancy species could be present in very large numbers and be considered common or frequent. For this reason, and to avoid misinterpretation, in this study we avoid the terms “frequent, common, and rare” and refer to high, medium, and low occupancy species to unambiguously state that these categories do not refer to abundance but to the small-scale geographic distribution in our study.

We used five analytical approaches to test for a number of hypotheses. First, we ran paired t-tests to test for differences in richness (number of species), diversity (Shannon Diversity Index), abundance (number of specimens), and number of exclusive species between artificial and natural substrates. We defined exclusive species as those that, for every location, were present in either the natural or the artificial substrate, but not in both. It is possible that the same taxonomic species contributes multiple times as an exclusive species, regardless substrate type. For example, species “A” could be present exclusively in the natural substrate in one location and exclusively in the artificial substrate in another location, contributing as an exclusive species in both locations. Regardless the variable, all paired t-tests had 10 replicates, i.e., one natural and one artificial value for location. A second analytical approach used log-linear models to test for differences in richness, abundance, and number of exclusive species as a function of substrate type, species occupancy, and species mobility. Because log-linear models are a type of multiway frequency table analysis, data for each cell in the table was a single value with the total number of species, total abundance, or total number of exclusive species under each respective category. Log-linear models were run with the three variables of interest (substrate type, species occupancy, and species mobility) and their two-way interactions. Third, we also tested for differences in richness, diversity, abundance, and number of exclusive species (all variables rank-transformed because of lack of assumptions) between artificial and natural substrates with a threeway analysis of variance applying "aov" function of the vegan package in R (Oksanen et al., 2016) with substrate type, species occupancy, and mobility as fully orthogonal, fixed factors (i.e., 180 data points for each variable; 3 levels of mobility x 3 levels of occupancy x 2 substrate types x 10 locations). We used a fourth analytical approach to test whether artificial substrates increasingly resembled their natural counterparts with time. To do so, we ran an analysis of covariance on the rank-transformed NAR using species occupancy and mobility as fixed factors and age of the artificial substrates as covariate. Because NAR was calculated for each species in our data set and many occurred in multiple locations, the total number of data points in this analysis was 492, i.e., there were multiple NAR values (multiple species) for each of the 10 age values (one for each location). Regressions in the analysis of covariance were highly replicated (between 32 and 93 data points depending on the mobility x occupancy combination). Finally, we also ran a permutational analysis of variance (PERMANOVA) of square-root transformed species abundance data to test for community level differences between natural and artificial substrates. We used a resemblance matrix based on Bray-Curtis distance and the "Adonis" function of vegan package (Oksanen et al., 2016) with 999 permutations.

1.3. Results

We found none non-indigenous or invasive species out of the 107 identified species quantified in our study (Appendix 1 for Chapter I). Overall, seven out of the 10 natural substrates had more species than their artificial counterparts, yet the total number of species failed to statistically differ between natural and artificial substrates (paired t-test, T=-0.918, df=9, p=0.382). The log-linear model fit well with the total number of species found in natural and artificial substrates (Likelihood Ratio χ^2=3.429, df=4, p=0.489). The same model without occupancy had a poor fit (χ^2=18.548, df=6, p=0.005), causing a significant change in the model (χ^2=15.119, df=2, p=0.001). The number of low occupancy species with medium and low mobility in natural substrates doubled and tripled those found in artificial substrates (Fig. 1.2a). We also found that the average number of species found in natural and artificial substrates might vary as a function of species occupancy and mobility (three-way ANOVA, see probability of three-way interaction term between substrate type, occupancy, and mobility, and probability of substrate type in Table 1.2a).

Similarly, eight out of 10 natural substrates had higher Shannon Diversity Index than their artificial counterparts, yet diversity failed to statistically differ between natural and artificial substrates (paired t-test, T=-1.983, df=9, p=0.079). We found that the average Shannon Diversity Index found in natural substrates was significantly larger than in artificial substrates (three-way ANOVA, significant substrate type, Table 1.2b), driven by the higher diversity values in natural than in artificial substrates for the low occupancy species with medium and low mobility (Fig. 1.3).

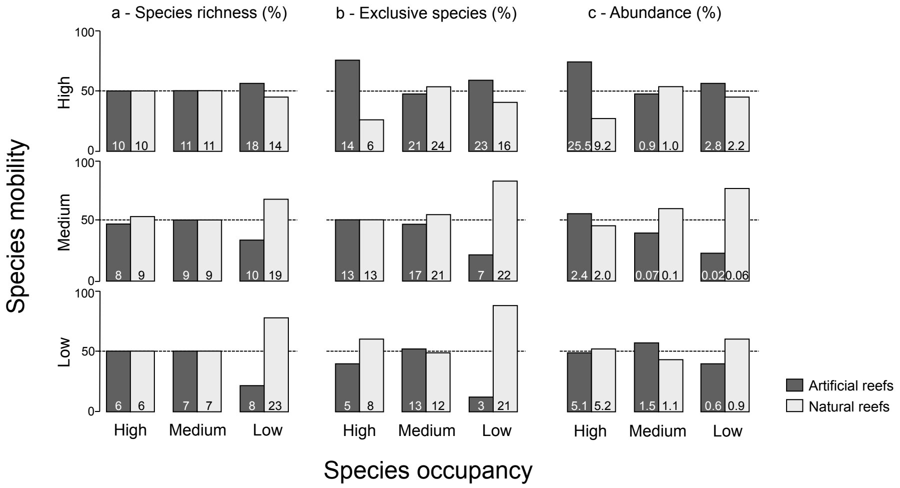


Figure 1.2. Percentage of a) species richness, b) exclusive species, and c) total species abundance found in artificial (dark bars) and natural (light bars) substrates. Numbers within bars are a) total number of species, b) total number of exclusive species, and c) total abundance (x10^3) pooled across substrates as a function of species occupancy (high, medium, and low occupancy, x-axis) and mobility (high, medium, and low mobility, y-axis).

Table 1.2. Summary of the three-way analysis of variance on a) species richness, b) Shannon diversity index, c) number of exclusive species, and d) total abundance of specimens with substrate type, species mobility, and species occupancy as fixed factors.

Variable	Factors	df	SS	MS	F	p
a. Richness	Substrate	1	3,234	3,234	3.46	0.064
	Mobility	2	11,193	5,596	5.99	0.003
	Occupancy	2	287,973	143,987	154.22	<0.001
	Substrate * Mobility	2	2,873	1,436	1.53	0.217
	Substrate * Occupancy	2	4,024	2,012	2.15	0.119
	Mobility * Occupancy	4	1,0408	2,602	2.78	0.028
	Substrate*Mobility*Occupancy	4	8,801	2,200	2.35	0.055
	Residuals	162	151,245	934		
b. Diversity	Substrate	1	7,618	7,618	5.27	0.022
	Mobility	2	6,210	3,105	2.14	0.119
	Occupancy	2	200,250	100,125	69.31	<0.001
	Substrate * Mobility	2	1,855	928	0.64	0.527
	Substrate * Occupancy	2	5,064	2,532	1.75	0.176
	Mobility * Occupancy	4	14,217	3,554	2.46	0.047
	Substrate*Mobility*Occupancy	4	11,800	2,950	2.04	0.09
	Residuals	162	234,025	1,445		
c. Exclusive species	Substrate	1	12,103	12,103	5.71	0.017
	Mobility	2	16,201	8,100	3.82	0.023
	Occupancy	2	20,717	10,359	4.89	0.008
	Substrate * Mobility	2	8,423	4,211	1.98	0.14
	Substrate * Occupancy	2	20,099	10,050	4.74	0.009
	Mobility * Occupancy	4	9,851	2,463	1.16	0.329
	Substrate*Mobility*Occupancy	4	21,138	5,284	2.49	0.044
	Residuals	162	343,088	2,118		
d. Abundance	Substrate	1	149	149	0.17	0.677
	Mobility	2	276,597	138,299	160.2	<0.001
	Occupancy	2	45,298	22,649	26.23	<0.001
	Substrate * Mobility	2	958	479	0.55	0.575
	Substrate * Occupancy	2	1,904	952	1.1	0.334
	Mobility * Occupancy	4	10,771	2,693	3.11	0.016
	Substrate*Mobility*Occupancy	4	9,928	2,482	2.87	0.024
	Residuals	162	139,847	863		

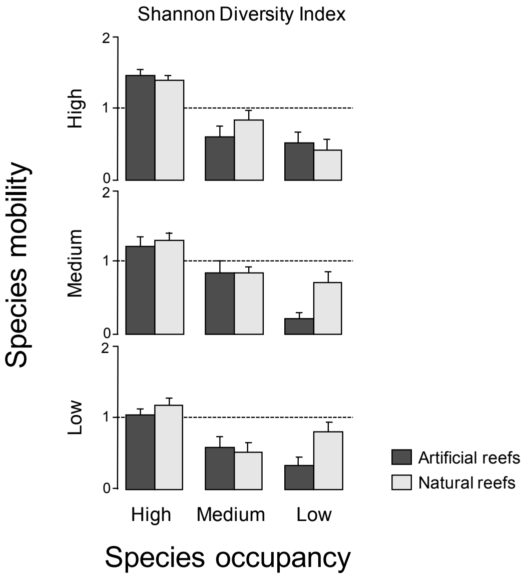


Figure 1.3. Mean (±1SE) Shannon diversity index of the species found in the 10 artificial (dark bars) and adjacent natural (light bars) substrates as a function of species occupancy (high, medium, and low occupancy, x-axis) and mobility (high, medium, and low mobility, y-axis).

Seven out of the 10 natural substrates had more exclusive species than their artificial counterparts, yet the total number of exclusive species failed to statistically differ between natural and artificial substrates (paired t-test, T=-0.918, df=9, p=0.382). The total number of exclusive species that were found in either natural or artificial substrates varied as a function of occupancy and mobility (Fig. 1.2b, χ^2= 9.886, df=2, p=0.007). High occupancy species with high mobility were more often seen exclusively in artificial than in natural substrates (56 *vs.* 42) while the opposite was true for low occupancy species with medium (36 *vs.* 56) and low (19 *vs.* 37) mobility (Fig. 1.2b). Substrate type also had an effect on the average number of exclusive species, although its effect varied as a function of mobility and occupancy (three-way ANOVA, significant substrate type effect and its interaction with occupancy and mobility, Table 1.2c).

The total number of specimens also failed to statistically differ between natural and artificial substrates (paired t-test, T=1.151, df=9, p=0.280). Yet, the total number of specimens in natural and artificial substrates varied as a function of occupancy and mobility (Fig. 1.2c, χ^2= 512.786, df=4, p<0.001). High occupancy species with high mobility were more abundant in artificial than in natural substrates (25.4 *vs.* 9.2) while the opposite was true for low occupancy species with medium (17 *vs*. 56) and low (600 *vs.* 893) mobility (Fig. 1.2c). We also found that the average number of specimens found in natural and artificial substrates varied as a function of species occupancy and mobility (three-way ANOVA, significant interaction term between substrate type, occupancy, and mobility, Table 1.2d).

NAR varied as a function of species occupancy, species mobility, and their interaction (p=0.005, p<0.001, and p=0.005, respectively, Table 1.3). Age had no effect on *NAR*, either directly (p=0.436, Table 1.3) or through its interaction with species occupancy and mobility (p=0.121, Table 1.3). Low occupancy species with medium and low mobility were more abundant in natural than in artificial substrates (Fig. 1.4). High mobility species showed negative *NAR* values regardless their occupancy (Fig. 1.4). Permutational analysis of variance (PERMANOVA) failed to detect differences in species abundances between natural and artificial substrates (Pseudo-F=1.064, df=1, p=0.354, Fig. 1.5).

Table 1.3. Summary of the two-way analysis of covariance on the *Natural-Artificial Ratio* (*NAR*) using species mobility and occupancy as factors and age of the artificial substrates as covariate.

Factors	*df*	*SS*	*MS*	*F*	*p*
Occupancy	2	194,601.6	97,300.8	5.281	0.005
Mobility	2	290,674.5	145,337.2	7.888	0.000
Age	1	11,182.5	11,182.5	0.607	0.436
Mobility * Occupancy	4	278,698.1	69,674.5	3.781	0.005
Mobility * Occupancy * Age	4	135,015.3	33,753.4	1.832	0.121
Error	478	8,807,322.7	18,425.3		

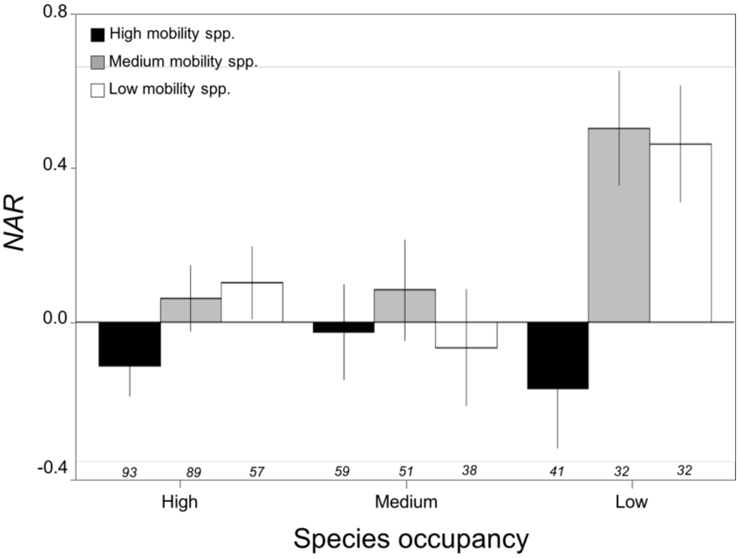


Figure 1.4. Mean (±1SE) *Natural-Artificial Ratio* (*NAR, y-axis*) of the species found in the 10 artificial and adjacent natural substrates as a function of species occupancy and mobility (x-axis). Positive *NAR* values are obtained with larger species abundance in natural than in artificial substrates, while negative *NAR* values are obtained with larger species abundance in artificial than in natural substrates. Numbers below bars are the number of NAR values (i.e., species) contributing to each occupancy x mobility combination. See Materials and methods for additional details.

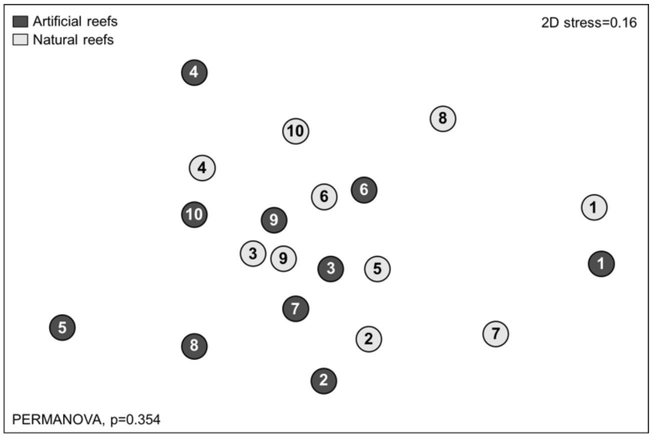


Figure 1.5. Non-metric multidimensional scaling (MDS) based on Bray-Curtis distance similarity matrix calculated from square-root transformed abundances of all species found in artificial (dark) and natural (light) substrates. Numbers within circles indicate locations as specified in Table 1.1. P value provided by permutational analysis of variance to test for differences between artificial and natural substrates. See text for additional details.

1.4. Discussion and Conclusion

Human alteration of coastal ecosystems is widespread and artificial substrates are becoming a significant habitat in shallow rocky communities (Airoldi and Beck, 2007). The proliferation of artificial structures in the sea, referred to as ocean sprawl (Firth et al., 2016), is a cause of concern because artificial substrates may not function as the natural substrates they often replace (Carr and Hixon, 1997; Airoldi and Beck, 2007; Burt et al., 2009). Many studies have evaluated whether communities in natural and artificial substrates differ, yet evidence is somehow contradictory and incomplete. For example, fish populations in artificial structures can be either larger (Jessee et al., 1985; Rilov and Benayahu, 2000; Granneman and Steele, 2015), similar (Santos et al., 2013; Ross et al., 2016), or smaller (Carr and Hixon, 1997; Rooker et al., 1997) than in natural reefs. Differences between natural and artificial substrates may vary depending on the variable recorded (e.g., species richness, species abundance, species diversity), the location investigated, the species quantified, or the complexity of the artificial structures, among others (Hunter and Sayer, 2009; Granneman and Steele, 2015). Our results showed biodiversity differences between adjacent natural and artificial substrates. These differences were majorly driven by the larger diversity of low occupancy species with medium or low mobility (i.e., rare benthic and sessile species) in natural substrates and the larger abundance of high occupancy and high mobility species in artificial substrates (i.e., common demersal fish species). Occupancy and mobility were, therefore, critical species traits to explain differences between substrate types. Failure to include these species traits resulted in non-significant differences between both substrate types. Our results suggest that the more common and mobile species create an illusion of natural communities in artificial substrates, by homogenizing both habitats and masking the negative effect that artificial substrates have in a large proportion of species. We found no evidence to support that these differences decreased over time, suggesting that artificial substrates are bad surrogates of their natural counterparts, at least over the 54-yr span investigated in our study.

There are reasons to expect that artificial substrates can mimic or surpass the biodiversity found in natural substrates (Baine, 2001). Artificial structures may provide additional habitats and refuge to those available in natural reefs, which could result in increased species richness, abundance, or diversity (Menge 1976; Jessee et al., 1985; Granneman and Steele, 2015). Out of the many possible artificial structures deployed in the ocean, artificial reefs have been widely used as a tool to help mitigate undesired trends such as habitat loss (Pickering and Whitmarsh, 1997) or to help preserve, restore, or enhance desired ecological functions such as diversity and production (Perkol-Finkel and Benayahu, 2005) or fisheries (Baine, 2001). Artificial reefs built with concrete blocks seem to increase both fish species and fish biomass (Pickering and Whitmarsh, 1997) as compared to artificial reefs built with pipes or natural reefs (Brock and Norris, 1989). Compared to natural reefs, the smaller size of artificial reefs can also explain higher species densities due to increase reef perimeter/area ratio (Jessee et al., 1985; DeMartini et al., 1989; Bohnsack et al., 1994). Most evidence for enhanced biodiversity (in a broad sense) by artificial reefs stem from fish data (Svane and Petersen, 2001), but increased invertebrate and algal populations have also been reported (Hunter and Sayer, 2009; Granneman and Steele, 2015). Whether the increased abundance, biomass, or diversity (in a broad sense) found in artificial reefs is due to increased production in the artificial structure or to attraction from surrounding environments, i.e., the production vs attraction debate (Pickering and Whitmarsh, 1997), remains unresolved.

Yet marine artificial structures can be deployed with no ecological/conservational goals in mind, for example, to provide shelter for boats as the breakwaters investigated in our study. These type of structures can show trends that diverge from those found in artificial reefs, with decreased biodiversity (in a broad sense) on artificial structures (Chapman, 2003, Airoldi et al., 2015). Our results provided evidence that the effect of artificial substrates varied as a function of the variable and species (or species group) investigated. Three set of data supported evidence for increased performance of artificial over natural substrates in our study. First, average *NAR* (*Natural-Artificial Ratio*) for high mobility species was negative, providing evidence for larger abundance of high mobility species in artificial than in natural substrates. Because *NAR* was calculated for every species in our study, the negative average values suggest that the larger abundance of high mobility species found in artificial substrates was a general pattern driven by many species. In fact, 80% of the high occupancy and 45% the low occupancy species with high mobility were more abundant in artificial substrates (as opposed to only 20% and 30% that were more abundant in natural substrates). Second, total and average abundance of high occupancy species were higher in artificial than in natural substrates. Third, the number of exclusive high mobility species with high occupancy found in artificial substrates doubled those found in natural substrates. Our results might suggest that the success of these species stem from their capacity to inhabit a variety of habitats (high occupancy) and to occupy new habitats as they become available (high mobility). All high mobility species in our study were demersal fish, so our study supports for the increased fish abundance and biomass found in many artificial reefs (Chapman, 2003), often deployed with specific conservation goals (as opposed to the coastal protection goals of the breakwaters investigated in our study). Increased fish abundance is a sought-after effect that can bring benefits to multiple stakeholders, including recreational and commercial fishing (Whitmarsh et al., 2008) or diving industry (van Treeck and Schuhmacher, 1999; Crabbe and McClanahan, 2007; Kirkbride-Smith et al., 2013), among others. Given that only high mobility species showed increased performance in the artificial substrates, our results could support for a stronger attraction than production effect in the attraction vs production debate (Pickering and Whitmarsh, 1997).

Our data showed stronger evidence for decreased performance of artificial over natural substrates, which was driven by low occupancy species with medium and low mobility. In our study, medium mobility species included multiple invertebrates and cryptic fish species. Adult organisms of these species are clearly more attached to the substrate than demersal fish and have a somehow reduced mobility. In our study, low mobility species included any sessile organism permanently attached to the substrate and, therefore, with highly restricted (i.e., nil) mobility. Other studies have also reported decreased artificial reef performance associated with sessile species, i.e., higher coral richness and diversity in natural habitats than in artificial reefs (Perkol-Finkel and Benayahu, 2004; Perkol-Finkel et al., 2005, 2006; Burt et al., 2009). Our data also showed that artificial substrates had lower numbers of low occupancy benthic and sessile species that were observed exclusively in either the natural or the artificial substrate, giving additional evidence for the decreased performance of artificial substrates in species richness. Yet, abundance of sessile species may be higher in artificial than natural reefs (Hunter and Sayer, 2009; Granneman and Steele, 2015). Even more, artificial reefs can be less diverse but, at the same time, hold higher abundance than natural reefs (Burt et al., 2009). We found the opposite, i.e., larger total abundance per species and larger average *NAR* of low occupancy benthic and sessile species on natural reefs, providing evidence for higher species density in natural than in artificial substrates. Because only medium and low mobility species with low occupancy showed decreased performance in the artificial substrates, these results could support for a weaker production than attraction effect in the attraction vs production debate (Pickering and Whitmarsh, 1997). If our data can be interpreted within this debate, our study might provide greater support for the attraction (improved performance of demersal fish, i.e., associated with the attraction effect) over the production effect (reduced performance of sessile species, i.e., associated with production effect) of the debate. Information on the size distribution of species in both substrate types (not analyzed in our study) could help shed more light into this unresolved debate.

Overall, and beyond the specific results, our findings suggest that artificial substrates missed an important component of biodiversity, the least widely distributed benthic and sessile species.

Despite their scarcity, these species were 40% of the total number of species in our study, representing a significant part of the biodiversity of the rocky littoral bottoms. Yet, because the species missing in our artificial substrates were the least apparent species in the community, artificial substrates gave an illusion of natural-like substrates driven by the most conspicuous species. In fact, and for all variables analyzed in our study, natural and artificial substrates failed to differ statistically unless we considered species occupancy and mobility. These species traits were, therefore, critical to find differences between natural and artificial substrates and provided evidence for the big impact that common species have at the community level, both statistically and at an observational, landscape scale. The large influence of common species at the community level exceeds biodiversity implications *per se*, linking biodiversity with ecosystem functioning (Grime, 1998). While common species are responsible for immediate effects, the filter and founder effects of the not-so-common species may become apparent at longer time scales and cannot be neglected (Grime, 1998).

Long-term data on the composition and abundance of species inhabiting artificial reefs is scarce, particularly with proper comparisons with natural reefs. In a 15-year study of artificial reefs off Rio de Janeiro, fish species richness, abundance, and biomass increased up to the 6-7th year to decrease thereafter although, unfortunately, no data is available from adjacent natural reefs (Neves dos Santos and Zalmon, 2015). Other studies have comparisons with natural reefs, but the artificial reefs have been few years underwater. Fish populations in young artificial reefs seem to be larger than in natural reefs (Bohnsack et al., 1994; Clark and Edwards, 1999; Chapman and Clynick, 2006) although fish assemblages may (Bohnsack et al., 1994; Clark and Edwards, 1999) or may not (Tupper and Hunte, 1998) differ. Data for mollusks showed an opposite pattern with lower diversity, richness, and evenness but larger number of specimens and dominance in artificial than natural reefs (Badalamenti et al., 2002). However, their natural and artificial reefs were associated with clear and turbid waters, which could act as a confounding factor (Badalamenti et al., 2002). Besides fish, Chapman and Clynick (2006) also quantified the algal and sessile invertebrate populations on their natural and artificial reefs, which were both similar.

At the other side of the age spectrum, data from a single 119-year old shipwreck and the adjacent reef where it sunk showed that natural-like communities developed only where the structure of the wreck matched the reef structure (Perkol-Finkel et al., 2006). Despite being underwater for over a century, wreck sections that differed structurally from natural reefs also differed ecologically (Perkol-Finkel et al., 2006). Likewise, sessile communities in natural reefs differed with those from breakwaters of varying age, even after 31 years underwater (Burt et al., 2011). Similarity between natural and breakwater communities increased with time (Burt et al., 2011), which could be interpreted as an example of directional replacement of species. In fact, turf algae dominated breakwaters until 1.5 years, followed by a peak in bivalves on the 3.5 to 5.5-year-old reefs, and then coral cover gradually increased with reef age (Burt et al., 2011). These transitions from short-lived, fast-growing, opportunistic species to long-lived, slow-growing, competitively superior species agrees with the directional replacement of species in classic succession although it does not guarantee stable communities equivalent to those found in surrounded natural reefs (Svane and Petersen, 2001). Other studies have shown that artificial reef communities may take over a decade to resemble those in natural reefs (Aseltine-Neilson et al., 1999; Abelson and Shlesinger, 2002; Perkol-Finkel and Beneyahu, 2004, 2007), but the resulting community may not be natural-like (Perkol-Finkel et al., 2006).

Our study is a snapshot comparison of multiple artificial substrates and their adjacent natural counterparts. For each location, natural and artificial substrates were equivalent in terms of orientation, wave exposure, depth, and slope. The artificial substrates we investigated differed in ecological conditions and spanned from 0 to 54 years underwater. We observed no major, community-level temporal trend in the presence and abundance of species. In the 20 reefs studied, we quantified presence and abundance of a total of 107 species. Detailed analyses at the species level or species-specific patterns along the 50-year timespan of our study are beyond the scope of this study. Our goal was to test whether communities inhabiting artificial substrates were equivalent to those found in natural substrates of the same area. As discussed previously, there are multitude examples with varying results often leading to contrasting conclusions. Our approach focused on many species to maximize ecological patterns over species specific responses, paired every artificial substrate with its adjacent natural reef to minimize community differences due to distinct geographic and environmental conditions, and used artificial substrates with varying numbers of years underwater to test for temporal trends in community organization. Overall, i.e., without considering species mobility and occupancy in our models, we found no statistical differences in diversity (broadly defined) between artificial and natural substrates. They seemed to be equivalent. These results were driven by the strong influence of common species, which minimized the large differences in low occupancy species with medium and low mobility. These benthic and sessile species were 40% of the species in our study and they were significantly less represented, both in terms of species number and abundance, in artificial substrates. Inclusion of species mobility and occupancy was therefore critical to describe the biodiversity loss associated with the artificial communities. Contrary to our expectations, age played no significant role to explain differences between natural and artificial substrates. Our results suggest that, regardless of directional replacement of species, communities developing in artificial substrates need not match their natural counterparts, as previously reported (Perkol-Finkel et al., 2006). This output agrees with the ecological succession following non-catastrophic disturbances, despite artificial substrates do offer a denuded substrate for primary succession (Platt and Connell, 2003). Given the current proliferation of artificial structures in our shallow marine environments, we might be building up a large biodiversity loss in shallow water marine communities around the globe. This unintentional loss is hard to detect as it seems to target the least conspicuous and less investigated benthic and sessile species. Fish species, the main target of many studies, seem to thrive in artificial substrates both in terms of number and abundance of species. Since communities inhabiting artificial substrates deviate from natural communities, artificial structures could lead to an increase of regional diversity (Connell and Glasby, 1999). Our results suggest otherwise that artificial substrates are not surrogates for natural communities (Burt et al., 2011). Understanding the strengths and weaknesses of artificial structures will sure lead to a more effective use of these habitats. Should we aim to minimize biodiversity loss and promote its conservation, reliance on artificial substrates as surrogates of natural reefs looks dubious. Strategies that lessen habitat destruction combined with alternative protection and restoration measures may provide more efficient mechanisms for biodiversity conservation (Abelson et al., 2016; Geist and Hawkins, 2016; Kollmann et al., 2016).

Chapter II

Measuring community recovery: unprotected marine areas have more resistance than partially protected areas to increase their diversity

This research is based on:

Sanabria-Fernandez JA, Alday J, Becerro MA, (In preparation). Measuring community recovery: unprotected marine areas have more resistance than partially protected areas to increase their diversity.

Picture: Underwater seascape from Cabo de Gata marine reserve. In the picture, you can see a group of *Salpa sarpa*. Jose A. Sanabria-Fernandez took this picture in 2014 during the sampling trip.

Abstract

Biodiversity is suffering an unprecedented decline. This diversity loss is leading to the degradation of ecosystem properties key for diversity conservation such as resilience and resistance to change. Understanding how communities resist change can help improve conservation strategies and increase the benefits of protection. Here, we quantified the density of fish, invertebrate, and sessile species of the marine reserve of Cabo de Gata and adjacent areas with no protection and used the multivariant distance between centroids as a measure of resistance to change. The rationale was that communities are more prone to become alike the closer they are multidimensionally to each other, i.e., the more similar they are in the number and abundance of species. Using the fully protected zones within the Cabo de Gata marine protected area as our target community, we identified geographic areas that had a low recovery cost and were more prone to recover diversity and become like fully protected zones. Our study found more diverse communities in terms of species richness and densities with increased protection. We also found that unprotected communities had larger resistance than partially protected communities to become like fully protected communities. Overall, our approach quantified the ecological cost of recovery, identified geographic areas with a low resistance to improve biodiversity, and could contribute to prioritizing areas to be preserved. Therefore, the correct application of this methodology can restructure conservation policies, increasing the benefits of protection on biological diversity.

2.1. Introduction

Biodiversity conservation is a major need of our times. Human activities are causing swift, profound, and ongoing environmental changes that are affecting the earth's system (Scholes, 2016). These abrupt ecological changes could lead the earth to an alternate state with adverse consequences for humanity (Scheffer et al., 2001; Lenton et al., 2008; Barnosky et al., 2011), making a strong argument for the beginning of a new era, the Anthropocene (Crutzen and Stoermer, 2000; Steffen et al., 2011; Lewis and Maslin, 2015). Out of nine planetary boundaries defined to prevent a global phase shift, biodiversity loss has surpassed its safety threshold (Rockström et al., 2009). Current extinction rates are 100 to 1000 times larger than background extinction rates (Alroy, 2015), providing support for the sixth global mass extinction (Barnosky et al., 2011; Dirzo et al., 2014; McCauley et al., 2015). Since the evolution of new species usually takes thousands of generations (Gavrilets, 2003), we may be facing a long-lasting biodiversity loss and an associated decline in ecosystem services. Thus, there is an urgent need to implement effective conservation measures to halt biodiversity loss, safeguard our beset natural resources, and restore biodiversity and ecosystem services (IPBES, 2019; EU2030 Biodiversity Strategy, 2020). Not surprisingly, biodiversity conservation is out of the academic box and has become an integral part of society with a presence in (most) political agendas (United Nations, 2000; Youatt, 2015; Lobo and Jacques, 2017).

Resilience is a measure of the persistence of systems. An extent of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables (Holling, 1973). This definition is multidimensional. It integrates persistence, resistance, and the existence of local asymptotic stability at multiple equilibria (Donohue et al., 2016). Therefore, resilience is a multifaceted concept, because includes multiple components. Also, Obura, (2005) suggests a cascade of stages in applying the resilience concept to coral bleaching that includes avoidance, resistance, tolerance, and resilience. Others have approached resilience as a combination of resistance and recovery (MacGillivray et al., 1995; Oliver et al., 2015). However, most of the literature indicates that resistance is inherent to the concept of resilience (Tilman and Downing, 1994; Holling, 1996; Côté, and Darling, 2010). In general, resistance is the ability of a community to remain unchanged when challenged by disturbances, i.e., resistance to remain (Grimm and Wissel, 1997). In this study, we adapted the resistance approach of Shade et al. (2012), based on distances between communities, as a concept of resistance to change. If we set a highly degraded, low diversity, unhealthy biological community as a starting point, it will present a high resistance to become a pristine, highly diverse, healthy community. This happens because the low diversity community has to change its biological composition tremendously to become similar to the high diversity community. This approach to resistance as the biological distance between communities can contribute to knowing the cost of change (in biological terms) among communities, presenting itself as a tool with full applicability in the management and conservation of biological diversity as we can measure the cost of any given community to become a highly diverse community (i.e., the cost of recovery).

Fueled by the Convention on Biological Diversity (CBD), the designation of protected areas has emerged as a relevant management tool to counteract current biodiversity trends (Secretariat of the CBD, 2014). Traditional designation of protected areas combines multiple biological, social, and aesthetic criteria to target biologically valuable areas that maximize conservation benefits (Roberts et al., 2003; Selig et al., 2014; Mcleod et al., 2019). Like their terrestrial counterparts, effective marine protected areas (hereafter, MPAs) are known to preserve biodiversity, enhance the biomass of threatened and fished species, and increase resilience against natural and anthropogenic disturbances (Halpern, 2003; Edgar et al., 2014; Sanabria-Fernandez et al., 2019). MPAs can also provide resistance against global stressors (Bates et al., 2013; Ardura et al., 2016) and faster recovery than unprotected areas (Bevilacqua et al., 2006; Caselle et al., 2015). Despite the relevance of these factors, the designation of protected areas often fails to consider their resistance and recovery potentials (Game et al., 2008; Abelson et al., 2016). Quantifying the community resistance to change and the potential for recovery would contribute to improved MPA design since, to be effective, MPAs need to shift from the unprotected state to an "improved" state. In other words, unprotected areas with high resistance to change their disturbing state will be poor candidates for effective MPAs.

But, what is the resistance of unprotected areas to become equivalent to protected areas in the absence of anthropogenic pressures? Can we use some metrics to rank unprotected areas according to their resistance to change? Moreover, resistance to change is critical but so is the direction of the change because, ultimately, MPAs aim to develop communities with increased biodiversity (in a broad sense) as compared to unprotected areas. Can we afford to protect any given area without understanding its potential to achieve its conservation goals? In this fragile context lies the need for our study, which is to report the application of a new conservation metric based on the resistance of the biological communities to change. Specifically, to calibrate our approach, we studied the benthic communities in areas with total, partial, and no protection areas of the Cabo de Gata marine reserve and adjacent waters. First, we quantified the biological community on fully protected, partially protected, and unprotected areas (i.e., the fish community, the invertebrate community, the sessile community, and the combination of these three partial communities). Second, we quantified the cost and the degree of change necessary for unprotected and partially protected communities to become like a fully protected community. And third, we investigated the species that were sensitive to the absence of protection since they are responsible for the resistance of unprotected areas to change. Our approach not only estimates the cost of recovery but also allows us to know the species or communities more prone to recover (or to forfeit if a protected area is no longer protected). This is in agreement with the major concerns of international conservation organizations. Our approach could, therefore, guide in the establishment of protected areas, helping select the best areas to preserve (most prone to achieve conservation goals) and increasing the efficiency of the protection figures.

2.2. Material and Methods

Study area

We sampled 28 locations located in the Cabo de Gata marine reserve and their adjacent waters in Almería province (southeast from the Iberian Peninsula). Specifically, eight of these locations were in the total protection zone, 10 in the partial protection zone, and 10 in localities adjacent to the reserve, but unprotected (Fig. 2.1). In this article, fully protected zones (FPZs) referred to the areas within the marine reserve with the strongest restrictions and levels of surveillance, i.e., No-take zones. Partially protected zones (PPZs) referred to the areas within the marine reserve but with limited surveillance and activities such as recreational fishing and scuba diving allowed. Finally, unprotected zones (UNZs) referred to areas with no surveillance outside the marine reserve but in adjacent waters. All sampled locations were shallow rocky reefs between 6 and 10 m deep.

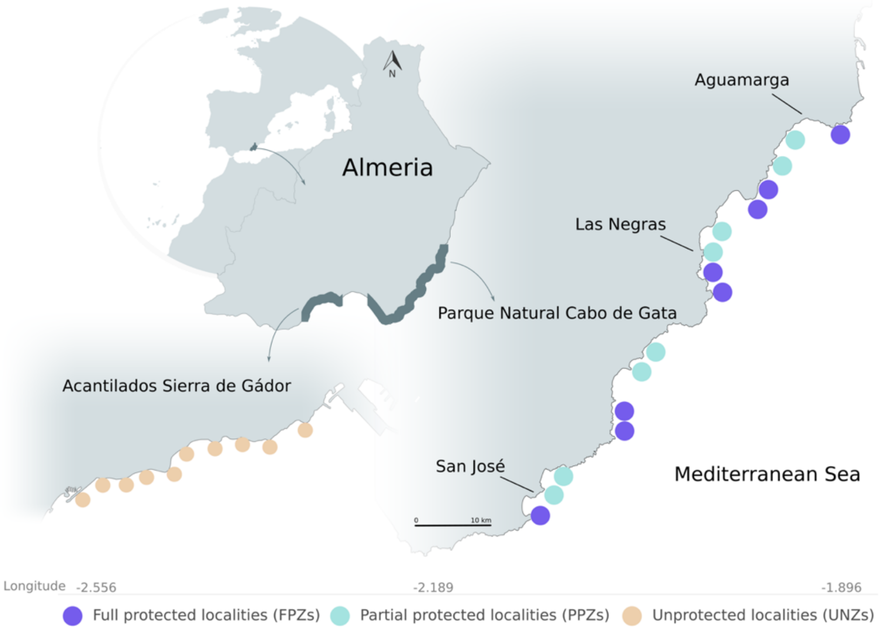


Figure 2.1. Map of the study area in the Almeria province (Mediterranean Sea). The circles represent the sampled sites (N=28). And the colors the protection status.

Data collection

At each sample location, we used the standardized visual census protocol of the Reef Life Survey program to obtain the marine biodiversity data (Edgar and Stuart-Smith, 2014). Firstly, we set up a line transect of 50 m long on a rocky reef and applied three methods to identify species 0.025 m of size. In method 1 (hereafter, fish community), we identified all the fish species and quantified their density and size, on a belt transect of 50 m long and 10 m wide (Fig. 2.2). In method 2 (hereafter, invertebrate community), we quantified the number and abundance of cryptic fish and mobile invertebrates in the 50 m long and 2 m wide transect (Fig. 2.2). Lastly, in method 3 (hereafter, sessile community), we took 20 photographs of the seabed along the transect to quantify the coverage of algae, phanerogam, and other sessile species (Fig. 2.2).

We used CPCe software (Kohler and Gill, 2006) to quantify the percentage of cover of sessile species. Specifically, Specifically, we randomly distributed 20 points over the central 0.2 x 0.2 m area of each photograph and identified the species underneath the points.

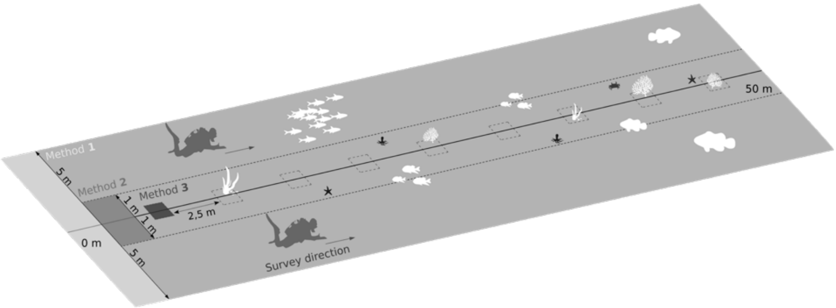


Figure 2.2. Reef Life Survey protocol outline. The three methods used and their technical specifications are represented.

Data analysis

We followed three sets of analyses to achieve the goals of the study. We first performed a Hellinger's transformation of the fish and invertebrate community to reduce the influence of high-density species (Oksanen et al., 2016). We also log-transformed (x+1) the percent cover of sessile organisms (Oksanen et al., 2016). Subsequently, we applied the "vegan" R package (Oksanen et al. 2016) to elaborate a dissimilarity matrix based on the Bray-Curtis distances for each of the fish, invertebrate, and sessile organism community. Finally, we used the fuse dissimilarity methodology to integrate the three matrices (containing data with various methods and units) into a single matrix (Bennion et al., 2015). Then, we used the richness of each taxonomic group (fish, invertebrate, and sessile) to compute a weighted sum of the dissimilarity matrices (Bennion et al., 2015). Subsequent analyses of global community composition relied on this fused species matrix.

The first set of analyses tested for differences in the composition of the biological community (fish, invertebrates, sessile organisms, and their combination) as a function of protection. We ran a Permutational Multivariate Analysis of Variance (permanova) trough "vegan" R package (Oksanen et al., 2016) on the fused species matrix (whole biological community) and on each community matrices separately (fish, invertebrate, and sessile organisms). Pair-wise comparisons between protection status were Bonferroni corrected (Sokal and Rohlf, 1995). To visualize the community plots, we used the "vegan" R package (Oksanen et al., 2016) and "ggplot2" (Wickham, 2016) R packages.

The second set of analyses strategy quantified the resistance (cost of change) and sensitivity (degree of change) of UNZ and PPZ communities to become like a biological community in an FPZ. In our study, we defined resistance as the distance between two communities and their multiple combinations in the different protection status, (i.e., the distance from UNZs to FPZs, and from PPZs to FPZs). Conceptually, a high distance value between UNZs and FPZs indicates that UNZs are very resistant to become like FPZs, i.e., UNZs show little capacity for recovery. On the other hand, we defined sensitivity as the difference between unity and resistance, i.e., the degree of community change from UNZs to FPZs, and from PPZs to FPZs. To compute resistance and sensitivity, we used FPZs as controls, i.e., the community of reference. In short, we defined a multivariate distance-based metric that measured the rate of change in community structure based on both functional identity and abundances. To do so, we calculated the distance of each locality within unprotected and partially protected zones to the metacommunity centroid of the fully protected locations (Anderson, 2006).

Finally, the third set of analyses determined the species and densities that were sensitive to the absence of protection. Specifically, we sought for which species, if any, changed their abundance when comparing UNZs or PPZs to FPZs. In other words, once again, FPZ functioned as a control, i.e., the community of reference. For each community (fish, invertebrates, and sessile organisms), we fit a set of generalized linear models to the multivariate density data with the "Mvabund" R package (Wang et al., 2016). We performed the data processing, statistical analysis, and results representation in R software (R Core Team, 2020).

2.3. Results

Protection status and community composition

The community composition as a whole varied with protection status (Permanova, $p<0.001$ for all comparisons, Fig. 2.3a, Table 2.1a). Specifically, the protection status accounted for 35 % of the total variance, showing significant differences in community composition between the three protection levels (Table 2.1a). The marine fish community varied with protection levels (Fig. 2.3b, Table 2.1b) and showed statistical differences between all protection levels (Table 2.1b). The invertebrate community also varied with protection (Fig. 2.3c, Table 2.1c), except for the FPZs vs PPZs comparison ($R^2=0.07$, $p=0.054$, Table 2.1d). The sessile community differed between the three levels of protection, with significant differences for all comparisons (Fig. 2.3d, Table 2.1d).

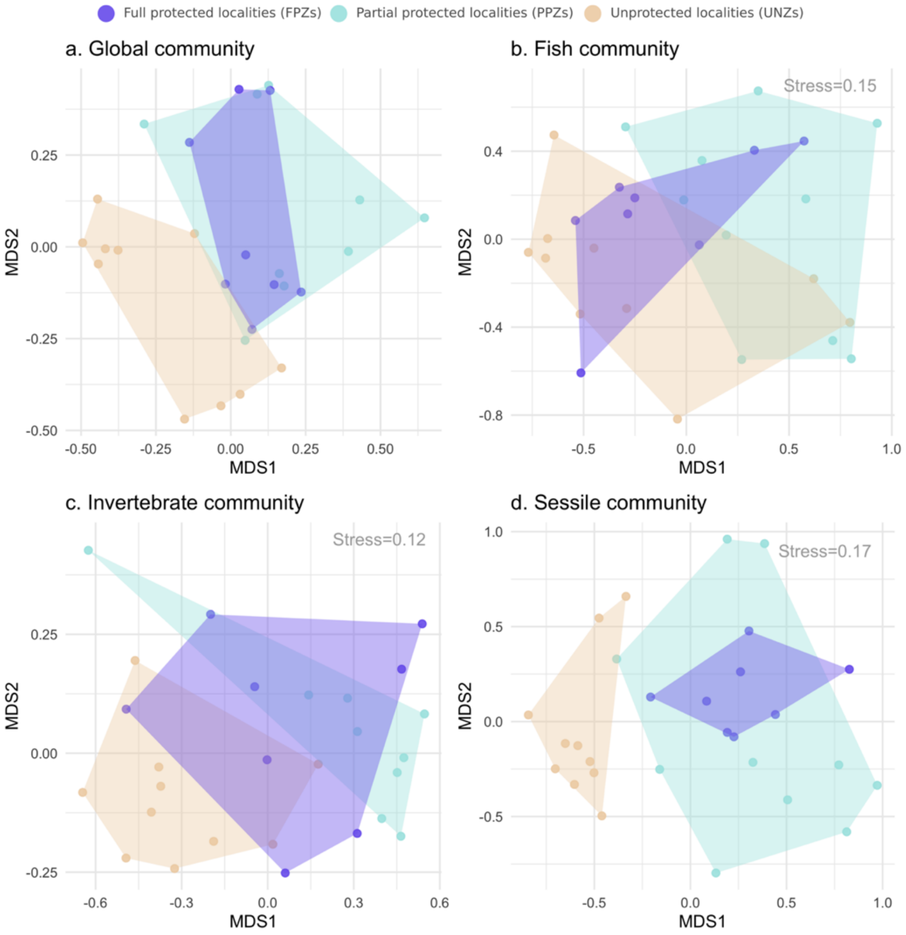


Figure 2.3. Non-metric multidimensional scaling (NMDS) ordination of species species-abundance matrices from the three monitoring types in Cabo de Gata.

Table 2.1. Summarized results of Permanova test. Significant differences are marked in bold.

	R^2	F	*P*
a) Gobal Community composition			
All localities	0.35	6.23	**0.001**
FPZs *vs* PPZs	0.11	3.90	**0.006**
FPZs *vs* UNZs	0.24	8.55	**0.001**
PPZs *vs* UNZs	0.23	8.53	**0.001**
b) Fish community			
All localities	0.17	2.63	**0.009**
FPZs *vs* PPZs	0.07	2.18	0.048
FPZs *vs* UNZs	0.10	3.08	**0.013**
PPZs *vs* UNZs	0.13	4.01	**0.007**
c) Invertebrate community			
All localities	0.30	5.15	**0.001**
FPZs *vs* PPZs	0.07	2.53	0.054
FPZs *vs* UNZs	0.23	7.77	**0.001**
PPZs *vs* UNZs	0.24	8.10	**0.001**
d) Sessile community			
All localities	0.31	5.52	**0.001**
FPZs *vs* PPZs	0.09	3.14	**0.010**
FPZs *vs* UNZs	0.22	7.90	**0.001**
PPZs *vs* UNZs	0.19	6.20	**0.001**

Community resistance and sensitivity: from unprotected to fully protected areas

The resistance and sensitivity of UNZ communities to become compositionally similar to FPZ communities was larger than those of PPZ communities (Table 2.2a). Our resistance values ranged from 0.52 for the sessile community to 0.09 for the invertebrate community, which showed the least resistance to change from PPZs to FPZs. The composition of the invertebrate community in PPZs and FPZs were very similar (Table 2.2c).

We found larger sensitivity to change compositionally from PPZ to FPZ communities than from UNZ to FPZ communities (Table 2.2a). Second, the sensitivity to change compositionally was greater than the resistance for fish and invertebrate communities (Table 2.2b,c). The sensitivity of the sessile community to change from PPZs to FPZs was greater than their resistance. But, the resistance to change from UNZs areas to FPZs was higher than their sensitivity (Table 2.2d).

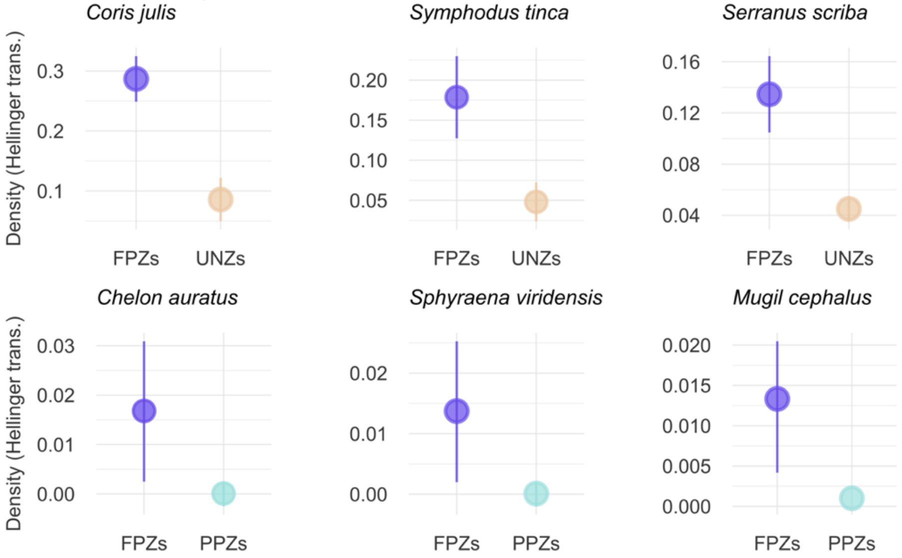
Table 2.2. Summarized results of compositional resistance and sensibility. Reported values are mean values ± SE.

	RD	Resistance	Sensitivity
a) Global community composition	0.35±0.02		
PPZs	0.53±0.03	0.32±0.07	0.68±0.07
UNZs	0.56±0.01	0.42±0.06	0.58±0.02
b) Fish community	0.33±0.06		
PPZs	0.50±0.05	0.23±0.07	0.77±0.07
UNZs	0.47±0.03	0.12±0.06	0.88±0.06
c) Invertebrate community	0.28±0.03		
PPZs	0.35±0.02	0.09±0.06	0.91±0.06
UNZs	0.37±0.02	0.18±0.05	0.82±0.05
d) Sessile community	0.33±0.03		
PPZs	0.58±0.03	0.44±0.05	0.56±0.05
UNZs	0.62±0.01	0.52±0.05	0.48±0.01

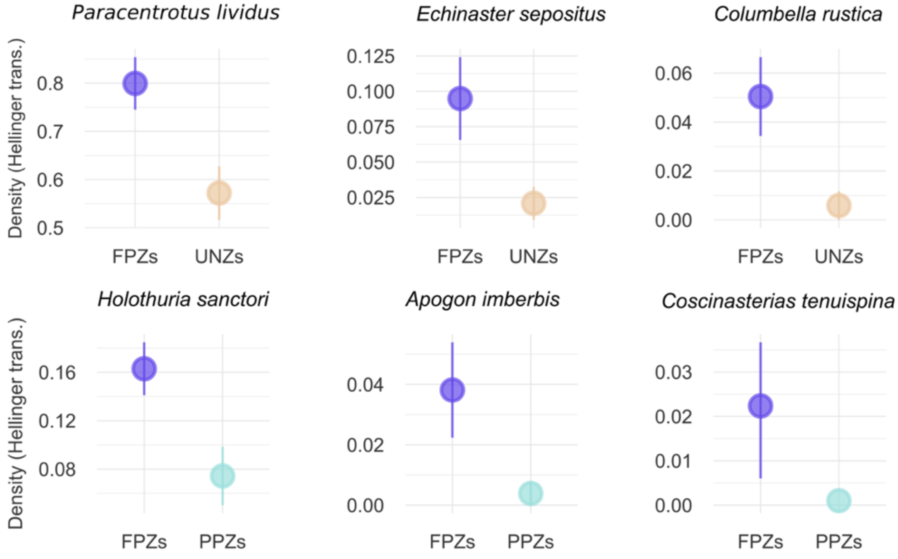
The most resistance and sensible species to change

Changes in resistance and sensitivity were responses that reflected the biological community when species density decreases, or even species disappear between different states of protection. Five fish species had higher densities within FPZs compared to UNZs or PPZs and only three species were exclusively present in FPZs (Fig. 2.4a, Table 2.3). Seven invertebrate species had a higher density within FPZs than in UNZs or PPZs, and 10 species were exclusively found within FPZs (Fig. 2.4b, Table 2.3). Five sessile species had greater coverage within FPZs than in UNZs or PPZs, and five species were exclusively found in FPZs (Fig. 2.4b, Table 2.3).

a. Fish community



b. Invertebrate community



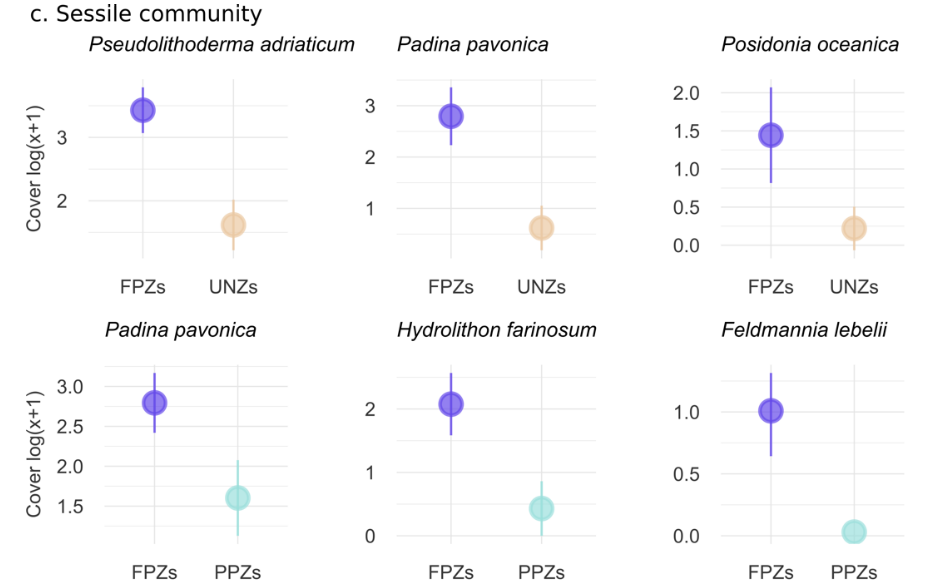


Figure 2.4. Representation a) fish, b) invertebrate, and c) sessile community, of the three species with the highest density or coverage within the FPZs and the comparison with the protection states. All these comparisons showed significant results $p<0.05$.

Table 2.3. Species that have a higher density or are present only in FPZs. All species have shown significant differences in the protection comparison (see Fig.2.4a, b, c).

	Protection comparative	
	UNZs vs FPZs	**PPZs vs FPZs**
a) Fish community		
	1. Coris julis	*1. Chelon auratus*
	2. Symphodus tinca	*2. Mugil cephalus*
	3. Serranus scriba	*3. Sphyraena viridensis*
	4. Diplodus vulgaris	
	5. Chromis chromis	
b) Invertebrate community		
	1. Echinaster sepositus	*1. Apogon imberbis*
	2. Columbella rustica	*2. Clibanarius aequabilis*
	3. Parablennius sanguinolentus	*3. Columbella rustica*
	4. Mitrea cornea	*4. Coscinasterias tenuispina*
	5. Muraena helena	*5. Echinaster sepositus*
	6. Percnon gibbesi	*6. Holothuria forskali*
	7. Parecentrotus lividus	*7. Holothuria sanctori*
		8. Muraena helena
		9. Parablennius rouxi
		10. Tripterigion melanurus
c) Sessile community		
	1. Pseudolithoderma adriaticum	*1. Padina pavonica*
	2. Padina pavonica	*2. Hydrolithon farinosum*
	3. Posidonia oceanica	*3. Feldmannia lebelii*
	4. Halopteris spp	
	5. Liagora viscida	
	6. Padina pavonica	
	7. Halopteris filicina	
	8. Amphiroa rigida	

2.4. Discussion

Marine Protected Areas are a key and essential tool to safeguard marine biodiversity (Hilborn, 2016). We are entrusting the future of marine biodiversity to a tool that can still substantially improve its functioning (Edgar et al., 2014). In this context, and to shed light on how to increase the benefits of biodiversity protection, we quantified the resistance (cost of change) and the sensitivity (degree of change) of the natural communities, two ecosystem properties that provide information on the resilience capacity of the biological community. Specifically, we analyzed whether biological communities varied with protection. Besides, we investigated the resistance and sensitivity (in biological terms) of the marine community to be transformed from the unprotected area or partially protected, to fully protected. Lastly, we tested which species increased their density or were only present in the areas of maximum protection. Overall our results showed that the biological composition and the resistance to change were dependent on the protection status, except some exceptions discussed below. Also, we identified the species that must appear or must increase their density for the UNZs and PPZs to become FPZs. Specifically, there were 8% of fish species, 17% of invertebrate species, and 14% of sessile species that are only in the areas of maximum protection, i.e., FPZs. For these reasons, this study provided a new approach to evaluate the cost and degree of change in marine communities and also identified the species more resistant or sensitive to change. Our approach has strong conservation applications because it allows incorporating resilience thinking into decision making. Also, because areas are well delimited geographically, our approach can detect the least resistant areas to preserve, which could lead to improve the efficiency of protection.

Currently, there are 26,984,530 km2 of marine protected areas globally (UNEP-WCMC, 2020). But the actual protection of such areas varies depending on their restrictions and enforcement, among other factors. For example, there are zones with intermediate restrictions in which certain selective fishing gears and sports such as scuba diving are allowed, called partial protection zones (PPZs in our study). There are also zones in which human activities are prohibited, these are the No-Take or fully protected zones (FPZs in our study). The latter are the areas that provide the greatest benefits to biodiversity conservation (Sala and Giakoumi, 2017). Paradoxically, these No-take are the protection zones with the least presence in our seas, occupying only 2.6% of the protected surface area (Marine Conservation Institute, 2020). We found that the marine community varied with protection, i.e., between UNZs, PPZs, and FPZs. However, Sciberras et al. (2013) did not show differences in marine fish density between partially and fully protected areas. In contrast, fish biomass was higher in the fully protected than in the partially protected areas (Sciberras et al., 2013, Campbell et al., 2017). Also, the structure of the invertebrate and sessile community is well-differentiated between UNZs and FPZs (Shears and Babcock, 2003). Overall, FPZs were the protection figures with the largest biodiversity benefits, and they are a vital instrument for conservation (Costello and Ballantine, 2015; Sala and Giakoumi, 2017). Nevertheless, even today, the selection of geographic areas to install a protection figure continues to be a challenge. Selig et al. (2014) proposed a methodology for detecting priority areas to be preserved based on species richness and human pressures. Also, Edgar et al. (2014) revealed the five factors that make a marine reserve effective, so an application of these factors could shed light on the detection of these priority areas to conserve. But unfortunately, the establishment of protection figures based on the biological capacity of recovery or resistance to change remains scarcely studied but fortunately undeferrable.

Establishing conservation strategies based on biological properties targetting resilience, such as the resistance or the sensitivity to change, can increase the efficiency of protection figures (Côté, and Darling, 2010). Our results showed that the resistance of the whole biological community (i.e., fish, invertebrates, and sessile organisms combined) to move from partially to fully protected zones is less than the resistance opposed by an unprotected community to become fully protected zones. The resistance of unprotected zones to become like a community in a fully protected zone was lower than that of a partially protected community (0.12 vs 0.23). A first plausible but unlikely scenario is that resistance reaches discrete values because the unprotected zones had a biological composition equivalent to the fully protected zones. A second perhaps more likely scenario might be the presence of poachers in the fully protected zones (Edgar et al., 2014). This would explain why the resistance between unprotected zones and fully protected zones is lower, despite the existence of significant differences between the communities. A third scenario might suggest that partially protected zones are receiving enormous pressure that moves them away from the fully protected zones (since certain extractive human activities are permitted), making the cost of recovery greater than that of the unprotected zones. This fact is undoubtedly worrying and needs to be addressed. Due to their high mobility capacity, fish may mask the clearer and more robust trends found with invertebrates or sessile organisms, similar to the masking function they play in artificial substrates (Sanabria-Fernandez et al. 2018). A potential way to clarify what is happening is to study illegal fishing pressure within the fully protected zones, and professional and recreational fishing in unprotected and unprotected zones, respectively (Arias et al., 2015; Harasti et al., 2019). However, establishing recurrent monitoring programs could provide extremely robust and enlightening results (Bates et al., 2013).

Compared to fish, benthic invertebrates are a group with reduced mobility (generally speaking) and may reflect more robust patterns (González-Duarte et al., 2014). In this sense, the resistance opposed by partially protected communities to become like communities in fully protected zones was small 0.09. The composition of both communities was similar and statistically not different. On the contrary, the resistance of unprotected zones communities to become like fully protected zones communities was 0.19, supported by significant differences between both communities. A potential interpretation of this interesting result is the existence of non-extractive pressures on the invertebrate community that is causing the degradation of this benthic community. For example, aquaculture installations (Silvert, 1992; Hargrave, 2010) or desalination plants (Ruso et al., 2007) can be modifying the nearby benthic community. In the same sense are the results of the sessile community, specifically, the resistance (cost of change) of the unprotected zones communities to become like fully protected zones communities was greater than their sensitivity (degree of change). This indicates that it is very costly (in biological terms) for this community to change. González-Duarte et al. (2014) showed that sessile communities or organisms are faithful indicators of the state of the environment around them. For this reason, our study may be indicating the presence of some non-extractive human pressure on this area that is modifying the entire invertebrate and sessile communities.

In this research, we used the distance that separates communities with different states of protection as a measure of the resistance to change. In other words, the path one community has to travel to become like the other one. We developed this approach from the idea of multivariate distances between communities of Shade et al. (2012). But, also Vasilakopoulos and Marshall (2015) and Vasilakopoulos et al. (2017) considered the concept of univariate distance to a tipping point as the relative resilience of the community. This distance can shed light on the properties of natural communities, such as resistance or resilience. Beyond using distances to detect priority areas to preserve, some approaches integrate the anthropogenic, environmental, and biological dimensions in the detection of these zones. For example, Green et al. (2009) and Davies et al. (2016) integrates the human, environmental, and biological dimensions in the detection of high marine resilience areas in tropical latitudes. However, these studies present a global vision of the system encompassing multiple factors and possibly masking an important fraction of the biological reality. On the contrary, our approach manages to obtain a faithful and real vision of biological resistance because it considers the entire biological composition of the community and respects the importance of each species, without distorting its reality.

Our conservation methodology has direct and potential applications to preserve the diversity of our seas. For example, the identification of areas with discrete values of resistance, being these firm candidates to be protected (because the cost of recovery in biological terms is small). This implies a reformulation of conservation policies because we could now estimate ahead of time how much the ecological cost of recovery is. And, it would allow us to elaborate on different recovery strategies, depending on the resistance of each area. To satisfactorily apply this approach, a broad and intense study of the geographical area is needed, but far from being a drawback, this can be a benefit for biodiversity because it allows the establishment of biodiversity monitoring and assessment programs in unprotected areas. Besides, this methodology has a wide range of applications in terrestrial, freshwater, and marine ecosystems that can be applied at multiple spatial and temporal scales depending on the objectives of the study. Overall, our approach offers a robust tool that could help prioritize areas more prone to improve in biodiversity, contributing to more efficient conservation measures.

Chapter III

Marine protected areas are more effective but less reliable in protecting fish biomass than fish diversity

This research is based on:

Sanabria-Fernandez JA, Alday J, Lazzari N, Riera R, Becerro MA, 2019. Marine protected areas are more effective but less reliable in protecting fish biomass than fish diversity. Marine Pollution Bulletin, 143, 24–32.

Picture: Underwater seascape from the Peñón de Vélez de la Gomera (Spanish territories in the African continent). In the picture you can see specimens of *Boops boops*, *Diplodus sargus*, and *Oblada melanura*. Jose A. Sanabria-Fernandez took this picture during an INBIOMAR 2019 research grant sampling trip.

Abstract

Marine protected areas (MPAs) provide multiple conservation benefits, thus raising the question of how good and consistent they are at their roles. Here, we quantified three components, namely, diversity, biomass, and other relevant variables, in numerous protected and unprotected areas across four marine ecoregions in Europe. We created a “global conservation status index” (CSI_{global}) as the sum of $CSI_{diversity,}$ $CSI_{biomass}$, and $CSI_{relevant}$. We then tested whether CSI and its three components varied as a function of protection and marine ecoregion. MPA efficiency, defined as the effect size of protection on CSI_{global}, was unreliable and varied with geography. $CSI_{biomass}$ and $CSI_{relevant}$ contributed to the unreliability of MPA efficiency, while $CSI_{diversity}$ was reliable. $CSI_{biomass}$ showed the major efficiency in protected areas (60%). Biomass of threatened species was the single largest variable that contributed to MPA efficiency. Our easy-to-use approach can identify high- and low-efficient MPAs and help to clarify their actual roles.

3.1. Introduction

Marine protected areas (MPAs) are one of the main management tools for the current human-driven biodiversity crisis. With increasing anthropogenic pressures, MPA is essential to preserve natural resources, biodiversity, and ecosystem properties (Micheli et al., 2012; Hilborn, 2016; Campbell et al., 2017). MPAs have steadily increased in the last decades to more than 5% of coastal areas under national jurisdictions and less than 1% of the high seas (Spalding et al., 2007) figures that keep on increasing with the establishment of some large MPAs, particularly in tropical waters (Devillers et al., 2015). MPAs are pivotal tools for coastal fisheries management and biodiversity conservation (Edgar et al., 2014). Yet, only 10% of the MPA surfaces are no-take zones, free of extraction, or habitat alteration activities, while 94% of MPAs allow fishing and other activities (Thomas et al., 2014; Costello and Ballantine, 2015; Campbell et al., 2017). Certainly, MPAs include a high range of areas, designs, uses, and management goals (Al-Abdulrazzak and Trombulak, 2012; Edgar et al., 2014; Pérez-Ruzafa et al., 2017), which could result in many benefits and varying degrees of protection efficiencies.

Besides MPAs, additional protection measures have been taken to contribute to biodiversity conservation, protection of threatened species, and restoration of fish stocks, including national parks, marine sanctuaries, natural parks, or natural monuments (Al-Abdulrazzak and Trombulak, 2012). Moreover, areas such as military zones can offer protection because of strong surveillance, highly restrictive access, and ban of extractive activities. All these protection measures can lead to the recovery of natural resources and other positive effects on natural communities (Russ et al., 2005; Weeks et al., 2010; Campbell et al., 2017).

The benefits of protection in marine communities are abundant, mostly focused on traits associated with diversity, biomass, or other relevant aspects related to protection. Protected areas are associated with larger species richness (Wantiez et al., 1997; Ciriaco et al., 1998; Edgar and Barrett, 1999; Barrett et al., 2007), larger trophic diversity (Shears and Babcock, 2003; Harmelin-Vivien et al., 2015), and larger functional diversity (Stelzenmüller et al., 2009; Villamor and Becerro, 2012; Guilhaumon et al., 2015) than unprotected areas. Protection also triggers an increase in fish biomass, particularly of commercial fish species (Barrett et al., 2007; Fenberg et al., 2012; Parravicini et al., 2014; Pérez-Ruzafa et al., 2017), likely as a result of decreased fishing pressures (e.g., larger biomass of fish over 20 cm; Edgar and Barrett, 1999; Barrett et al., 2007; Stuart-Smith et al., 2017). However, the biomass of other groups of species such as fish species in the IUCN Red List (Nieto et al., 2015) has received less attention (Willis et al., 2003; Afonso et al., 2011; Harmelin-Vivien et al., 2015). Other relevant variables unevenly used to assess the effects of marine protection include abundance of higher carnivores (Cole, 1994; Harmelin et al., 1995), vulnerability of fish community (Cheung et al., 2007; Stuart-Smith et al., 2017; Vasconcelos et al., 2017), and fish size (Shears and Babcock, 2003; Sciberras et al., 2013). Overall, most available evidence supports for a positive effect of protection on all these traits, providing ample MPA benefits in terms of fish diversity, fish biomass, and relevant traits of the fish community.

The variability in MPA traits and benefits also points toward the possibility that MPAs may be inconsistent in their multiple roles, leading to varying degrees and contrasting levels of efficiency (Dichmont et al., 2013; White et al., 2014). In fact, the positive effects of protection are unevenly spread across MPAs, and numerous studies fail to provide evidence for the expected beneficial effects of protection. Literature on the so-called paper parks provides ample evidence that MPAs can be inefficient (Bustamante et al., 2014; Gallacher et al., 2016) due to multiple factors (Rife et al., 2012; Edgar et al., 2014). Often, the protection effects of MPAs, e.g., increase in species richness or abundance, are noticeable after sufficiently long periods together with suitable control sites (Stobart et al., 2009; Chirico et al., 2017). Moreover, many studies that assessed MPA efficiency have focused on one rather than several benefits (McClanahan et al., 1999; Vanderklift et al., 2013), which could account for differences associated with the specifics of each benefit, MPA, or geographic region investigated (Caveen et al., 2015; Fletcher et al., 2015; Hughes et al., 2016).

Studies examining the effects of protection on multiple benefits over large geographic scales can provide opportunities to advance our understanding on how good MPAs are at achieving their multiple benefits and how reliable MPAs are at providing such benefits. In this study, we followed this approach to shed some light on the relationship between protection and their benefits. We used fish communities across south-western Europe to investigate how fish diversity, fish biomass, and relevant protection-related benefits contributed to the overall differences between fish communities in protected and unprotected areas and tested whether these benefits were consistent or varied as a function of geography. We investigated more than 20 protected sites distributed in four marine ecoregions of the world (Spalding et al., 2007) in the Atlantic-Mediterranean confluence area. We used species richness, trophic diversity, and functional diversity to evaluate MPA benefits on fish diversity; biomass of commercial fish, biomass of large fish, and biomass of threatened fish species to evaluate MPA benefits on fish biomass; and fish vulnerability, fish size, and abundance of higher carnivores as other MPA benefits on fish communities. Our results showed evidence for a small but consistent protection effect on fish diversity as opposed to larger and geographically variable protection effects on biomass and other relevant variables that resulted in unreliable MPA efficiency in our study area.

3.2. Material and Methods

Study area and field survey

We sampled a total of 372 sites that are mostly scattered along, but not limited to, the coast of Spain, Portugal, and North Africa (Fig. 3.1). The locations included 22 MPAs from four marine ecoregions (Alboran Sea; Azores, Madeira and Canary, hereafter Canary Is.; South European Atlantic Shelf, hereafter Atlantic; and Western Mediterranean) defined by Spalding et al. (2007) as “areas of relatively homogeneous species composition, clearly distinct from adjacent systems." The species composition of each ecoregion is likely to be determined by the predominance of a small number of ecosystems or a distinct suite of oceanographic or topographic features (Spalding et al., 2007, Table 3.1). In this paper, we define MPA broadly to accommodate for the multiple protection measures available in our study area, including marine reserves, national parks, natural parks, and no-access military zones with strong enforcement. Specific goals of these 22 MPAs include biodiversity conservation (17 MPAs), fish stock restoration (12 MPAs), national defense (4 MPAs), and protection of endangered species (1 MPA). Our sampling design covered many protected and unprotected sites in each of the four ecoregions investigated, providing a good representation of both factors. All sampling was conducted in the summers of 2014, 2015, and 2016.

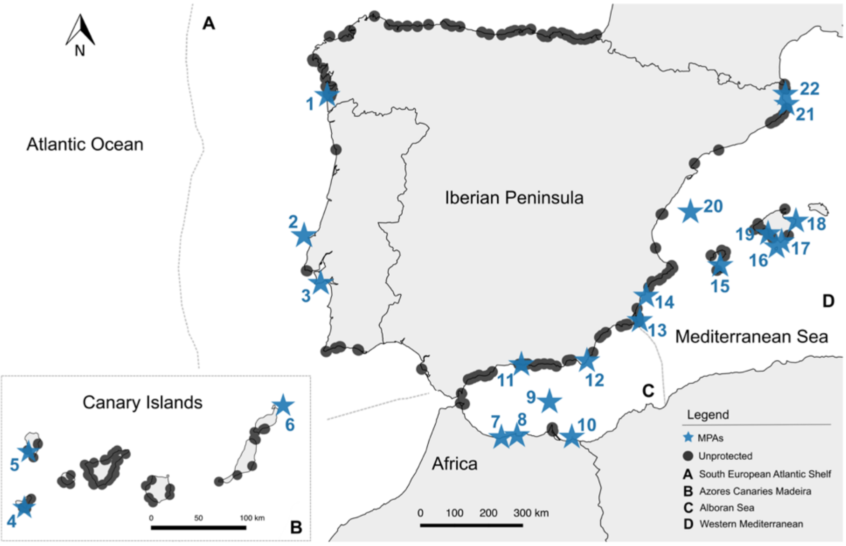


Figure 3.1. Location of the 22 marine protected areas (stars) and hundreds of localities (circles) investigated in our study, spanning more than four marine ecoregions of the world (A, B, C, and D; Spalding., 2007). See Table 3.1 for detail

Table 3.1. Marine protected areas investigated in our study, showing the code to find its location in Figure 3.1, marine ecoregion, protected area name, protection status, and goals as specified in their official sites.

Map code	Marine ecoregion	Protected area	Protection status	Goals
1	South European Atlantic Shelf	Islas Cíes	National Park	Biodiversity conservation
2	South European Atlantic Shelf	Archipielago de las Berlengas	Marine Reserve	Biodiversity conservation Fish stock restoration
3	South European Atlantic Shelf	Da Arrabida	Natural Park	Biodiversity conservation
4	Azores, Madeira and Canary Is.	Punta de la Restinga - Mar de las Calmas	Marine Reserve	Biodiversity conservation Fish stock restoration
5	Azores, Madeira and Canary Is.	Isla de la Palma	Marine Reserve	Biodiversity conservation Fish stock restoration
6	Azores, Madeira and Canary Is.	Isla de la Graciosa e islotes del Norte de Lanzarote	Marine Reserve	Biodiversity conservation Fish stock restoration
7	Alboran Sea	Peñón de Vélez de la Gomera	Military Area	National defense
8	Alboran Sea	Islas Alhucemas	Military Area	National defense
9	Alboran Sea	Isla de Alboran	Military Area and Marine Reserve	Biodiversity conservation Fish stock restoration National defense
10	Alboran Sea	Islas Chafarinas	Military Area	Biodiversity conservation National defense
11	Alboran Sea	Maro Cerro Gordo	Natural Park	Biodiversity conservation
12	Alboran Sea	Cabo de Gata-Níjar	Marine Reserve	Biodiversity conservation Fish stock restoration
13	Western Mediterranean	Cabo de Palos e Islas Hormigas	Marine Reserve	Biodiversity conservation Fish stock restoration
14	Western Mediterranean	Isla de Tabarca	Marine Reserve	Biodiversity conservation Fish stock restoration

15	Western Mediterranean	Freus de Ibiza y Formentera	Marine Reserve	Biodiversity conservation Fish stock restoration
16	Western Mediterranean	Archipielago de Cabrera	National Park	Biodiversity conservation
17	Western Mediterranean	Migjorn de Mallorca	Marine Reserve	Biodiversity conservation Fish stock restoration
18	Western Mediterranean	Cala Ratjada	Marine Reserve	Biodiversity conservation
19	Western Mediterranean	Bahía de Palma	Marine Reserve	Biodiversity conservation
20	Western Mediterranean	Islas Columbretes	Marine Reserve	Biodiversity conservation Fish stock restoration
21	Western Mediterranean	Islas Medas	Natural Park	Biodiversity conservation
22	Western Mediterranean	Cabo de Creus	Natural Park	Endangered species protection

We used the Reef Life Survey protocol (Edgar and Stuart-Smith, 2014) to quantify the number, abundance, and size distribution of the fish community at each site. Briefly, in each sampled site, we took at least two underwater visual surveys along 50-m long × 10-m wide transects (Edgar and Stuart-Smith, 2014), with all conspicuous fish (>25 mm size) identified and their abundances and sizes estimated. We restricted sampling between 6- and 15-m deep to minimize the influence of depth on fish communities.

Conservation Status Index (CSI)

Our quantitative data allowed us to calculate multiple variables from which we selected nine mostly unrelated traits to characterize fish communities (Table 3.2). These selected variables provided quantitative information on the status of each fish community in terms of diversity (species richness, trophic diversity, and functional diversity), biomass (biomass of commercial species, biomass of large specimens, and biomass of threatened species), and relevant traits (vulnerability, size community, and abundance of higher carnivores; Fig. 3.2). We calculated species richness as the total number of fish species in each transect. To calculate trophic diversity, we categorized every fish specimen into its respective trophic group, i.e., benthic invertivore, browsing herbivore, higher carnivore, planktivore, or scraping herbivore, and we computed the Shannon-Weaver diversity index as natural logarithm on the abundance of these trophic groups. To calculate functional diversity, we assigned all fish specimens to their corresponding levels of eight functional traits (water column position, preferred substrate, trophic group, dial activity pattern, habitat complexity, gregariousness, trophic breadth, and maximum length) and calculated Rao-Q following Stuart-Smith et al. (2013). Information on the trophic groups and functional traits of every fish species is available in FishBase (www.fishbase.com), (Froese and Pauly, 2000).

We used our observed abundance of fish size groups to estimate biomass of fish species (Ln transformed) based on species-specific length-weight relationships available in FishBase (Froese and Pauly, 2000). We defined large specimens as fish individuals larger than 200 mm length (hereafter biomass >200 mm). We used Spanish Commercial List of Marine Fishes (http://www.mapama.gob.es/es/pesca/temas/mercados-economia-pesquera/fichas_sp_comerciales.aspx) to assign fish species to the commercially interesting species group and the European Red List of Marine Fishes of the International Union for Conservation of Nature (IUCN) to assign fish species to the threatened species group (Nieto et al., 2015).

We also used FishBase information (Froese and Pauly, 2000) to quantify the abundance of higher carnivores (log transformed) and to assign vulnerability values to every fish specimen in our data set. Then, we used the community-weighted mean as a vulnerability index. We calculated fish size as the community-weighted mean of the total length of the observed fish specimens in each site.

We defined the global conservation status index (CSI_{global}) as the sum of the nine variables investigated, which was standardized between 0 and 100 to give equal possible weight to their contribution to CSI_{global} (Fig. 3.2). The simple addition of standardized variables also allowed for (i) an easy partitioning of the CSI_{global} into its three components of diversity ($CSI_{diversity}$), biomass ($CSI_{biomass}$), and relevant traits ($CSI_{relevant}$) by simply considering their respective variables and (ii) straight ecological interpretation as each variable value contributed directly and proportionally to CSI_{global} (Fig. 3.2).

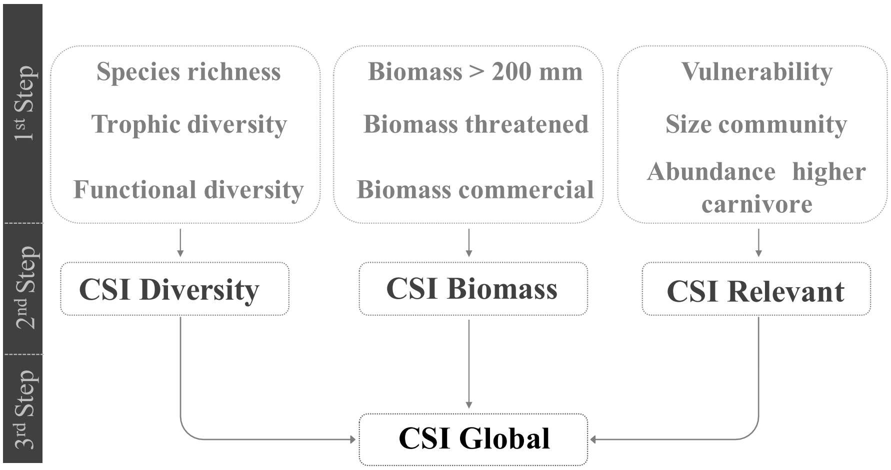


Figure 3.2. Summary of the hierarchical structure followed to calculate the CSI_{global}. We used nine individual variables that were standardized to give equal weight to each variable. Second, related variables were pooled to generate the $CSI_{diversity}$, $CSI_{biomass}$, and $CSI_{relevant}$. The CSI_{global} is the sum of the $CSI_{diversity}$, $CSI_{biomass}$, and $CSI_{relevant}$.

Testing MPA efficiency

We defined MPA efficiency as the difference in CSI between protected and unprotected sites, i.e., the effect size of protection. Thus, larger CSI values in protected sites would show evidence for an efficient MPA with further analyses of the three CSI components (or nine individual variables) pointing to specific benefits over unprotected sites. Equal or larger CSI values in unprotected sites would define inefficient MPAs.

We used general additive mixed models (GAMMs; Wood, 2017) to analyze ecoregion (i.e., Alboran Sea, Canary Is., Atlantic, and Western Mediterranean) and protection (i.e., protected and unprotected) effects on CSI_{global}, $CSI_{biomass}$, $CSI_{diversity}$, and $CSI_{relevant}$ components. Here, GAMM models were fitted using ecoregion and protection as fixed factors and sampling sites nested with protection as random factors to account for hierarchical pseudoreplication. Moreover, we selected GAMM models because we can correct the autospatial correlation including latitude and longitude as tensor product interaction covariable (Wood, 2017). All statistical analyses were conducted in R software environment (R Core Team, 2015) using mgcv package for GAMM (Wood, 2017). We tested three null hypotheses: no interaction between ecoregion and protection, no CSI differences between protected and unprotected sites, and no CSI differences among the four ecoregions. Because we defined MPA efficiency as the difference in CSI between protected and unprotected sites, a significant protection factor indicated efficient (or inefficient) MPAs, while a significant interaction term stressed spatial inconsistencies in MPA efficiency (or inefficiency). In other words, the model actually tested for the role of geography (ecoregion) in CSI, MPA efficiency (protection), and reliability of MPA efficiency across ecoregions (interaction).

Afterward, we tested the differences in MPA efficiency matrix between the four marine ecoregions by using permutational multivariate analysis of variance with the function “Adonis” of vegan package (Oksanen et al., 2016). Here, we applied Euclidean distance to the matrix comprising $CSI_{biomass}$, $CSI_{diversity}$, and $CSI_{relevant}$ variables with 999 permutations. The pairwise comparisons between ecoregions were calculated using “adonis.pairwise” function from the EcolUtils package (Salazar, 2015). We also calculated and plotted MPA efficiency as the CSI effect size of protection (protected minus unprotected sites). By examining the effect size of the three CSI components and corresponding standardized variables, we also quantified whether MPAs were more efficient in some specific benefits and whether such benefits remained consistent across the ecoregions. All the results are reported as mean ± standard error for protected and unprotected areas. The supplementary data (see appendix for Chapter III) and the R codes used to compute the CSI index are in the Git repository: https://github.com/Sanabria-Fernandez/Conservation-Status-Index

3.3. Results

Global Conservation Status Index (CSI_{global})

MPA efficiency was unreliable and varied significantly with the ecoregions (Table 3.3., CSI_{global}, p-interaction<0.001, Fig. 3.3a). We found larger CSI values in protected areas than in unprotected areas in the Canary Is. (4.51 ± 0.42 and 2.70 ± 0.11; t=5.06, p<0.001) and Western Mediterranean (2.94 ± 0.19 and 1.87 ± 0.07; t=3.09, p=0.002) ecoregions and no CSI_{global} differences in the Atlantic (2.57 ± 0.54 and 1.83 ± 0.06; t=1.39, p=0.163) and Alboran Sea (2.56 ± 0.12 and 2.27 ± 0.13; t=0.84, p=0.4) ecoregions (Fig. 3.3a). The Canary Is. had the largest protection effect size (1.818), followed by the Western Mediterranean (1.069), Atlantic (0.737), and Alboran Sea (0.286) ecoregions (Fig. 3.3a and Fig. 3.6).

Biomass Conservation Status Index ($CSI_{biomass}$)

MPA efficiency was unreliable and varied significantly with the ecoregions (Table 3.3, $CSI_{biomass}$, p interaction<0.001, Fig., 3.3b). We found larger $CSI_{biomass}$ values in protected areas than in unprotected areas only in two out of four ecoregions (Fig. 3.3b): Alboran Sea (1.01 ± 0.09 and 0.66 ± 0.06; t=2.28, p=0.022) and the Canary Is. (1.9 ± 0.16 and 0.87 ± 0.07; t=4.21, p<0.001). There were no significant differences in the Western Mediterranean (1.12 ± 0.11 and 0.56 ± 0.05; t=1.73, p=0.083) and Atlantic (0.74 ± 0.21 and 0.55 ± 0.02; t=-0.14, p=0.88) ecoregions. Specifically, the biomass > 200 mm was significantly greater with protection (0.33 ± 0.01 and 0.24 ± 0.01; F= 10.31, p=0.001), and the biomass of commercial species showed significant differences at the ecoregion level, for example, in the Canary Is. (average=0.28 ± 0.01) and

Western Mediterranean (average=0.25 ± 0.01); (F=5.07, p=0.001) ecoregions. The biomass of threatened species varied significantly between protected and unprotected areas irrespective of the ecoregion (F=8.84, p interaction<0.001). Alboran Sea (0.45 ± 0.08 and 0.21 ± 0.05) and the Canary Is. (0.40 ± 0.06 and 0.26 ± 0.06) showed the highest values inside the protected areas.

Diversity Conservation Status Index ($CSI_{diversity}$)

We did not find significant differences in the $CSI_{diversity}$ among the studied ecoregions nor between ranges of protection (0.85 ± 0.02 and 0.79 ± 0.01; Table 3.3, Fig. 3.3c). An independent analysis of $CSI_{diversity}$ components showed that only species richness (F=12.07, p<0.001) and trophic diversity (F=3.73, p=0.01) exhibited significant differences between the ecoregions. However, there was a significant ecoregion*protection effect over functional diversity (F=3.3, p interaction=0.02).

Relevant Conservation Status Index ($CSI_{relevant}$)

There was a significant interaction between ecoregion and protection for relevant conservation status index (Table 3.3, $CSI_{relevant}$, p interaction<0.001, Fig. 3.3d). We found larger $CSI_{relevant}$ values in protected areas than in unprotected areas in three out of four ecoregions (Fig. 3.2d): the Canary Is. (1.51 ± 0.25 and 0.83 ± 0.05; t=4.41, p<0.001), the Atlantic (1.22 ± 0.36 and 0.80 ± 0.05; t=2.03, p=0.042), and the Western Mediterranean (0.88 ± 0.11 and 0.49 ± 0.01; t=3.151, p=0.001). However, there were no $CSI_{relevant}$ differences in the Alboran Sea (0.74 ± 0.06 and 0.84 ± 0.07; t=-0.77, p=0.441). In detail, the vulnerability (F=3.21, p interaction=0.02), size community (F=5.58, p interaction<0.001) and the abundance of higher carnivores (F=6.13, p interaction<0.001) varied significantly with the ecoregions. For more information on the $CSI_{biomass}$, $CSI_{diversity}$, $CSI_{relevant}$, and CSI_{global} values of each protected and unprotected area, see Table S3.1.

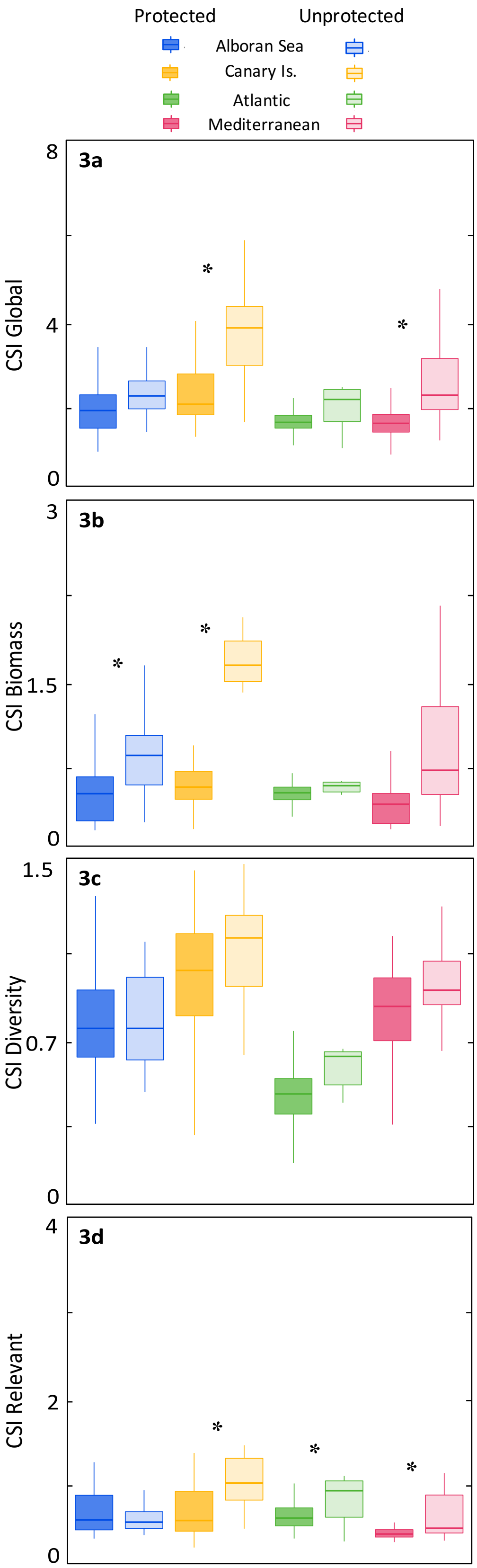


Figure 3.3. Boxplots representation of the conservation status index (CSI_{global}, 3.3a; $CSI_{biomass}$, 3.3b; $CSI_{diversity}$, 3.3c; and $CSI_{relevant}$, 3.3d) in protected and unprotected areas of the four ecoregions investigated in our study. * indicates significant differences ($p<0.05$) between protected and unprotected areas within each ecoregion. See Table 3.3 for the statistical details.

Table 3.2. Correlation matrix showing the strength of the association (coefficient of determination) between the nine variables investigated in our study. * indicates significant differences ($p<0.05$).

	1	2	3	4	5	6	7	8	9
Biomass threatened species (1)	1								
Abundance of higher carnivores (2)	0.19^*	1							
Biomass > 200 mm (3)	0.09^*	0.12^*	1						
Trophic diversity (4)	0.09^*	0.04^*	0.00	1					
Species richness (5)	0.11^*	0.06^*	0.01^*	0.12^*	1				
Biomass commercial species (6)	0.05^*	0.13^*	0.25^*	0.00	0.12^*	1			
Vulnerability (7)	0.02^*	0.00	0.00	0.11^*	0.01^*	0.00	1		
Functional diversity (8)	0.01^*	0.01	0.06^*	0.17^*	0.00	0.00	0.18^*	1	
Large specimens (9)	0.01	0.00	0.06^*	0.00	0.15^*	0.00	0.19^*	0.01^*	1

Table 3.3. General additive mixed model (GAMM) on CSI_{global}, $CSI_{diversity}$, $CSI_{biomass}$, and $CSI_{relevant}$ as a function of marine ecoregion (four levels) and protection status (two levels). A significant interaction factor supports for spatial unreliability in MPA efficiency for that variable. A significant protection factor supports for significant MPA efficiency. See text for details of individual indexes.

Variable	Effect	F	p-value
CSI_{global}	Ecoregion	2.786	0.041
	Protection	0.714	0.399
	Ecoregion*Protection	8.895	<0.001
$CSI_{biomass}$	Ecoregion	1.941	0.125
	Protection	5.281	0.022
	Ecoregion*Protection	7.090	<0.001
$CSI_{diversity}$	Ecoregion	0.267	0.849
	Protection	0.014	0.904
	Ecoregion*Protection	1.055	0.368
$CSI_{relevant}$	Ecoregion	4.777	0.002
	Protection	0.598	0.439
	Ecoregion*Protection	6.905	<0.001

Marine protected areas efficiency

Overall, the three components of biomass, diversity, and relevant contributed 60.01%, 14.41%, and 25.58%, respectively, to MPA efficiency (Fig. 3.4a). These contributions varied significantly between ecoregions (F=26.59, p<0.001, Fig. 3.4b), with $CSI_{biomass}$ being the largest contributor in three out of four ecoregions and $CSI_{diversity}$ in none of them (Fig. 3.4b). Biomass of threatened species (48.7%) and abundance of higher carnivores (26.9%) were the largest contributors to MPA efficiency (Fig. 3.5). Biomass of large fish (9.3%), trophic diversity (8%), and species richness (7.4%) were less important contributors to MPA efficiency, while the contribution of the remaining variables was either marginal or negative, i.e., biomass of commercial fish (2.1%), vulnerability (0.1%), functional diversity (-1.1%), and fish size (-1.4%) (Fig. 3.5). Biomass of threatened species was consistently a major contributor to MPA efficiency, although the magnitude of the contribution varied largely among ecoregions (from 81.1% in Alboran Sea to 19.3% in the Atlantic, Fig. 3.6). Vulnerability was consistently a minor contributor, with positive or negative effect sizes close to zero in all ecoregions (Fig. 3.6). The contribution of the remaining variables to MPA efficiency was highly unreliable among the ecoregions (Fig. 3.6).

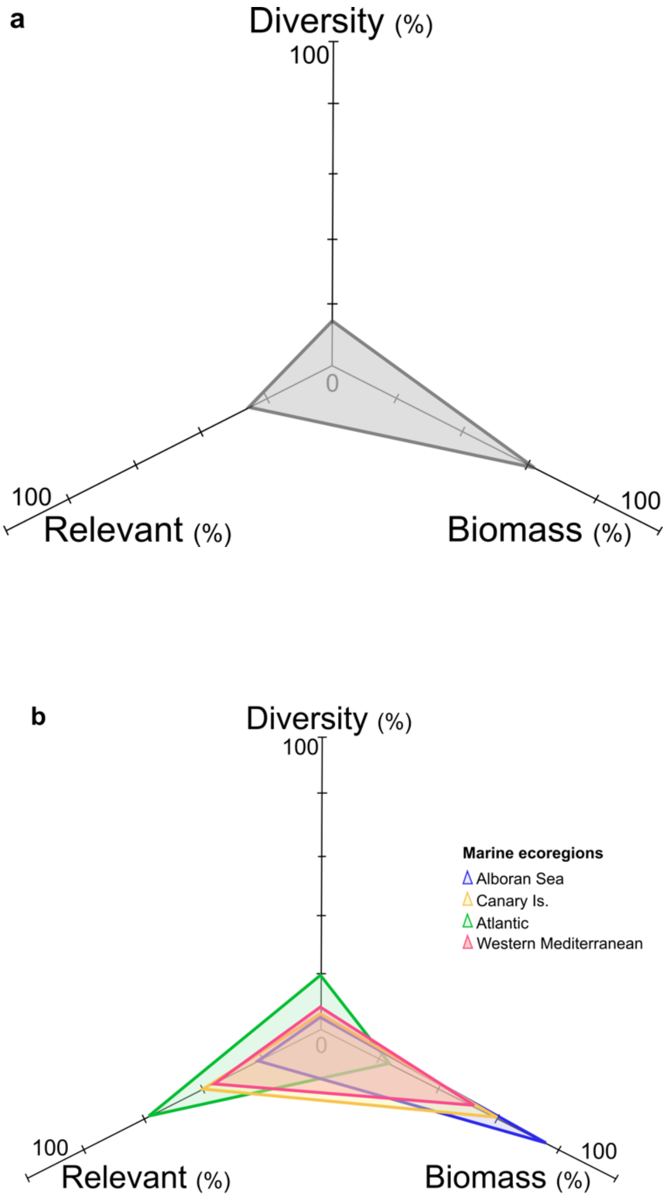


Figure 3.4. (A). Percentage contribution of the three components of diversity, biomass, and other relevant traits to the total MPA efficiency. (B). Percentage contributions as in (A) but disclosed for each ecoregion.

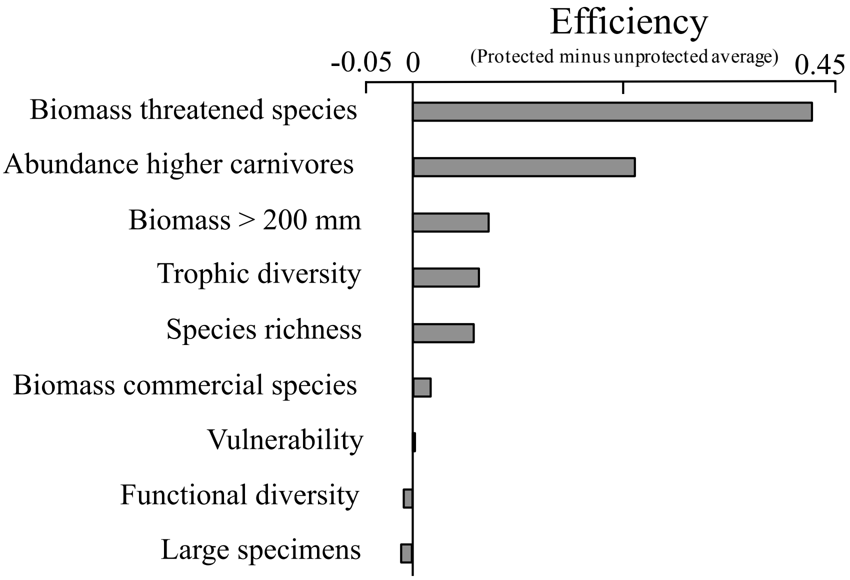


Figure 3.5. MPA efficiency, defined as the effect size between protected and unprotected areas, for each of the nine variables investigated in our study.

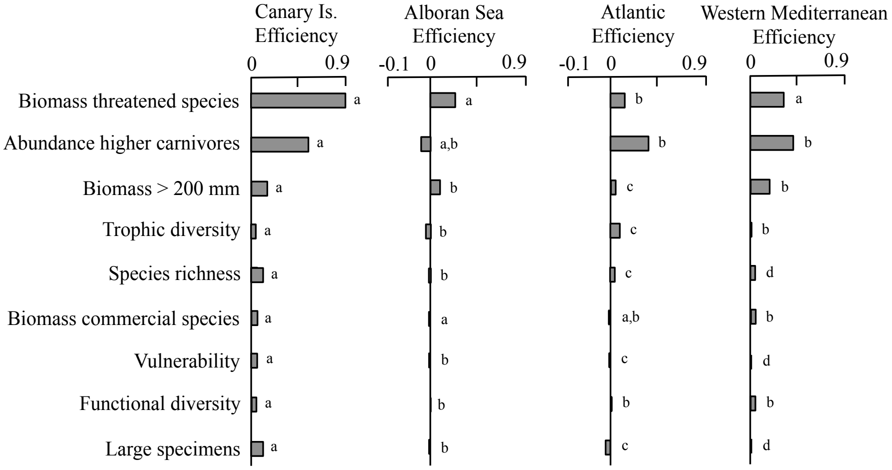


Figure 3.6. MPA efficiency, defined as the effect size between protected and unprotected areas for each ecoregion for each of the nine variables investigated in our study. Letters show significant differences between ecoregions for each of the nine variables investigated. Statistical results based on the "Adonis" (vegan package in R; Oksanen et al., 2016) and "Adonis.pairwise" (EcolUtils package in R; Salazar, 2015). See text for additional details.

3.4. Discussion

MPAs are becoming one of the most prevalent tools to promote biodiversity conservation and sustainable use of marine resources (Gaines et al., 2010; Spalding et al., 2013). Available evidence supports for multiple benefits of protection and points to ineffective MPA management when benefits are missing (Rife et al., 2012). These arguments may lead to believe that MPAs would excel at all their multiple roles under good management practices. Although good management is imperative for effective protection, MPAs differ in many aspects that could contribute to differences in their degree of efficiency at one or multiple roles regardless of their management practices (Villamor and Becerro, 2012). Here, we analyzed nine protection benefits in numerous MPAs of four marine ecoregions of the world and tested whether MPA efficiency was reliable or varied as a function of ecoregion. Our results showed the existence of large differences in MPA efficiency across ecoregions, with varying degree of efficiency at protecting multiple roles. Our results warned against the belief that implementation of an MPA may lead to the achievement of every protection-related benefit as we still lack predictive knowledge on how protection benefits apply into specific protected areas. Our approach may help quantify the degree of achievement of MPA objectives and the circumstances under which MPAs accomplish certain benefits more efficiently.

MPA efficiency varied significantly between ecoregions. We found effective MPAs with larger CSI values in protected areas than in unprotected areas in the Canary Is., Western Mediterranean, and Atlantic ecoregions and ineffective MPAs in the Alboran Sea ecoregion. MPAs in the Canary Is. were the most efficient in our study area, driven by high CSI values in protected areas as compared to those in the remaining geographic regions. Although the causes underlying the good conservation status of MPAs in the Canary Is. are diverse, the high fishing pressure throughout unprotected areas in the archipelago (García-Mederos et al., 2015) and the decrease in density of the voracious sea urchin *Diadema africanum* and associated regime shifts in protected areas (Sangil et al., 2012) are likely contributors. Difficulties in surveillance, enforcement, and monitoring may underlie the inefficiency of MPAs in the Alboran Sea ecoregion, as it occurs in other vast offshore MPAs in the ocean (Wilhelm et al., 2014). In addition, the major unprotected sampled points in this ecoregion have been conducted in the Spanish coastal zone; hence, a gap exists in the unprotected Moroccan coastal area. An extensive sampling survey in the northern African coast is needed to shed light on the effects of protection in the Alboran Sea ecoregion.

Biomass-related traits were the largest contributors to MPA efficiency in our study, which was mostly explained by the contribution of the biomass of threatened species within the studied MPAs. The strong positive effect of protection on the biomass of threatened species (49% efficiency) was in contrast with the weak effect of protection on the biomass of commercial species (2% efficiency). Further, the biomass of threatened species was consistently a major contributor to MPA efficiency, while the contribution of the biomass of commercial species to MPA efficiency varied substantially between ecoregions. In the Atlantic ecoregion, the biomass of threatened species was the second major contributor to MPA efficiency. Although the Atlantic is a hotspot of threatened fish species (Nieto et al., 2015), biomass was minor because threatened species were accidental in our sampling stations. These results contrasted with the specific goals of the 22 MPAs investigated in this study. Twelve out of 22 MPAs included commercial fish stock restoration as a specific goal, while only 1 MPA (Cabo de Creus, Western Mediterranean) was designed to protect endangered species. It seems, therefore, that the sought-after goal of fish stock restoration is at risk in the MPAs investigated herein, making these MPAs an unreliable tool to protect coastal fisheries in our study area. Increased biomass of commercial fish species is a common benefit of protection (Barrett et al., 2007; Fenberg et al., 2012; Parravicini et al., 2014; Campbell et al., 2017; Pérez-Ruzafa et al., 2017) and failure to achieve this goal may rely on the small-size of no-take zones, as suggested by other studies (Claudet et al., 2008). The biomass of large fish (>200 mm) was similar within the studied MPAs from the Canary Is. and Western Mediterranean. However, this biomass was surprisingly lower in the Alboran Sea and Atlantic ecoregions, though these ecoregions are characterized by a high productivity. Hence, the efficiency of MPAs regarding biomass is reliable but showed a high spatial variability among ecoregions, perhaps due to suboptimal MPA surveillance to control illegal fishing.

The effect of protection on fish diversity was reliable but small in the studied MPAs. MPAs were not only a successful conservation tool to preserve biodiversity but, they also seemed to promote an increase in biodiversity within the studied protected areas. Our results suggest that MPAs may function as both biodiversity conservation and restoration areas. European MPAs have demonstrated evidence of preserving biodiversity of local ecosystems (Fenberg et al., 2012) through the re-establishment of biological variables, e.g., trophic interactions that characterized unfished ecosystems. The importance of functional diversity has recently increased in the marine realm because of the advantages of using functional traits as surrogates of the status of coastal environments (Stuart-Smith et al., 2013); further, it has been demonstrated that functional diversity greatly contributes to the stability of marine communities (Bates et al., 2013). In our study, functional diversity showed the highest values in the Canary Is. ecoregion though we found no differences associated with protection in the studied ecoregions.

MPA efficiency on other traits associated with the fish community was highly variable among the ecoregions. We found higher $CSI_{relevant}$ values in protected areas than in unprotected areas of the Canary Is., Western Mediterranean, and Atlantic. These differences were mostly driven by the abundance of higher carnivores, which was the second largest contributor to MPA efficiency in our study. Our results showed large abundances of higher carnivores within MPAs, which is likely a consequence of the impact of fishing on the density and structure of fish assemblages (Clemente et al., 2009; Guidetti et al., 2014). Yet, the Alboran Sea showed higher abundances of higher carnivores in unprotected areas. Illegal fishing associated with suboptimal surveillance could lead to these unexpected results in the Alboran Sea. Vulnerability was a minor contributor to MPA efficiency regardless of the ecoregion, probably because of the dominance of species with low vulnerability and high to medium resilience in the studied ecoregions, as it has been shown in other coastal environments (Vasconcelos et al., 2017). Vulnerability showed slightly higher values in protected areas than in unprotected areas of the Canary Is. (1.7%), which is likely to be associated with larger fish size (5.6%). The effect of protection on fish vulnerability was virtually nonexisting in the remaining ecoregions.

The lack of a consistent trend regarding MPA efficiency in the studied ecoregions may be explained by the high spatial unreliability of most of the variables investigated in our study. Except for the biomass of threatened species and vulnerability, the remaining seven variables showed high spatial variability that prevented reliable protection effects. This spatial variability is multifaceted because it is dependent upon fish characteristics, such as fish mobility and spill-over effect (Pérez-Ruzafa et al., 2008; Le Quesne et al., 2009) and features regarding protection measures (Edgar et al., 2014) such as size of no-take zones (Claudet et al., 2006), time of creation (Babcock et al., 2010), and enforcement (Brown et al., 2017). The lack of expected benefits in the studied MPAs may be partially explained by the geographic variations of unreliability among ecoregions because these benefits need to be considered at a broad scale. Former studies have demonstrated that MPA characteristics such as number of years of protection, size, isolation, and surveillance are significant factors for the effective operation of MPAs (Stewart et al., 2009; Edgar et al., 2014).

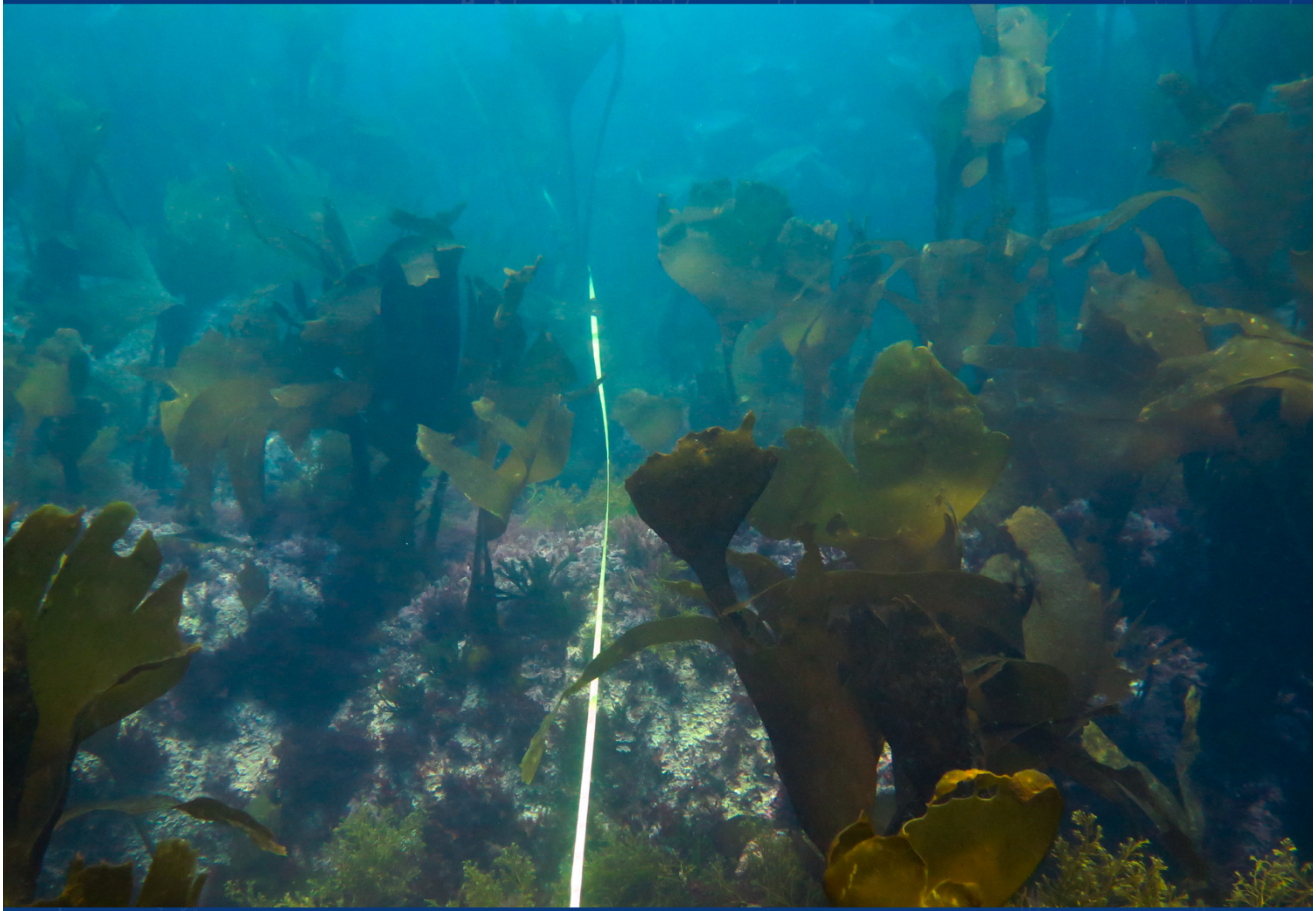
In short, we have found that MPA efficiency greatly varied among the ecoregions because some variables were more reliable than others, but we still lack predictive knowledge to understand how the multiple benefits of protection apply to specific MPAs. Our study showed that traits associated with fish biomass contributed the most to MPA efficiency, but the magnitude of the effect was unreliable. Contrarily, traits associated with fish diversity were minor but reliable contributors to MPA efficiency. Because we used nine distinct variables to calculate CSI values and multiple MPAs in each of the four ecoregions investigated, our MPA efficiency was ecologically and geographically inclusive, allowing for a broader view than more localized studies with fewer numbers of variables or MPAs.

3.5. Conclusions

The present study showed that MPA efficiency was unreliable and varied with ecoregion, highlighting contrasting differences between effective and ineffective MPAs in multiple geographic areas. Biodiversity conservation, the largest conservation goal present in 17 out of 22 MPAs in our study, is a benefit that MPAs reliably provide in our study area, even though the magnitude of the effect is small. Biomass-related traits were the largest contributors to MPA efficiency, yet the effect of protection on the magnitude of these traits was highly variable. Much work is needed to be done to have a successful fish stock restoration goal in our study area. A 2% MPA efficiency on the biomass of commercial fish species seems to be a low benefit for the second largest protection goal present in 12 out of 22 MPAs in our study. Understanding the environmental and management reasons for this failure is critical to bring this figure more in line with its relevance. On the contrary, MPAs in our study were highly efficient to increase over 60% the biomass of threatened species—a goal only present in one of the 22 MPAs investigated in our study. Different conservation needs between commercial and threatened species might be responsible for such contrasting levels of efficiency. Our approach also represents an opportunity to assess the circumstances under which some variables positively respond or fail to respond to protection. Additionally, because our approach integrates multiple variables grouped in several categories, we could easily incorporate other socio-economic variables to evaluate educational, economic, or cultural benefits associated with MPAs, which along with ecological variables would provide a more comprehensive and accurate vision of the actual roles that MPAs play in our socio-ecological systems.

Chapter IV

Quantifying patterns of resilience: What matters is the intensity, not the relevance, of contributing factors



This research is based on:

Sanabria-Fernandez JA, Lazzari N, Becerro MA, 2019. Quantifying patterns of resilience: What matters is the intensity, not the relevance, of contributing factors. Ecological Indicators, 107, 105565.

Picture: Underwater seascape from the Sisargas Archipelago in Galicia (Spain). In the picture you can see kelp forest habitat. Natali Lazzari took this picture during a MARINERES 2016 research grant sampling trip.

Abstract

Ecological resilience, broadly defined as the magnitude of the disturbance a system needs to shift to an alternative stable state, is becoming a critical trait in the Anthropocene era. However, we are far from having baseline resilience data to guide decision makers toward more resilient ecological systems. In the last decade, the resilience assessment framework has taken a sum of products approach to obtain a resilience indicator based on the relevance and the intensity of multiple factors. While factor intensity relies on quantitative data, estimates of factor relevance rely on ordinal data with a lesser understanding of their relative importance to resilience, which may have consequences in the value of the resilience indicator. Here, we computed three resilience indicators to test for the quantitative impact that changes in factor relevance might cause to the resilience indicator. We defined the Inclusive Resilience Indicator of a Site (IRIS) as a relevance-free indicator based exclusively on factor intensity. We also computed the Relative Resilience Potential (RRP) and an RRP with random relevance values (RRP_{rrv}) as indicators based on both intensity and relevance. To calculate these three indicators in rocky reefs of the Alboran Sea, we quantified 17 biological, environmental, and human-related factors known to influence resilience. We used correlation analyses, Linear Mixed Models, and Generalized Additive Models to compare the three resilience indicators and to examine their spatial patterns. We found highly significant positive correlations between the RRP, RRP_{rrv}, and IRIS indicators ($r>0.9$, $p<0.001$ for all comparisons). All three indicators had equivalent resilience values ($p=0.440$), provided non-significant differences in their predictions ($p=0.097$), and exposed the same resilience gradients in the Alboran Sea ($p<0.001$ for all indicators). IRIS accounted for 94% and 99% of the variance associated with RRP and RRP_{rrv}, respectively, suggesting that the intensity-based IRIS can estimate resilience without the uncertainties associated with factor relevance. The new IRIS indicator proposed in our study may facilitate the acquisition of baseline data needed to further advance in the ecological and management implications of marine resilience.

4.1. Introduction

Resilience is a broad and complex concept that is increasingly getting the attention of many research disciplines, from mental health (Hu et al., 2015) to economics (Martin, 2012) or politics (Gladfelter, 2018) (Fig. 4.1). Notably, resilience science has come through in environmental and ecological research (Fig. 4.1), becoming a very active field that has resulted in many understandings of the same broad concept of resilience. Originally, ecological resilience referred to the ecosystem ability to cope with change without shifting to an alternative stable state (Holling, 1973). Other definitions focus on the ecosystem capacity to resist and to recover from disturbance (engineering resilience, Walker et al., 1969; Holling, 1996). The concept of resilience has evolved over the years integrating numerous levels of comprehension (see Müller et al., 2016 and references therein) and biological organization (Gunderson and Holling, 2002; Micheli et al., 2012; Rice et al., 2013). Along with this conceptual development, we also have a great variety of empirical observations with a high diversity of approaches (Müller et al., 2016). These advancements provide, for example, increased appreciation of the multiple factors that regulate resilience (Bernhardt and Leslie, 2013; Barnett and Baskett, 2015; Ling et al., 2014; Oliver et al., 2015; van de Leemput et al., 2018), which is the first step toward a better understanding of natural patterns of resilience and an opportunity for more resilient ecosystems through proper management actions. Both topics are critical because, despite the progress in this field, quantification of resilience remains somehow elusive in ecological systems. Lack of resilience data prevents further development of this research area and hinders management, as it is hard to manage what is not measured (Spears et al., 2015).

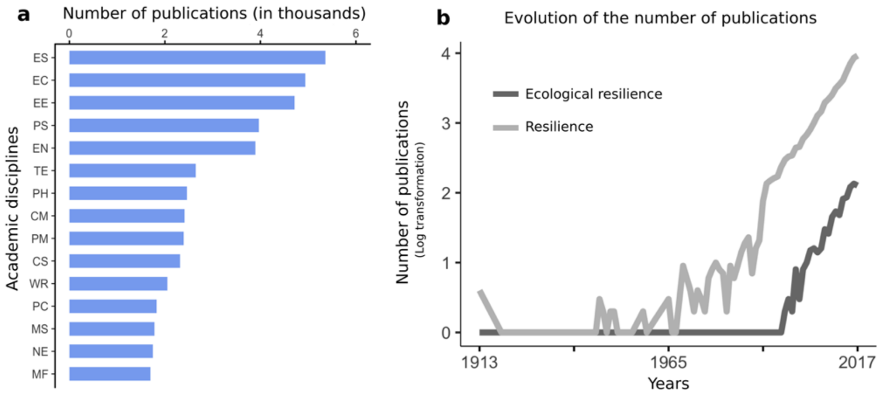


Figure 4.1. (a) Top 15 disciplines in the ISI Web of Science core collection based on the number of papers with the term "Resilience" in the title or abstract: (ES) Environmental sciences, (EC) Ecology, (EE) Engineering electrical electronic, (PS) Psychiatry, (EN) Environmental studies, (TE) Telecommunications, (PH) Public environmental occupational health, (CM) Computer science theory methods, (PM) Psychology multidisciplinary, (CS) Computer science information systems, (WR) Water resources, (PC) Psychology clinical, (MS) Multidisciplinary sciences, (NE) Neurosciences, (MF) Marine freshwater biology. (b) Total number of publications in the ISI Web of Science core collection with the terms "Resilience" (light gray) and "Ecological resilience" (dark gray) in the title, abstract, or keywords of the scientific article over the last 104 years.

Resilience also is a sought-after ecosystem trait, from the conservation and management perspective, particularly relevant in an era when human-driven activities have raised biodiversity loss to mass extinction levels (Barnosky et al., 2011; Pimm et al., 2014). Resilience can offer relevant information on the current status of natural communities and on their risk of collapse (Holling, 1973; Obura, 2005) or it can be a useful tool to identify locations with strong recovering capacity. As an example, organizations such as the Convention on Biological Diversity seeks to enhance ecosystem resilience (Aichi Biodiversity Target 15, Leadley et al., 2014) and the United Nations Environment Programme World Conservation Monitoring Centre includes resilience as one of four design principles in marine protected areas (UNEP-WCMC, 2008). The UNEP-WCMC also warns about the current knowledge gap in marine resilience and urges to take steps to resolve it (UNEP-WCMC, 2008). Unfortunately, a decade later, the resilience status of marine ecosystems remains unknown (Díaz et al., 2019).

As a complex concept, quantifying resilience is a challenge that needs integration of numerous factors including biological, environmental, or anthropogenic (Maynard et al., 2010; Maynard et al., 2015). Specifically, factors determine the ecological resilience of a system (Thrush et al., 2009; McClanahan et al., 2012; Timpane-Padgham et al., 2017) including biological (Gunderson, 2000; Rice et al., 2012; Ling et al., 2014), environmental (Wernberg et al., 2009; Maynard et al., 2010; Wernberg, 2010; McClanahan et al., 2012), and anthropogenic elements (Levin and Lubchenco, 2008; Piola and Johnston, 2008; Gladstone et al., 2013). A compelling, meaningful resilience indicator should include multiple factors of the biological, environmental, and anthropogenic dimensions of resilience so that the influence of a single factor does not bias the broader resilience concept. Based on this knowledge and rationale, the resilience assessment framework established an approach to calculate a site-specific resilience indicator with strong management implications (Maynard et al., 2010). The approach has been adapted and used to assess resilience in several tropical locations (Ladd and Collado-Vides, 2013; Maynard et al., 2015). In contrast, studies on the ecological resilience of temperate rocky reefs are scarce (Behrens and Lafferty, 2004; Strain et al., 2015) and mostly focused on the response to climate change (Bates et al., 2013; Bernhardt and Leslie, 2013) or overfishing in kelp forests (Steneck et al., 2002; Ling et al., 2009). The need for site-specific quantitative resilience data in temperate systems is clear, as phase shifts are occurring in many temperate systems worldwide (Ling et al., 2014; Wernberg et al., 2016).

The resilience assessment framework could be instrumental in gaining knowledge about the resilience of temperate systems. Although the resilience assessment method embraces the ecological resilience definition of Holing, (1973), their indicator does not quantify the exact magnitude needed for a specific disturbance to shift the local system to an alternative stable state. Their approach is broader and relies on the relative contribution of multiple individual factors to the overall resilience of a site (Maynard et al., 2010). Thus, the resilience assessment framework approach quantifies the Relative Resilience Potential indicator, which can be used to expose resilience patterns (Maynard et al., 2010). The contribution of each factor is the product of two components that estimate a) the relative importance of each factor to resilience (i.e., factor relevance) and b) the impact of each factor to a site (i.e., factor intensity). The overall resilience indicator of a site takes a sum of products approach as the sum of the contributions of every factor (Maynard et al., 2010; Ladd and Collado-Vides, 2013; Maynard et al., 2015). The current definition of the Relative Resilience Potential indicator relies on truly quantitative data to estimate factor intensity and ordinal data to estimate factor relevance (Maynard et al., 2015). Although the ordinal data are based on the best available ecological information on resilience (Obura and Grimsditch, 2009; McClanahan et al., 2012; Graham et al., 2015; Maynard et al., 2015), we have a limited understanding of the relative importance of factor relevance to resilience (Maynard et al., 2015). For example, although factor relevance can vary spatially and ordinal data should be re-evaluated accordingly (Maynard et al., 2010), factor relevance has been used as a constant at the local and regional scales investigated in previous studies (Maynard et al., 2010; Ladd and Collado-Vides, 2013; Maynard et al., 2015). As a quantitative indicator, the Relative Resilience Potential indicator is somehow restricted by the uncertainties associated with the ordinal nature of factor relevance. A resilience indicator without the factor relevance limitations would prove more reliable as it would be free of the possible restrictions associated with our current incapacity to accurately quantify factor relevance. In the present study, we proposed a novel resilience indicator based exclusively in factor intensity, the Inclusive Resilience Indicator of a Site (IRIS), and compared its performance with the latest iteration of the Relative Resilience Potential indicator (RRP, Maynard et al., 2015). We also computed an RRP with randomized relevance values (RRP_{rrv}) to further investigate the effect that the ordinal values of factor relevance have on the resilience indicators. We hypothesized that there were no differences between the three resilience indicators (first null hypothesis) and, consequently, that the three resilience indicators exposed the same pattern of resilience (second null hypothesis). Failure to reject these hypotheses would make the more straightforward intensity-based IRIS indicator better suited to provide baseline resilience data to help track natural patterns of resilience and the consequences that management actions have on the resilience of our oceans.

4.2. Material and Methods

Study area and field survey

The Alboran Sea marine ecoregion of the world (hereafter the Alboran Sea) is located in the western Mediterranean basin, spreading from the Gibraltar Strait to Cartagena in the Iberian Peninsula and to Arzew Gulf in Algeria (Spalding et al., 2007, Fig. 4.2). The strong Atlantic influence makes this Mediterranean region unique, with high productivity and diversity differentiated from the western Mediterranean (IUCN, 2009).

We used the Reef Life Survey underwater protocol (Edgar and Stuart-Smith, 2014) to identify and quantify the abundance of fish, invertebrate, and sessile species in 54 unprotected sites spread over 500 km of the Alboran sea, from Gibraltar to Cartagena including some locations in North Africa. Briefly, we used underwater visual surveys to run three quantification methods along the same 50m-long tape. The first method used a 10m-wide transect centered along the 50m-long tape (Edgar and Stuart-Smith, 2014) to identify and estimate the abundance of all conspicuous fish (total length over 2.5 cm). Then, we identified all mobile benthic invertebrates larger than 2.5cm in a 2m-wide transect centered along the same 50m-long tape (method 2). Finally, we took 20 photographs evenly distributed every 2.5m along the same 50m-long tape to calculate the percent cover of sessile organisms and bare rock (method 3). All surveys were above 15m deep to minimize the variation of coastal communities associated with depth.

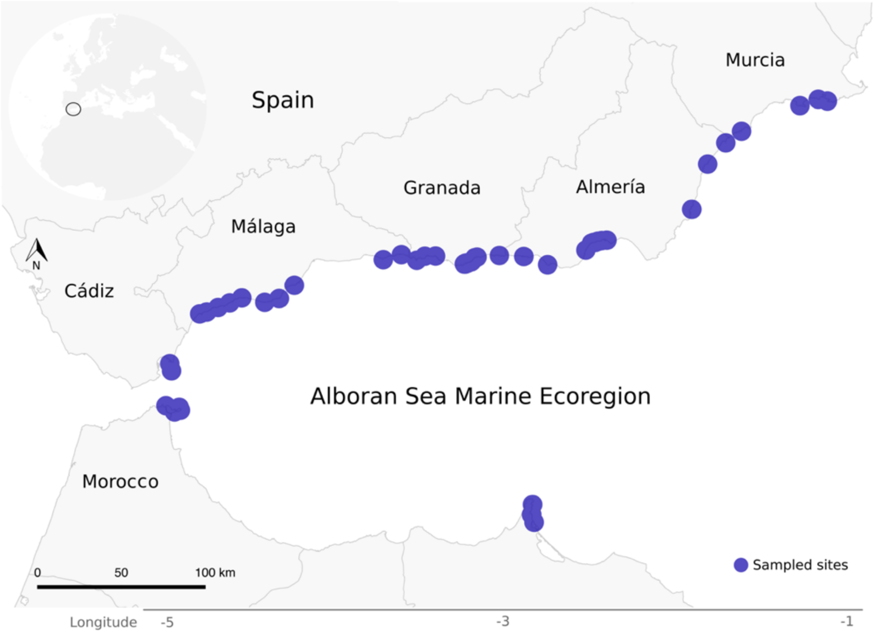


Figure 4.2 Map of the study area in the Alboran Sea marine ecoregion. The circles represent the sampled sites (N=54).

Resilience factors justification

In this paper, we referred to the overall resilience metrics as indicators and used the term (contributing) factor(s) to refer to the quantitative variables used to calculate the indicators (Table 4.1). We also summarized all the initialisms used in our study in Table 4.2 to facilitate access to their full description.

The resilience assessment framework uses a sum of products approach that relies on the relevance and intensity of multiple factors to estimate the Relative Resilience Potential indicator of a site (RRP, Maynard et al., 2010; Ladd and Collado-Vides et al., 2013). We selected 17 contributing factors that are known to affect the resilience of temperate systems (Table 4.1). We used the best evidence available in the literature to estimate the direction and strength of the influence between each contributing factor and resilience in temperate systems (Table 4.1). We classified Factor Relevance (hereafter FR) as highly, moderately, or slightly relevant. Factors with a strong influence on resilience classified as highly relevant. Factors with a weaker influence on resilience or with higher uncertainty classified as moderately relevant. Factors with the weakest influence on resilience classified as slightly relevant. Finally, we assigned an FR value of 3, 2, and 1 to highly, moderately, and slightly relevant contributing factors, respectively (Table 4.1).

The intensity of a factor relied on the actual measurement (truly quantitative data) of each factor in each site. In our study, Factor Intensity (hereafter FI) was the normalized value (between 0 and 1) of the quantitative measurement.

Table 4.1. Justification, quantification, and link to increased resilience of the 17 factors contributing to resilience. Factors were selected based on the best available resilience literature in temperate systems. All 17 factors were used to compute the three resilience indicators used in our study.

FR - Factor relevance	Contributing factor	Rationale and supporting literature	Factor quantification	Link to increased resilience	Data source
Highly relevant (FR=3)					
	Macroalgal cover (MC)	Macroalgae are essential components of littoral rocky reefs in temperate seas. They are primary producers providing oxygen and tridimensional habitat for invertebrate and fish (Mann, 1973; Dayton, 1985; Carr, 1989; Poloczanska et al., 2007; Giakoumi et al., 2012; Strain et al., 2015).	We analyzed the MC in 20 high-quality photographs taken along 50m-long transects in each site (for a total of 1,380 photographs). In each photograph, we used a centered digital square of 400 cm^{2} to randomly select 5 points (Cresswell et al., 2017) using CPCe software (Kohler and Gill, 2006). We calculated percent cover as the number of algal points over the total number of points for each transect (100).	↑ MC	Method 3 of Reef Life Survey
	Fishing pressure (FP)	Overfishing is causing the degradation and fragmentation of marine communities (Micheli and Halpern, 2005; Baskett et al., 2006; Ling et al., 2009; Barnett and Baskett, 2015).	We quantified FP as the total number of metric tons fished yearly in each province divided by the longitude of the coast (km).	↓ FP*	Andalusian Multi-Territorial Information System (https://www.juntadeandalucia.es/institutodeestadisticaycartografia/sima/index2.htm)
	Anthropogenic pollution (AP)	Pesticides, chemical, metal, and liquid pollutants increase the likelihood of disease in macroalgae, invertebrates, and fishes (Folke et al., 2004; Levin and Lubchenco, 2008; Piola and Johnston, 2008; Wernberg et al., 2009).	We quantified the number of sewage emissaries in the vicinity of our sampling sites (≤ 5km).	↓ AP*	MAPA Ministry Spanish Government (https://www.mapa.gob.es/es/)
	Community richness (CR)	Species richness is intrinsically linked to community stability (Yachi and Loreau, 1999;	We quantified the number of fish and invertebrate species present in our sampling sites.	↑ CR	Method 1 & 2 of Reef Life Survey

	Bernhardt and Leslie, 2013; Borja et al., 2013).			
Invertebrate herbivory (IH)	Increased abundance of invertebrate herbivores, i.e., sea urchins, is shifting macroalgae dominated communities to barren grounds (Ling et al., 2014; Kraufvelin, 2017).	We used the total abundance of sea urchins in each site (*Arbacia lixula*, *Paracentrotus lividus,* and *Sphaerechinus granularis*) as an estimate of IH intensity.	↓ IH*	Method 2 of Reef Life Survey
Sea urchin fish predators (SUFP)	The abundance of fish species that feed on juvenile or adult sea urchins, controls sea urchin populations and contributes to enhancing macroalgal cover (McClanahan, 1995; Shears and Babcock, 2002; Guidetti and Dulčić, 2007; Clemente et al., 2010).	We used the total abundance of the 8 fish species in our species list known to feed on sea urchins as an estimate of the intensity of the fish top-down control on sea urchins. See supplementary Table 1 for the list of species for Chapter IV.	↑ SUFP	Method 1 of Reef Life Survey & FishBase information (www.fishbase.com)
Abundance of top predators (ATP)	The abundance of top predator fishes is a proxy of ocean health. Their presence and abundance point to more resilient, fully functional communities (Jackson, 2001; Crowder and Norse, 2008; Llope et al., 2011).	We used the total abundance of 16 fish species categorized as higher carnivores to estimate ATP in each of our sampling sites. See supplementary Table 2 for the list of species for Chapter IV.	↑ ATP	Method 1 & Method 2 of Reef Life Survey) & FishBase information (www.fishbase.com)
Moderately relevant (FR=2)				
Free anthropogenic physical pressures (FPP)	Impacts from divers, snorkelers, or anchors increase the susceptibility of disease in macroalgae and invertebrates (Claudet et al., 2010; Gladstone et al., 2013; Riera et al., 2016; Siciliano et al., 2016).	We quantified the total number of dive centers within a distance of 10 km from each sampling site.	↓ FPP*	Database of Spanish Underwater Activities (www.bajoelagua.com)
Fish functional diversity (FFD)	High values of functional diversity provide marine communities a better response to disturbance since the system is likely to have traits that enhance recovery (Folke et al., 2004; Bates et al., 2013; Nash et al., 2017).	We used the {FD} package in R (Laliberté et al., 2014) to calculate FFD using thermal physiology, life history strategy, feeding ecology, behavior, habitat use, and geographic range breadth traits (total of 10).	↑ FFD	Method 1 of Reef Life Survey & FishBase information (www.fishbase.com)

Trophic redundancy (TR)	Redundancy of fish species in trophic levels confers robustness because trophic groups remain functional despite the loss of a species (Folke et al., 2004; Micheli and Halpern, 2005; Rice et al., 2012).	We categorized every fish species (68 in total) as planktivore, benthic invertivore, browsing herbivore, higher carnivore, and scrapers. See supplementary Table 3 for the classification of all fish species found in our study for Chapter IV.	↑ TR	Method 1 of Reef Life Survey & FishBase information (www.fishbase.com)
Vulnerability of the fish community (VFC)	Fish are major components of most marine communities. Fish vulnerability depends on intrinsic traits (Cheung et al., 2007; Hughes et al., 2005; Berkes et al., 2006).	We calculated VFC as the average of the vulnerability (estimates from FishBase) of every fish specimen observed in each site (community-weighted mean).	↓ VFC*	Method 1 of Reef Life Survey & FishBase information (www.fishbase.com)
Human population (HP)	Ocean sprawl, recreational fishing activities, or water pollutants are directly related with the size of human population and have strong impacts on biodiversity and resilience (Borja et al., 2013; Ladd and Collado-Vides, 2013)	We used the total number of inhabitants of the municipality of the sampling site.	↓ HP*	Andalusian Multi-Territorial Information System (https://www.juntadeandalucia.es/institutodeestadisticaycartografia/sima/index2.htm)
Sea urchin invertebrate predators (SUIP)	The abundance of invertebrate species that feed on juvenile or adult sea urchins controls sea urchin populations and contributes to enhancing macroalgal cover (Shears and Babcock, 2002; Clemente et al., 2007). Contrary to SUFP above, we classified SUIP as moderately relevant because of the reduced mobility of invertebrates.	We used the total abundance of the four invertebrate species in our species list that are known to feed on sea urchins (*Charonia lampas, Charonia tritonis, Coscinasterias tenuispina*, and *Marthasterias glacialis*) as an estimate of the intensity of the invertebrate top-down control on sea urchins.	↑ SUIP	Method 2 of Reef Life Survey
Slightly relevant (FR=1)				
Proximity to the nearest city (PNC)	Although the area of influence of human activities reaches the whole planet, some impacts on the environment get diluted with increasing distance to the source (Stuart-Smith	We quantified in meters the distance in a straight line between our sampling sites and the nearest city.	↑ PNC	Quantum Geographic Information System software (QGIS, 2018)

	et al., 2008; Borja et al., 2013).			
SSTmax deviation (SSTD)	Deviation from the average maximum sea surface temperature (SSTmax) is a major cause of stress in marine organisms, increasing their susceptibility to disease (Wernberg et al., 2009; Wernberg, 2010).	We calculated SSTD as the difference between the SSTmax value of a site and the average of the SSTmax values of all 54 sites in our study.	↓ SSTD*	Bio-ORACLE Database (www.bio-oracle.org)
Nitrate deviation (ND)	Nitrates play a major role in marine productivity. Anthropogenic activities are increasing the nitrate concentration of marine systems, often leading to eutrophication (Wernberg et al., 2009; Strain et al., 2015).	We calculated ND as the difference between the ND value of a site and the average of the ND values of all 54 sites in our study.	↓ ND*	Bio-ORACLE Database (www.bio-oracle.org)
Phosphate deviation (PHD)	Phosphates also play a major role in marine productivity. Anthropogenic activities are increasing the phosphate concentration of marine systems, often leading to eutrophication (Wernberg et al., 2009).	We calculated PHD as the difference between the PHD value of a site and the average of the PHD values of all 54 sites in our study.	↓ PHD*	Bio-ORACLE Database (www.bio-oracle.org)

* We used the inverse value of the factor so that larger factor values were always associated with increased resilience.

Resilience indicators computation

In our study, we tested whether changes in the criteria to assign ordinal values to factor relevance may lead to differences in resilience, i.e., we tested for the importance of factor relevance in the resilience indicators. To do so, we used 17 contributing factors to calculate three resilience indicators with varying criteria to assign FR values. First, we calculated the Relative Resilience Potential (RRP), a resilience indicator that takes into account both the relevance (FR) and intensity (FI) of every factor. The RRP assigns FR values based on the available ecological literature on resilience (Maynard et al., 2015). Second, we calculated a modified version of the RRP that used randomized FR values (RRP_{rrv}) rather than values based on the best ecological evidence. Finally, we calculated the Inclusive Resilience Indicator of a Site (IRIS), which is an intensity-based resilience indicator that did not consider factor relevance. An irrelevant FR role should render no differences between the three indices.

Relative Resilience Potential (RRP)

The RRP is a resilience indicator defined by Maynard et al. (2015) as:

$$\mathrm{RRP} = \sum_{\mathrm{k}=1}^{\mathrm{N}} (\mathrm{FR_k} \times \mathrm{FI_k})$$

where k refers to each contributing factor, FR is factor relevance, FI is factor intensity, and N is the total number of factors.

The FI value was the min-max normalized value of each contributing factor. Thus, FI values of each of the 17 contributing factors ranged between 0 and 1, regardless of their original units. The product FI x FR measured the Factor Contribution to Resilience (FCR), and the sum of all 17 FCRs provided the estimate of the resilience of a site. Final RRP values ranged between 0 and 1 as they were min-max normalized again.

Relative Resilience Potential with random relevance values ($\mathrm{RRP_{rrv}}$)

The $\mathrm{RRP_{rrv}}$ was the average of 1004 RRP values. Most RRP values (1000) were calculated assigning random FR values of 1 to 3 rather than the corresponding value based on the best available evidence. The remaining 4 RRP values were the observed RRP value (as explained in the previous section) and the expected RRP value obtained if all factors had the same FR of 1, 2, or 3.

Inclusive Resilience Indicator of a Site (IRIS)

Conceptually, we defined IRIS as the RRP value when all FR equaled one. Thus, IRIS values accounted for just factor intensity, i.e., factor relevance had no influence on IRIS. In practice, we defined IRIS as

$$\mathrm{IRIS} = \frac{\sum_{k=1}^{N} \mathrm{FI}_k}{N}$$

where k refers to each contributing factor, FI is factor intensity, and N is the total number of factors. As for the RRP, FI values were the min-max normalized value of each contributing factor. Contrary to RRP, we divided the sum of all FIs over the total number of contributing factors (N=17 in our study). Thus, possible IRIS values ranged between 0 and 1, but these maximum and minimum values were extremely unlikely to occur since a single site should have the maximum (or minimum) values for all contributing factors. The lack of normalization in the final computational step in IRIS differed from that in the RRP (and $\mathrm{RRP}_{\mathrm{rrv}}$) approach and did not force IRIS values to spread toward the end values of the range. The R code of the IRIS indicator is available in the next git repository: https://github.com/Sanabria-Fernandez/Inclusive-Resilience-Indicator-of-a-Site-IRIS-.

Statistical analysis

To test for the first hypothesis of our study, we used Linear Mixed Effects Models (LMEs) using the “nlme” R package (Pinheiro et al., 2018). We tested for differences in resilience values as a function of the resilience indicator (fixed effect factor with three levels: RRP, RRPrrv, and IRIS) and site (random effect factor with 54 levels). LMEs allowed estimating and accounting for the covariance among sites to address the spatial pseudoreplication associated with this type of sampling design. We also tested for differences in the coefficient of variation between resilience indicators using “cvequality” R package

(Marwick and Krishnamoorthy, 2018). To test whether the three resilience indicators behaved similarly, we evaluated their coefficients of determination with lm() function of “stats” (R Core Team, 2016).

To test for the second hypothesis of our study (spatial patterns of resilience in the Alboran Sea) we used Generalized Additive Models (GAMs) with the “Gam” R package (Hastie, 2017). To do so, we computed a GAM for each resilience indicator (RRP, RRP_{rrv}, and IRIS) using a loess smoothing function with longitude as a factor (Zuur et al., 2009). GAMs were selected applying the Akaike Information Criteria (Zuur et al., 2009). To test whether resilience indicators differed in their predictive capacity, we tested whether the GAM fit values and their coefficients of variation differed between resilience indicators using the same methodology explained earlier. We also used the coefficients of determination to test whether the values predicted by the three resilience indicators behaved similarly.

Finally, to analyze the factors that contributed the most to high and low resilient areas, we selected those sites with the highest or lowest 5% of the resilience values. We, then, analyzed the contribution of each factor to the final resilience indicator (i.e., their FCRs). For this assessment, we used only the IRIS indicator, so the FCRs equaled to factor intensity (FI). We set up a threshold FI value of 0.8 or 0.2 to identify the most relevant factors. Factors with an FI higher than or equal to 0.8 had a large influence to increase resilience values, while factors with an FI lower than or equal to 0.2 had a large influence to decrease resilient values. We performed the statistical analyses in R software (R Core Team, 2016).

Table 4.2. Initialisms used in our study with their full name

Initialisms	Full name
RRP	Relative Resilience Potential
RRP_{rrv}	Relative Resilience Potential with random relevance values
IRIS	Inclusive Resilience Indicator of a Site
FR	Factor Relevance
FI	Factor Intensity
FCR	Factor Contribution to Resilience

4.3. Results

The 17 resilience factors used to calculate the three resilience indicators in our study were complementary (average of the correlation coefficient=0.019). We found no differences in resilience values between the three resilience indicators (RRP, RRP_{rrv}, and IRIS, p=0.44, Table 4.3, Fig. 4.3a). Resilience indicators differed in their coefficients of variation (p<0.001, Fig. 4.3a), with IRIS showing a lower coefficient of variation than RRP and RRP_{rrv} (in percentage, 15.48, 41.98 and 40.85, respectively). The three resilience indicators were highly correlated (R>0.9 and p<0.001 for all comparisons, Fig. 4.4a,b) and we found significant longitudinal gradients in resilience with all three indicators (p<0.01 for all indicators, Table 4.4, Fig. 4.5). The percentage of deviance explained varied between resilience indicators (in percentage, RRP_{rrv}=67.0, IRIS=37.0, and RRP=24.5).

Table 4.3. Linear Mixed Effects Model (LME) on **(a)** observed and **(b)** fitted resilience values as a function of the resilience indicator (fixed factor, RRP, RRP_{rrv}, and IRIS) and site (random factor, 54 sites). Fitted values resulted from significant GAMs.

(a)	**LME-observed resilience values**	*DF*	*F-value*	*p-value*
	Intercept	159	1279.6	<0.001
	Resilience indicator	159	0.82	0.440
(b)	**LME-fitted resilience values**	*DF*	*F-value*	*p-value*
	Intercept	159	3662.7	<0.001
	Resilience indicator	159	2.36	0.097

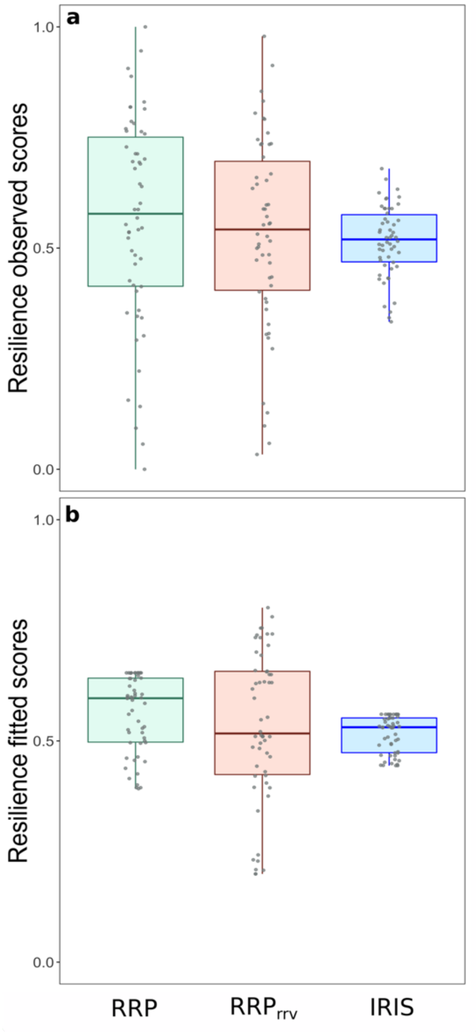


Figure 4.3. Boxplot representations of the RRP, RRP_{rrv}, and IRIS resilience indicators. (a) Observed resilience values. (b) Fitted resilience scores obtained by significant GAMs. Gray dots show the actual observed or fitted resilience values for each site.

Table 4.4. Generalized Additive Model (GAM) on observed resilience values with geographical longitude as a factor. We ran an independent GAM for each resilience indicator (RRP, RRP_{rrv}, and IRIS).

(a)	**RRP**	**DF**	**Mean Sq**	**F-value**	**p-value**
	Longitude	2	0.11	2.6	0.001
	Residuals	49.91	0.040		
(b)	**RRP_{rrv}**	**DF**	**Mean Sq**	**F-value**	**p-value**
	Longitude	2	0.26	11.5	<0.001
	Residuals	36.42	0.020		
(c)	**IRIS**	**DF**	**Mean Sq**	**F-value**	**p-value**
	Longitude	2	0.03	8.5	<0.001
	Residuals	49.91	0.004		

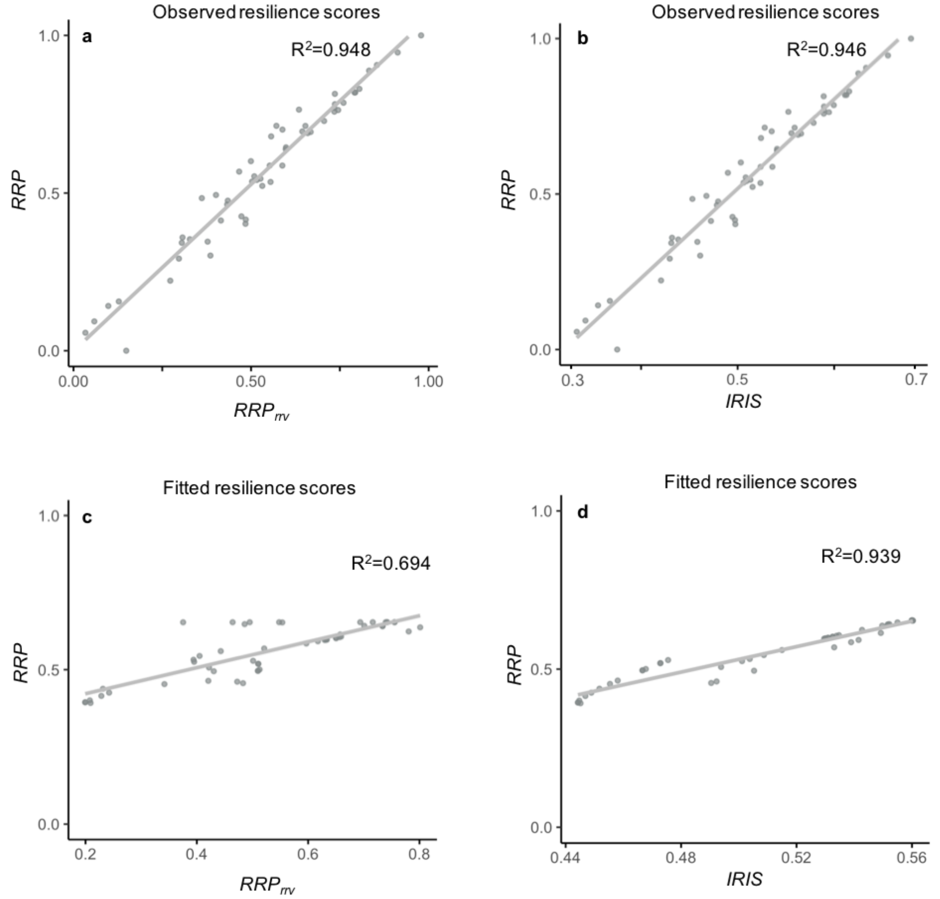


Figure 4.4. Relationship between the RRP, RRP$_{rrv}$, and IRIS resilience indicators. Graphics (a) and (b) based on observed resilience values. Graphics (c) and (d) based on fitted resilience scores obtained by significant GAMs.

We found no differences in the fitted values predicted by the GAMs for the three resilience indicators ($p=0.097$, Fig. 4.3b). Predicted resilience values differed in their coefficients of variation ($p<0.001$, Fig. 4.3b), with IRIS showing the lowest coefficient of variation (in percentage, 8.04, 41.98, and 40.85 for IRIS, RRP, and RRP_{rrv}, respectively). Fitted resilience values for the three resilience indicators were strongly correlated ($R>0.8$ and $p<0.001$ for all comparisons, Fig. 4.4c,d) and all three GAMs predicted the same spatial pattern of resilience with low resilient areas at longitudes between -5° and -4° and high resilient areas at longitudes between -3° and -2° (Fig. 4.5). IRIS categorized in low, medium, regular, and high resilience showed a longitudinal pattern (Fig. 4.6). Anthropogenic physical pressures, anthropogenic pollution, human population, invertebrate herbivory, and fishing pressure contributed highly to high resilient areas (Fig. 4.7a). Sea urchin invertebrate predators, proximity to the nearest city, phosphate deviation, abundance of top predators, fishing pressure, invertebrate herbivory, and nitrate deviation contributed highly to low resilient sites (Fig. 4.7b).

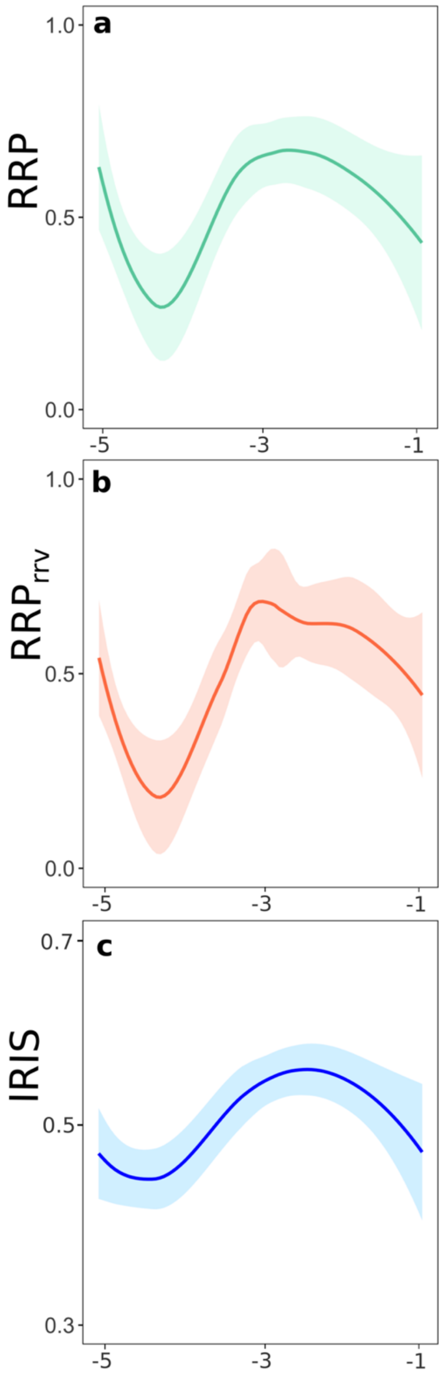


Figure 4.5. Longitudinal gradient of the (a) RRP, (b) RRP_{rrv}, and (c) IRIS resilience indicators along the Alboran Sea. Mean and 95% confidence intervals obtained by significant GAMs.

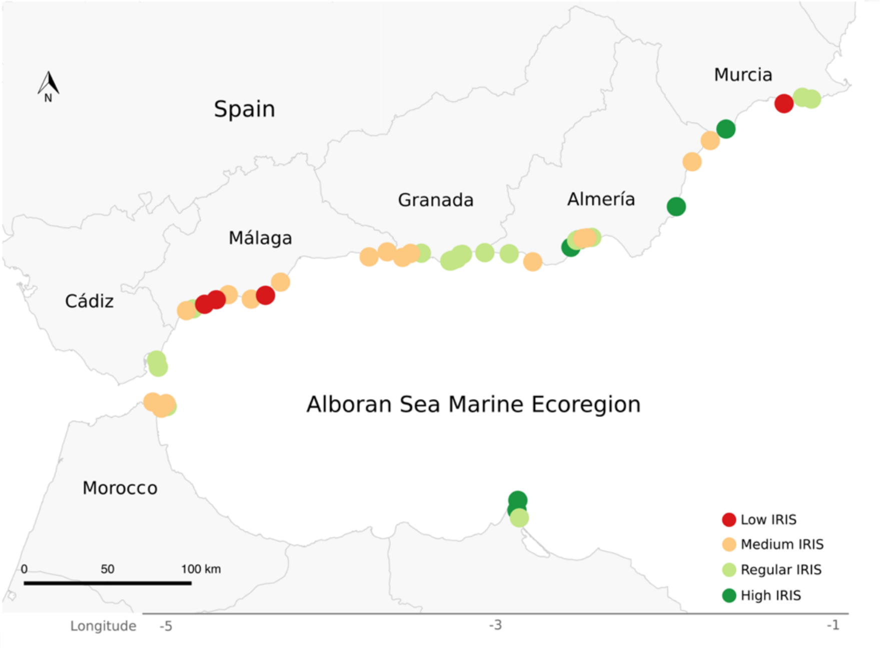


Figure 4.6. Map of the observed IRIS values in the Alboran Sea. We colored sites with low (red), medium (orange), regular (soft green) and high (dark green), IRIS values to better convey the information. See text and Table 4.4 for more information on the significant resilience gradients observed with RRP, RRP_{rrv}, and IRIS.

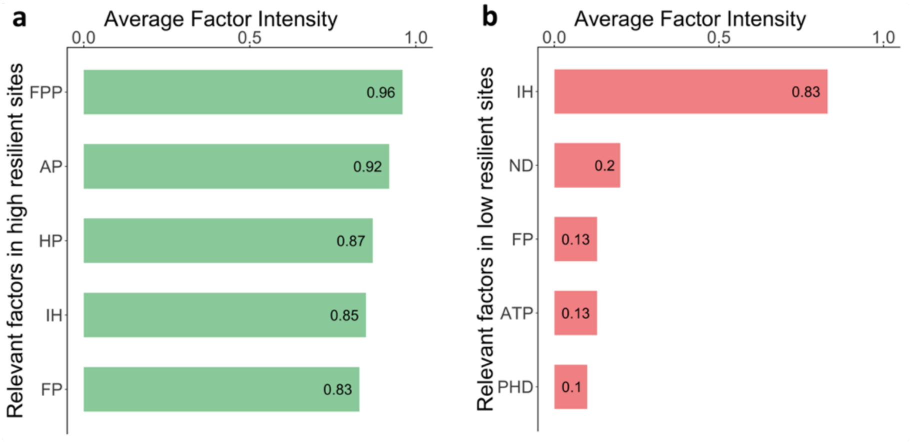


Figure 4.7. Average factor intensity (FI) values of the most relevant factors contributing to high (a) and low (b) resilient sites. We defined the most relevant factors as those with an FI ≥ 0.8 or an FI ≤ 0.2. Notice we found no factor with an FI ≤ 0.2 in high resilient sites. Invertebrate herbivory was the only factor with an FI ≥ 0.8 in low resilient sites, but also contributed to high resilient sites. (FPP) Anthropogenic physical pressures, (AP) Anthropogenic pollution, (HP) Human population, (IH) Invertebrate herbivory, (ND) Nitrate deviation, (FP) Fishing pressure, (ATP) Abundance of top predators and (PHD) Phosphate deviation.

4.4. Discussion

Resilience, first defined as the persistence of systems (Holling, 1973), is a critical ecosystem trait with substantial implications in management. Despite the extensive development of the resilience research in ecology, site-specific quantitative estimates of resilience remain elusive, hindering the development of this field. International programs such as the Convention on Biological Diversity or the United Nations Environmental Program actively support the acquisition of resilience data (Aichi Biodiversity Target 15, Leadley et al., 2014). And yet, the recent global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and

Ecosystem Services brought to light the lack of awareness on this particular field (Díaz et al., 2019). Finding pragmatic solutions to build a resilience baseline is, therefore, essential. The resilience assessment framework has successfully quantified the relative resilience potential of some tropical reefs, and its approach could undoubtedly contribute to generating resilience data (Maynard et al., 2010; Ladd and Collado-Vides et al., 2013; Maynard et al., 2015). In our study, we embraced the resilience assessment approach to quantify resilience, analyzed the relative resilience potential indicator, and simplified its computation topropose a new resilience indicator that it is easier to calculate and could support the acquisition of broadscale resilience data (Fig. 4.8).

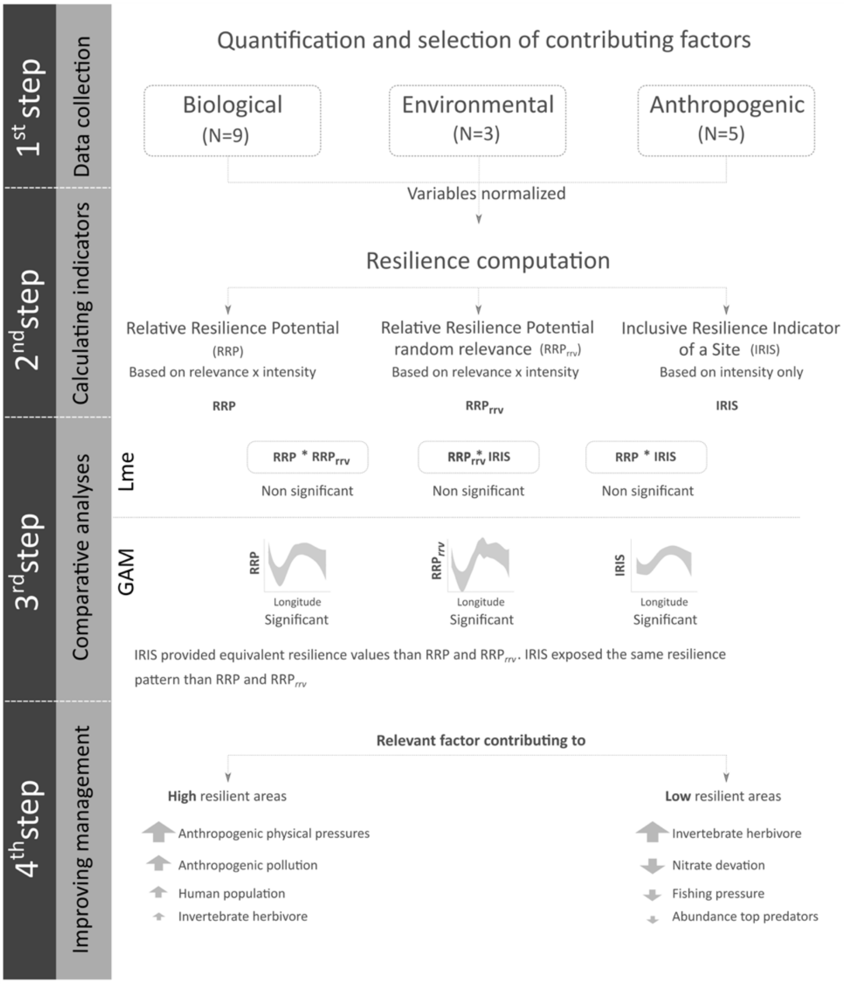


Figure 4.8. Workflow of our study with the four essential steps, most relevant methods, and main results.

The resilience assessment framework takes a sum-of-products approach to calculate an indicator of the relative resilience potential of a site that adds together the multiplicative effect of the relevance and the intensity of multiple factors known to contribute to resilience (Maynard et al., 2010; Ladd and Collado-Vides et al., 2013; Maynard et al., 2015). While factor intensity relies on actual quantitative data, factor relevance relies on ordinal data that are categorized based on available literature (McClanahan et al., 2012).

Lack of information on the relevance of some factors and the uncertainties associated with wrong assignments could deter otherwise interested scientists and policymakers from generating resilience data. In our study, we tested whether an intensity-based resilience indicator (IRIS) could function as the current Relative Resilience Potential indicator of reference (RRP, Maynard et al., 2015), which would get rid of the least supported and most dubious section of the indicator. We found that the intensity-based IRIS had similar resilience values and detected and predicted the same longitudinal resilience pattern than the RRP. Further, an RRP calculated with random factor relevance values (RRP_{rrv}) was also equivalent to the original RRP, which used ordinal values assigned to each factor after reviewing the literature. We, therefore, accepted our null hypothesis of no difference between the three resilience indicators investigated in our study. We also accepted our second hypothesis as the three indicators exposed the same pattern of resilience in the Alboran Sea. These results are supported by the strong positive correlation between IRIS and RRP, despite IRIS having less variation and no data on factor relevance. Our study also revealed a small number of highly influential factors contributing to the high and low resilient areas in the Alboran Sea. These factors were strongly and negatively associated with human activities prone to management practices (e.g., eutrophication or fishing). Based on our results, we recommend the use of IRIS as a suitable indicator to assess resilience in temperate rocky reefs (Fig. 4.8).

There are a large variety of approaches to estimate the complex concept of resilience. A number of studies approximate to resilience with related ideas such as ecosystem degradation, stability, or phase shifts (Steneck et al., 2002; Thibaut and Connolly, 2013). Other studies focus on the resilience to specific factors such as storms or temperature (Wernberg et al., 2010; Bates et al., 2013) and others investigate statistical concepts to obtain generic indicators of resilience not often used in the field (Dakos et al., 2015; Scheffer et al., 2015). Although many of these and other studies discuss the implications of their findings to resilience, few studies empirically estimate the broader concept of resilience. With the diversity of approaches available, the need for a resilience assessment framework that allows comparable quantification of resilience is clear (Nyström et al., 2008).

Supported by a number of studies on the factors that affect the capacity of coral reefs to cope with disturbance (Salm et al., 2001; West and Salm, 2003) and the interest to establish a protocol to measure resilience (Obura 2005; Obura and Grimsditch, 2009), Maynard et al. (2010) established a resilience assessment framework that has allowed ranking coral reef sites as a function of resilience (Maynard et al., 2010; Ladd and Collado-Vides 2013; Maynard et al., 2015). The approach taken by the resilience assessment framework to quantify resilience is very encouraging. First, it uses a large number of factors known to contribute to resilience, avoiding a strong influence from a single factor (e.g., temperature). Second, since not all the factors contribute the same to resilience neither they are constant in space nor time (McClanahan et al., 2012), the resilience assessment framework uses an indicator that accounts for both the relevance and the intensity of every contributing factor (Maynard et al., 2015). Third, factor intensity uses min-max normalized values of the factors, so that the factors' original units or scales have no influence on factor intensity nor on the overall resilience metric. Fourth, the approach can be easily extrapolated to other locations, regions, or systems of interest (Maynard et al., 2015). To do so, it is necessary to adjust the list of contributing factors to include those driving resilience in the area of interest (Maynard et al., 2015). It may also be necessary to re-assess the relative importance of the contributing factors and re-evaluate factor relevance based on appropriate ecological literature for the area of interest (Maynard et al., 2010).

Meanwhile, our knowledge of the ecological resilience of rocky reefs is limited (Díaz et al., 2019). Our priority was to adapt the resilience assessment framework approach to temperate rocky reefs. In our study, we used 17 contributing factors to calculate resilience, which is similar to the number of factors used in other studies using the resilience assessment framework (Maynard et al., 2010; Ladd and Collado-Vides, 2013; Maynard et al., 2015). Ecological evidence in temperate systems allowed adjusting the list of contributing factors more easily than estimating FR. Contrary to the considerable information on FR in the tropics, the relative importance of the factors contributing to resilience is less investigated in temperate systems and created uncertainties in our criteria to assign the ordinal FR values. Our results showed that, as currently estimated, FR plays a minor role in the RRP indicators. Resilience values failed to differ between the RRP and the RRP_{rrv}. Since RRP_{rrv} used a random assignment of FR values rather than the RRP assignments based on the ecological evidence, variation in the criteria to establish the relevance of certain factors seems to have little impact on the resilience indicator. Resilience values also failed to differentiate between the RRP and the relevance-free IRIS, suggesting a negligible role of FR in the resilience values. Given the constant nature of FR and the sum-of-products nature of the RRP, FR could potentially introduce a three-fold difference in RRP values (i.e., when all FR values equaled one vs. all FR values equaled three). In practice, this is impossible since there are multiple factors with FR values of one to three.

An additional consequence of the constant nature of FR is that factor intensity (FI) is the source of resilience variation between sites. The strong positive correlations found between the three resilience indicators in our study further illustrated this influence. The implications are far from trivial. Since it is FI (and not FR) what currently drives the patterns of resilience, struggling with the uncertainties (and possible deterrent effects) associated with FR to advance in our ecological understanding of resilience is completely unnecessary. It is realistic to argue that FR will play the same role than FI when we advance in our capacity to obtain site-specific quantitative estimates of FR. As for now, our study showed that the three resilience indicators found the same longitudinal pattern of resilience and predicted the same expected resilience values along the longitudinal gradient of the region despite the intensity-based IRIS used no FR data.

The simplicity of the intensity-based IRIS could facilitate the collection of widespread resilience data to understand patterns and trends in resilience and promote resilience-based management. However, the capacity of the IRIS to quantify resilience is not a free meal and has a number of limitations. IRIS relied on a quantitative database of 17 independent environmental, social, and biological factors, which may be challenging to collect. Of course, factors need to vary, as a constant variable would contribute to the final resilience values but not to the resilience patterns. The need for variation is also associated with site ranking. IRIS (and RRP) provides a relative value of resilience as it is based on the normalization (i.e., ranking) of sites. The relative nature of IRIS can be an important limitation, as resilience values are dependent on i) the exact contributing factors and ii) the actual sites used in the study. Given the large number of factors contributing to resilience that are used in the resilience assessment approach, we believe that the final resilience value of a site is robust enough as to not vary significantly with a small variation in the number (or nature) of the contributing factors. Similarly, given a large enough number of sites, we believe that the resilience pattern exposed would remain the same, despite changes in the actual sites selected in the study. A simple corollary of this limitation seems clear: the more number of contributing factors and the more number of sites, the better. Beyond its limitations, the relative nature of IRIS also is a strength, as resilience has to be assessed as relative when producing rankings meant to inform decisions (Maynard et al., 2010). In fact, previous studies using the resilience assessment framework have strong management implications (Walker et al., 2002, Maynard et al., 2010, Ladd and Collado-Vides, 2013, Maynard et al., 2015). The simplicity of the intensity-based IRIS could facilitate the collection of widespread resilience data to understand patterns and trends in resilience and promote resilience-based management, for example in the Andalusian coastal marine social-ecological systems (Lazzari et al., 2019). Moreover, IRIS could be easily adapted to report species-specific resilience levels, to target threatened, invasive, or commercially interesting species rather than the whole community (Micheli et al., 2012).

Additionally, IRIS could point to high resilient sites worth preserving, as for example, sites with high IRIS values or sites with low IRIS values but prone to improvements through management actions. In our study, the longitudinal patterns of resilience exposed two specific geographic areas with high and low resilience sites, respectively. We found that high resilient sites had low population density, low anthropogenic pollution, low physical and fishing pressures, and a large abundance of invertebrate herbivores. Areas with no fishing pressures are known to have increased resilience (Barnett and Basket, 2015) and sea urchins are known to function as drivers of resilience in temperate rocky reef systems (Ling et al., 2009). However, the abundance of invertebrate herbivores was also a relevant factor in low resilient sites, so its contribution to the differences between high and low resilient sites was minimal. Low resilient sites were close to cities, had high nitrate and phosphate concentrations, a large fishing pressure, and a low abundance of top predators. A high abundance of top predators is associated with high resilient sites (Llope et al., 2011). Proximity to nearby cities and fisher access points also influence fish communities (Stuart-Smith et al., 2008) and ocean sprawl reduces the number and abundance of many benthic and sessile species, which could play an important role in the resilience of the system (Sanabria-Fernandez et al., 2018). The influential factors found in our study are prone to management practices that could result in increased resilience, providing an example of how our IRIS-based approach can help prioritize specific management actions to increase resilience. Biological factors such as (functional) diversity (Bates et al., 2013), trophic redundancy (Micheli and Halpern, 2005; Rice et al., 2012), macroalgal cover (Carr, 1989; Poloczanska et al., 2007) or environmental factors such as temperature (Wernberg et al., 2009; Wernberg, 2010) played a less influential role in the resilience of the Alboran sea marine ecoregion of the world.

4.5. Conclusions

The intensity-based Inclusive Resilience Indicator of a Site (IRIS) was as reliable and accurate as the Relative Resilience Potential (RRP) used by the resilience assessment framework, which is based on both factor intensity and factor relevance. Our study showed evidence that, as currently estimated, factor relevance played a negligible role in resilience, as supported by the non-significant differences between the three indicators and by the same spatial pattern of resilience they exposed along the Alboran Sea. We also showed that the inconsequential capacity of factor relevance to influence resilience was restricted to the final quantitative resilience value and only factor intensity accounted for the variation in resilience between sites. IRIS accounted for 94 % and 99% of the variance of RRP and $RRP_{rrv,}$ respectively. We, therefore, suggest that the intensity-based IRIS can produce proper baseline resilience data to increase our understanding of the spatial and temporal patterns in resilience, which can help boost resilience-based management decisions. Indeed, our IRIS-based analysis of the most influential factors contributing to the resilience of the Alboran sea suggests that improved management practices to reduce eutrophication and fishing pressures could boost the resilience of this diverse ecoregion of the world.

Chapter V

Enhancing and preserving marine resilience trough management actions: How to identify top resilient areas and make them more resilient

This research is based on:

Sanabria-Fernandez JA, Lazzari N, Becerro MA, (In preparation). Enhancing and preserving marine resilience trough management actions: How to identify top resilient areas and make them more resilient.

Picture: Underwater seascape from the Peñón de Vélez de la Gomera (Spanish territories in the African continent). In the picture you can see specimens of *Chromis chromis, Coris julis, and Serranus scriba*. Natali Lazzari took this picture during an INBIOMAR II 2020 research grant sampling trip.

Abstract

Resilience, an essential property of natural systems, is declining as we lose biological diversity. Resilience loss increases the fragility and vulnerability of natural communities, which can degrade to a point of no return and lead to collapse. In the current state of biodiversity loss, how to preserve and improve resilience have become conservation priorities. Here, we quantified the marine resilience of temperate rocky reefs by integrating 17 biological, management, and environmental factors. We then identified areas with extremely high and low resilience values (top and bottom resilient areas, respectively). We also went one step further and recalculated our resilience indicator assigning maximum values to every management factor, which allowed evaluating how much we can improve resilience through management actions and the actual contribution of every management factor to the overall resilience improvement. Both arguments are critical in environmental policy decision making. Briefly, we found 13 top and 21 bottom resilient areas, distributed over the five marine ecoregions of Southwestern Europe waters. Through management actions, we could foster resilience by 11.77% although the actual magnitude of the resilience improvement varied with ecoregion. Our study not only helped prioritize areas to preserve but also stressed the factors that must be managed to maximize resilience. Our study provided, then, a two-for-one approach that can benefit marine conservation by incorporating resilience into decision making.

5.1. Introduction

Natural ecosystems are losing resilience tremendously (Oliver et al., 2015; Bruno et al., 2019). This loss is becoming evident at different geographic and ecosystem scales (Oliver et al., 2015). From terrestrial (Scheffer and Carpenter, 2003; Hirota et al., 2011), to freshwater (Scheffer, 2009) and marine communities (Mumby et al., 2007; Vasilakopoulos and Marshall, 2015). Also, this resilience erosion is directly impacting on the conservation of biological communities, making them fragile and vulnerable to future disturbances (Gunderson et al., 2009; Folke et al., 2004). Because of that, resilience conservation has become an unprecedented priority in the current era, based on two challenges, i.e., preserving and enhancing it. In detail, the first requires the identification of areas with high resilience, and the subsequent implementation of conservation policies to preserve it (Green et al., 2009). Conversely, the second challenge is to identify areas with poor resilience scores and to enhance it through management actions. In other words, the future of resilience depends on conservation and management being focused and oriented in the same direction (Folke et al., 2004; Maynard et al., 2010; Anthony et al., 2015; Mcleod et al., 2019).

Detection of pristine resilient areas is a required step to safeguard it in a short to medium-term future (Green et al., 2009; Davies et al., 2016). In this regard, today, various approaches are being developed to preserve the resilience from terrestrial to marine habitats. For example, in riparian systems, Fremier et al. (2015) are implementing a connectivity network that would facilitate species migration and foster resilience. Also, in marine terms, some studies seek to implement a marine resilience reserve network against climate change (Green et al., 2009). Also, protecting resilience from a socio-ecological perspective is already a reality for coral reefs (Davies et al., 2016). Then, a potentially effective way to safeguard resilience is to know which and where geographic areas with great resilience are located before implementing protection, i.e., top resilience areas. In this way, targeted protection would be applied to preserve this vital trait. However, to keep and to enhance the resilience of natural communities does not depend uniquely on protection, also the management should be included (Scheffer et al., 2001; Folke et al., 2004; Fischer et al., 2009; Maynard et al., 2010; Bruno et al., 2019).

Management is a key tool for improving and increasing the resilience of biological communities (Hughes et al., 2003; Mumby and Steneck, 2008; Morecroft et al., 2012). To be effective, management should be specific and prioritize the pressures that cause resilience loss (Hughes et al., 2003; Mumby and Steneck, 2008; Morecroft et al. 2012; Gibbs and West, 2019). For example, in the coral communities are being managed the density of coral snails, as coral reefs with a low density of coral snails increase their resilience to thermal events (Shaver et al., 2018). Furthermore, today there are strategies to build resilience from an integrative perspective, involving biological, environmental, and anthropogenic dimensions (Maynard et al., 2010; Maynard et al., 2015; Sanabria-Fernandez et al., 2019). In contrast, the resilience of rocky reefs at temperate latitudes remains a pending issue today. Reducing local factors such as human activities, erosion, and nutrient concentration is known to enhance the resilience of certain algal species (Perkol-Finkel and Airoldi, 2010; Strain et al., 2015). But, numerous anthropogenic pressures lead to resilience loss, and, even today, they are poorly managed, if managed at all (Seidl, 2014; Wu et al., 2017; Chambers et al., 2019). For example, oceanic resources overfishing produced the kelp forest collapse in the Aleutian Islands (Estes et al., 1998). Not only the overfishing but also the pollution caused by the pesticides and chemical pollutants increase the likelihood of disease in marine biological communities, losing resilience (Folke et al., 2004; Piola and Johnston, 2008; Wernberg et al., 2009). Likewise, recreational activities such as scuba divers, snorkelers, or anchor impacts increase the susceptibility of disease in macroalgae and invertebrates provoking the dismantling of the benthic structure and associated resilience loss (Gladstone et al., 2013; Siciliano et al., 2016). Fortunately, now we have the opportunity to manage the factors that degrade resilience and, then, we will be able to turn these factors into their main drivers (Folke et al., 2004; Maynard et al., 2010; Ladd and Collado-Vides, 2013; Anthony et al., 2015).

In this fragile scenario for resilience, international programs such as Convention on Biological Diversity seek to enhance the ecosystem resilience trough the Aichi Biodiversity Target 15 (Leadley et al., 2014). More recently, the International Union for Conservation of Nature (IUCN) established the Resilience Thematic Group in 2017 (www.iucn.org/es/node/25175). But beyond these international efforts, the resilience status of marine ecosystems remains a great challenge (Díaz et al., 2019). Contributing to this need, here we quantified the resilience through the integration of multiple factors belonging to the biological, environmental, and management dimensions of temperate rocky reefs (Sanabria-Fernandez et al., 2019). Then, we identified areas with extremely high resilience values (top resilient areas), these being priorities to preserve. Conversely, we detected areas with low resilience values (bottom resilient areas), these being priorities to management. Lastly, we quantify how much you can improve resilience with the highest level of management. Advancing to build a resilience management framework for rocky reefs can be global, but at the same time, a particular solution to enhance and to preserve the resilience of the natural systems.

5.2. Material and Methods

Study area

We carried out this study in the rocky reefs of the Iberian Peninsula, North Africa, and Balearic and Canary Archipelagos. We surveyed 300 locations scattered in five marine ecoregions of the world defined by Spalding et al. 2007 (Fig 5.1, South European Atlantic Shelf, hereafter Atlantic; Azores Canaries Madeira, hereafter Canaries; Sahara Upwelling, hereafter Sahara; Alboran Sea, hereafter Alboran; and Western Mediterranean, hereafter Mediterranean).

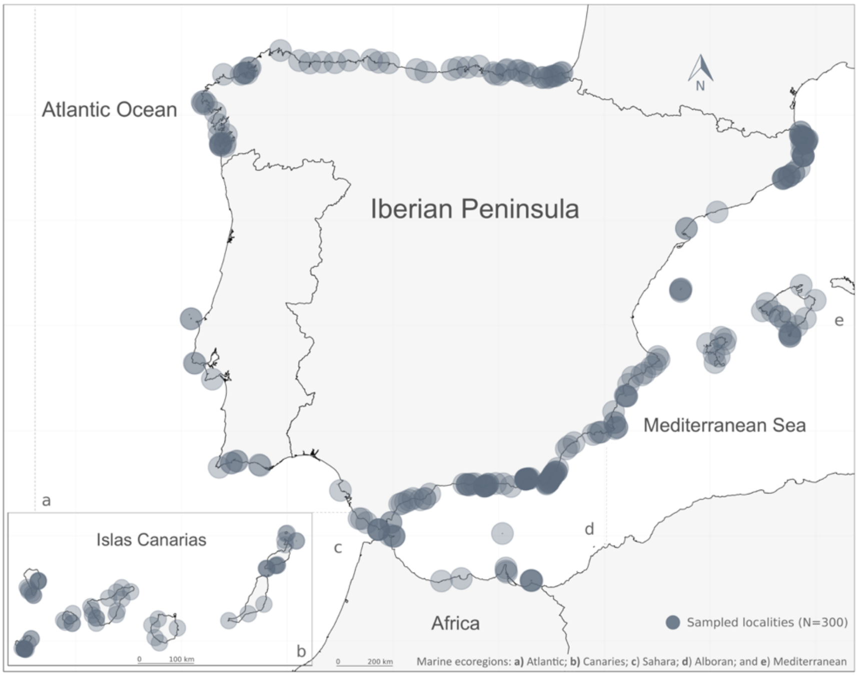


Figure 5.1. Map of study area involving five marine ecoregions.

Resilience factors

Seventeen are the factors quantified in this study, as the main resilience regulators in temperate rocky reefs. We computed the seventeen factors at each sampling location and categorized them into biological, environmental, and management dimensions (Sanabria-Fernandez et al., 2019).

Biological resilience factors

We have calculated nine biological resilience factors (Table 5.1). To obtain the biological data, we applied three methods of Reef Life Survey underwater visual census protocol (RLS, hereafter). Specifically, with method 1 we quantified the species density and size of each fish species surveyed at 50m long x 10m wide. With method 2, we counted the density of the species of mobile macroinvertebrates in 50m long x 2m wide. Lastly, with method 3, we collected information on the algal cover through 20 photo quadrats of the seabed taken every 2.5m along 50m (Edgar and Stuart-Smith, 2014). All samples were between 6 and 12 meters deep, and each sample location had a minimum of two transects.

Environmental resilience factors

In terms of environmental factors, we obtained information of three for each sample location (Table 5.1) (Bio-Oracle v2.0; Assis et al., 2017) with a resolution of 9 x 9km^2. Subsequently, the average of each factor was calculated at the ecoregion level. And lastly, we quantified the difference between the calculated average and the observed scores at each location (Sanabria-Fernandez et al., 2019).

Management resilience factors

Concurrently, we calculated five management factors that affect the resilience of temperate rocky reef communities. Specifically, these factors are the fishing pressures, anthropogenic pollution, anthropogenic physical pressures, human population, and proximity to the nearest city. We obtained the information from National, regional, and provincial government databases (see Table 5.1 for details).

Table 5.1. Here we present the 17 factors that affect the marine resilience of rocky reefs in temperate seas (Sanabria-Fernandez et al., 2019).

Dimension	Resilience factor	Link to increased resilience	Factor quantification
Biological	Macroalgal cover (MC)	↑ MC	We analyzed the MC in 20 high-quality photographs taken along 50 m-long transects in each site. In each photograph, we used a centered digital square of 400 cm^2 to randomly select 5 points using CPCe software (Kohler and Gill, 2006). We calculated percent cover as the number of algal points over the total number of points for each transect (100).
Biological	Community richness (CR)	↑ CR	We quantified the number of fish and invertebrate species present in our sampling sites.
Biological	Invertebrate herbivory (IH)	↓ IH*	We used the total abundance of 6 species of sea urchins as an estimate of IH intensity.
Biological	Sea urchin fish predators (SUFP)	↑ SUFP	We used the total abundance of the 14 fish species in our species list known to feed on sea urchins as an estimate of the intensity of the fish top-down control on sea urchins.
Biological	Abundance of top predators (ATP)	↑ ATP	We used the total abundance of 31 fish species categorized as higher carnivores to estimate ATP in each of our sampling sites
Biological	Fish functional diversity (FFD)	↑ FFD	We used the {FD} package in R (Laliberté et al., 2014) to calculate FFD using thermal physiology, life history strategy, feeding ecology, behavior, habitat use, and

			geographic range breadth traits (total of 10).
Biological	Trophic redundancy (TR)	↑ TR	We categorized every fish species (133 in total) as planktivore, benthic invertivore, browsing herbivore, higher carnivore, and scrapers.
Biological	Vulnerability of the fish community (VFC)	↓ VFC*	We calculated VFC as the average of the vulnerability (estimates from FishBase) of every fish specimen observed in each site (community-weighted mean).
Biological	Sea urchin invertebrate predators (SUIP)	↑ SUIP	We used the total abundance of the 10 invertebrate species in our species list that are known to feed on sea urchins as an estimate of the intensity of the invertebrate top-down control on sea urchins.
Anthropogenic	Fishing pressure (FP)	↓ FP*	We quantified FP as the total number of metric tons fished yearly in each province divided by the longitude of the coast (km).
Anthropogenic	Anthropogenic pollution (AP)	↓ AP*	We quantified the number of sewage emissaries in the vicinity of our sampling sites (≤ 5km).
Anthropogenic	Free anthropogenic physical pressures (FPP)	↓ FPP*	We quantified the total number of dive centers within a distance of 10 km from each sampling site.
Anthropogenic	Human population (HP)	↓ HP*	We used the total number of inhabitants of the municipality of the sampling site.
Anthropogenic	Proximity to the nearest city (PNC)	↑ PNC	We quantified in meters the distance in a straight line between our sampling sites and the nearest city.
Environmental	SSTmax deviation (SSTD)	↓SSTD*	We calculated SSTD as the difference between the SSTmax value of a

			site and the average of the SSTmax values of each marine ecoregion of the study.
Environmental	Nitrate deviation (ND)	↓ ND*	We calculated ND as the difference between the ND value of a site and the average of the ND values of each marine ecoregion of the study.
Environmental	Phosphate deviation (PHD)	↓ PHD*	We calculated PHD as the difference between the PHD value of a site and the average of the PHD values of each marine ecoregion of the study.

* We used the inverse value of the factor so that larger factor values were always associated with increased resilience.

Quantifying resilience - Inclusive resilience indicator of a site - IRIS

Quantifying original resilience – IRIS $_{Original}$

We computed the resilience indicator in each of the 300 surveyed sites. To do this, we used the scores of 17 resilience factors from the three dimensions, i.e., biological, environmental, and management. Each factor was normalized by min-max, obtaining 0 and 1. And then, we run the IRIS formula described in Sanabria-Fernandez et al. (2019). IRIS is based exclusively on the factor scores, namely factor intensity, hereafter, FI. In detailed, we defined IRIS as:

$$\mathrm{IRIS} = \frac{\sum_{\mathrm{k}=1}^{\mathrm{N}} \mathrm{FI}_{\mathrm{k}}}{\mathrm{N}}$$

where k refers to each contributing factor, FI is factor intensity, i.e., the min–max normalized value of each contributing factor. And N is the total number of factors (17 in our study). We computed the IRIS at the ecoregion level and renamed IRIS as IRIS $_{Original.}$

Quantifying artificial resilience - IRIS $_{Artificial}$

In this section, we built the IRIS Artificial. To do this, we assigned artificially the maximum scores to each management factor, i.e., 1. And, we calculated the IRIS artificial at the ecoregion level following the same formula that in the last section. The rest of the factors (biological and environmental) were equals. In other words, the values obtained in the IRIS Artificial represents the "hypothetical" maximum values of resilience under the best possible management scenario.

Finding the Top and Bottom resilience areas

For every ecoregion, we identified the top and bottom resilience areas. We defined top and bottom areas as those areas that fell outside the central part of a sigmoidal Weibull distribution. To assign the threshold levels, we used the IRIS $_{Original}$ to build a cumulative frequency distribution and adjusted a sigmoidal Weibull log-based curve through the "drc" R package (Ritz et al., 2015). Then, we used the third derivative to the Weibull curve as threshold levels to determine IRIS $_{Original}$values that had extremely high, medium, or extremely low resilience values. Top resilient areas had resilience values higher than the upper third derivative, bottom resilient areas had resilience values lower than the bottom third derivative, and areas with resilience values between both thresholds were considered moderate resilient areas.

How much the management factors can be improved?

Knowing how much can improve each management factor, we calculated the difference between the Artificial Management Factor (i.e., it is always 1, the maximum possible value to achieve) and the Original Management Factor at each location. The results of the difference are between 0 and 1, and it informs us how much and where the management factor can be improved. For example, a value close to 1 would be informing us that this factor can be substantially improved. And vice versa with the results of the differences close to 0.

Statistical analyses and plotting

We followed four statistical strategies to achieve our study aims. Firstly, to study the possible differences between IRIS $_{Original}$ vs IRIS $_{Artificial}$, we developed a Generalized Additive Mixed Model (GAMM) applying the "mgcv" R package (Wood, 2017). We built the GAMM model with two fixed factors crossed i.e., IRIS (Original or Artificial) and the ecoregion (Atlantic, Canaries, Sahara, Alboran, and the Mediterranean). Here, we included the locations as a random effect to avoid spatial auto replication. Secondly, we developed the GAMM models between IRIS Original and IRIS Artificial at the ecoregion level. And here, the localities of each ecoregion were included too as a random factor. Thirdly, we tested whether the improvement of management factors, i.e. artificial factor minus original factor scores, depends on the ecoregion. To do this, we used Linear Mixed Model (LME) applying the "lsmeans" R package (Lenth, 2016), with two fixed factors, i.e., the management factors (AP, FP, FPP, HP and, PNC), and the ecoregions (Atlantic, Canaries, Sahara, Alboran, and the Mediterranean). Also here, we included the locations as a random effect. And fourthly, we tested the difference between factors (artificial minus original), using LME models, at each ecoregion with the localities as a random effect. Lastly, we used the “ggplot2” R package (Wickham, 2016) to create the figures. We performed the statistical analyses, and representation in R software (R Core Team, 2020).

5.3. Results

Identifying Top and Bottom resilience areas trough IRIS Original

We identified 13 top and 21 bottom resilient areas scattered in the five ecoregions (Fig. 5.2 and Table 5.2). The Atlantic, Alboran, and Canaries ecoregions obtained 2 top resilient areas. Followed by the Mediterranean with 3, and the Sahara ecoregion obtained 4 top resilient areas. In contrast, the Atlantic and Alboran showed the highest number of bottom resilient areas, 6 each ecoregion. Followed, by the Mediterranean with 5, and the Canaries with 4 bottom resilient areas (Fig. 5.2 and Table 5.2).

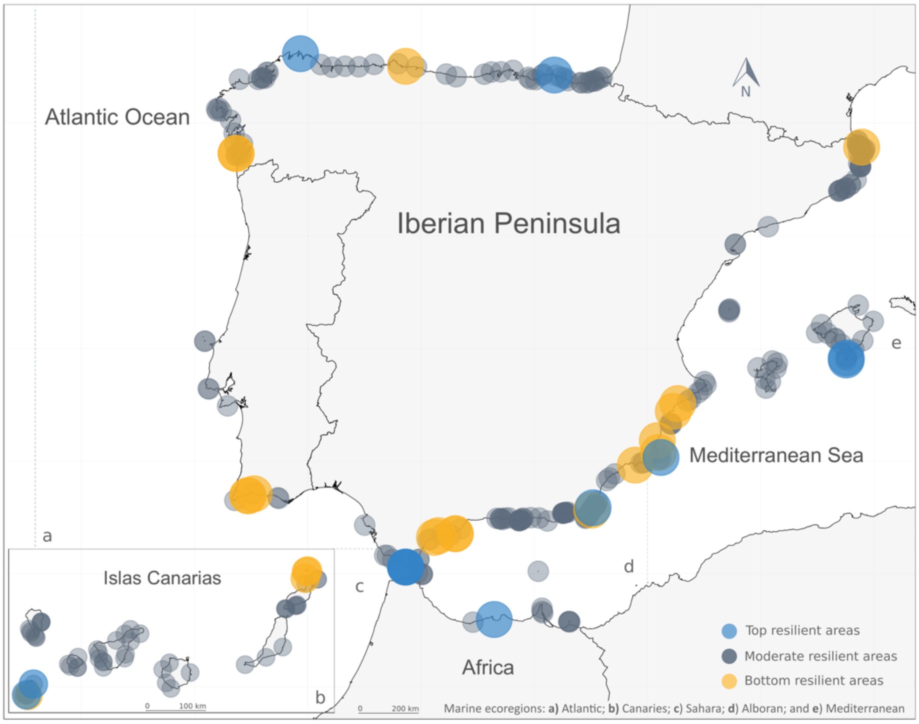


Figure 5.2. Map representing the geographical location of the Top (blue, N= 13) and Bottom (yellow, N= 21) resilience areas detected.

Table 5.2. Scores and numbers of the Top and Bottom resilience areas detected in each ecoregion (average ± standard deviation).

Top and Bottom marine resilience areas - IRIS		
Ecoregion	Average top resilience scores	Average Bottom resilience scores
Alboran	0.7 ± 0.09 (n=2)	0.4 ± 0.03 (n=6)
Atlantic	0.64 ± 0.05 (n=2)	0.37 ± 0.02 (n=6)
Canaries	0.67 ± 0.02 (n=2)	0.43 ± 0.02 (n=4)
Mediterranean	0.69 ± 0.01 (n=3)	0.42 ± 0.01 (n=5)
Sahara	0.61 ± 0.01 (n=4)	NA (n=0)

IRIS $_{Artificial}$ versus IRIS $_{Original}$

Resilience is significantly higher due to management at the ecoregion level (Interaction between IRIS (Artificial and Original) and ecoregions; F=3.41 and p= 0.009). Furthermore, in all comparisons between IRIS Artificial and Original at the ecoregion level, obtained high and significant scores for the IRIS $_{Artificial}$ (Figure 5.3 and Table 5.3). The Spain original resilience scores are 88.23% of artificial resilience, this result indicates that the resilience could increase up to 11.77% through management actions. Specifically, the management can enhance the resilience in all ecoregions (Sahara 16.82%, Atlantic 14.22%, Alboran 11.6%, the Canaries 10.7%, and Mediterranean 10.2%).

Table 5.3. List of ecoregions studied with the average scores of IRIS $_{Original}$ and scores of IRIS $_{Artificial}$ that would be improve it trough management actions. We included GAMM results of tested IRIS $_{Original}$ versus IRIS $_{Artificial}$ at ecoregion level.

Ecoregion	Average IRIS $_{Original}$	Average IRIS $_{Artificial}$	p-value
Atlantic	0.5 ± 0.06	0.59 ± 0.04	<0.001
Canaries	0.56 ± 0.06	0.63 ± 0.05	<0.001
Sahara	0.52 ± 0.14	0.62 ± 0.1	0.001
Alboran	0.57 ± 0.08	0.64 ± 0.06	<0.001
Mediterranean	0.54 ± 0.06	0.6 ± 0.06	<0.001

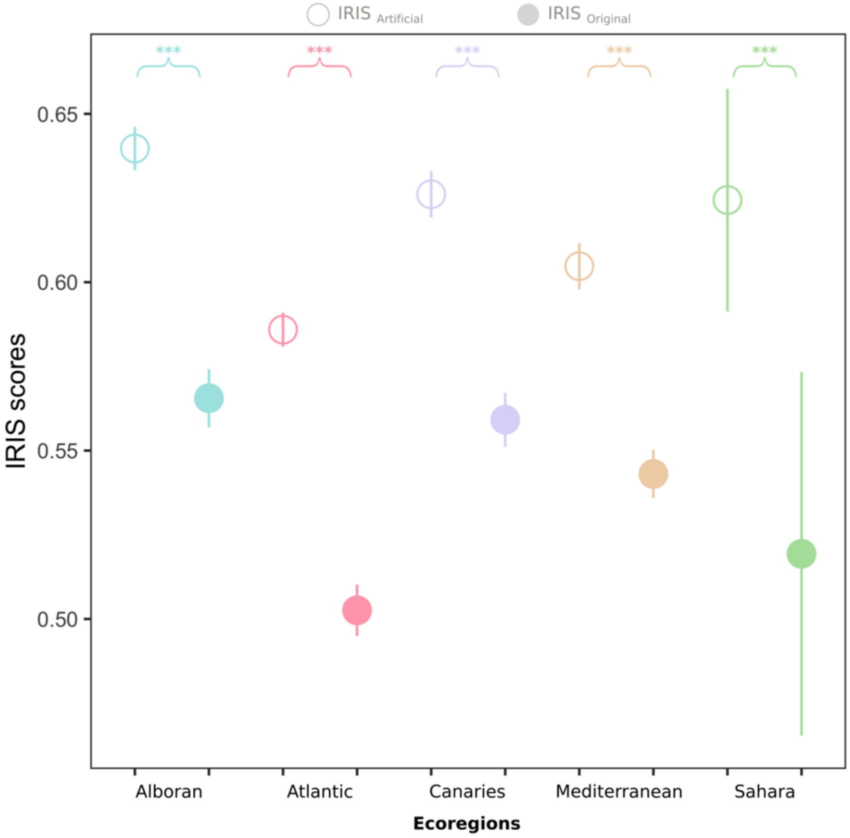


Figure 5.3. Representation of the IRIS $_{Artificial}$ and IRIS $_{Original}$ scores (average ± error) by ecoregion. The *** represents significant results from GAMMs models (p<0.001).

How much can increase the management factors?

Improvement of management, i.e., the difference between the Artificial and Original management factor, depends on the ecoregion, and the management factor studied (the interaction between ecoregions and management factors, F-value=10.91, p-value <0.001). Specifically, the improvement of each factor (i.e., Anthropogenic pollution, Fishing pressure, Free anthropogenic physical pressures, Free anthropogenic physical pressures, and Human population) showed differences between the ecoregions (Figure 5.4 and Table 5.4).

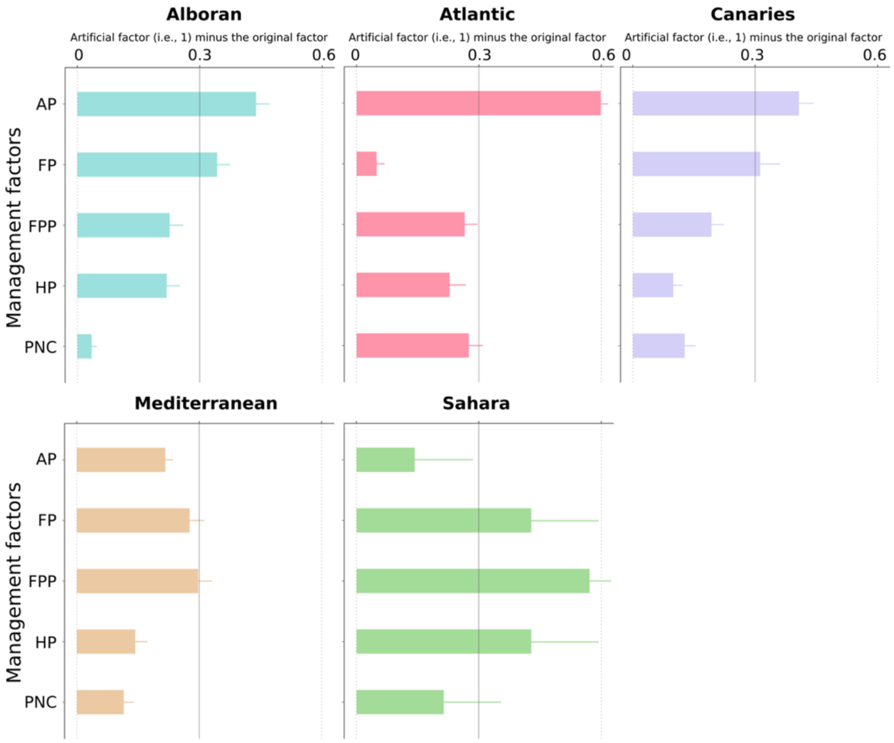


Figure 5.4. Figure showing the difference between the Artificial (i.e., always 1) and original values of each management factor at the ecoregion level. The management factors are: AP (Anthropogenic pollution); FP (Fishing pressure); FPP (Free anthropogenic physical pressures); HP (Human population); PNC (Proximity to the nearest city).

Table 5.4. Ecoregions studied with the values of the difference between the Artificial and Original management factor (average ± error), for each of the factors. We include the results of the LME models.

Management factors	Alboran	Atlantic	Canaries	Mediterranean	Sahara	p-value
AP	0.44 ± 0.03	0.59 ± 0.04	0.41 ± 0.04	0.22 ± 0.02	0.14 ± 0.13	<0.001
FP	0.34 ± 0.03	0.05 ± 0.02	0.31 ± 0.05	0.28 ± 0.04	0.42 ± 0.2	<0.001
FPP	0.23 ± 0.03	0.26 ± 0.03	0.19 ± 0.03	0.3 ± 0.03	0.57 ± 0.12	0.008
HP	0.22 ± 0.03	0.23 ± 0.04	0.1 ± 0.02	0.14 ± 0.03	0.42 ± 0.2	<0.004
PNC	0.03 ± 0.01	0.27 ± 0.03	0.13 ± 0.03	0.11 ± 0.02	0.21 ± 0.14	<0.001

5.4. Discussion

Resilience is an essential and fundamental property that keeps the health of biological communities (Peterson et al., 1998; Gunderson et al., 2009; Folke et al., 2004). Unfortunately, this metric is degrading, enhancing the fragility and vulnerability of the natural communities (Gunderson et al., 2009). Because of this and to stop this negative trend, society needs strategies to preserve and enhance resilience. A potential pathway to recover the resilience of natural communities is to apply efficient management actions, and this is a priority challenge without precedent in the current era (Folke et al., 2004; Fischer et al., 2009). In this fragile scenario, our study contributes to shedding light on the knowledge to safeguard and manage the resilience of temperate rocky reefs from two perspectives. The first of them is to identify highly resilient geographic areas, to implement conservation measures to preserve the resilience, i.e., top resilient areas, (13 in our study). On the other hand, we identified geographic areas with bottom resilience (a total of 21), where proper management policies could enhance resilience. Moreover, our results are suggesting that the management actions, i.e., regulation of anthropogenic activities, could improve the resilience in all our ecoregions. Also, we can improve all the management factors in different ecoregions. Overall, our approach not only helps to preserve but also to foster the resilience of temperate rocky reefs trough an integrative management perspective.

Improving resilience depends significantly on the ecoregions. We have found that artificial resilience, i.e., IRIS Artificial, is higher than the original resilience in all ecoregions. In other words, management can increase marine resilience. Specifically, the resilience of the Sahara ecoregion can increase by 16.82%, followed by Atlantic 14.22%, Alboran 11.6%, the Canaries 10.7%, and finally Mediterranean 10.2%. An empirical example of improving resilience through management is that of Strain et al. (2015), which increased the resilience of certain species of algae from a local geographic scale. This fact is important to know, but difficult to scale to higher geographical proportions, due to the great heterogeneity of the coastal marine environment. Instead, the Coastal marine socio-ecological systems (Lazzari et al., 2018), composed of socio-economic and environmental variables, may become the potential unit of marine resilience management (Walker et al., 2002; Folke, 2006).

We have identified 21 areas with low resilience (7% of N=300) distributed heterogeneously in four of the five ecoregions studied. So, we found areas in a fragile equilibrium with a high risk of collapse if this has not already happened. Specifically, resilience scores in bottom resilient areas could increase by up to 23.4% due to improved management factors. And in line with our results, management of the factors that erode resilience is extremely urgent and necessary if we are to avoid the collapse of natural communities (Kennedy et al., 2013; Maynard et al., 2015; Bruno et al., 2019). For example, in our case, the five manageable factors show urgent and unavoidable improvement (AP 57.3%, FPP 46.58%, FP 41.8%, HP 38.7%, and PNC 25.4%). The factor that requires the most management is anthropogenic pollution (AP) since it is known that the contribution of nutrients, pesticides, and other anthropogenic contaminants reduces the resilience of marine communities (Piola and Johnston, 2008; Wernberg et al., 2009). Fishing pressure is also a clear factor in the erosion of resilience (Estes et al., 1998; Llope et al., 2011; Neubauer et al., 2013). For example, on coral reefs habitats, this management occurs on fishing pressure of the herbivorous trophic fish species (Chung et al., 2019). But, the management or regulating several factors at once is highly unusual but can be highly effective in boosting resilience (Maynard et al., 2010). In this way, Strain et al. (2015) addressed the management of two factors, erosion and nutrients, to build the resilience of selected macroalgae species at the Mediterranean Sea. Here, we go one step further and showed that proper management of multiples human factors that erode resilience is the first step to build up to it.

Some studies address patterns of marine resilience from multiple perspectives and at different geographic scales (Maynard et al., 2010; Mumby et al., 2013; Ladd and Collado-Vides, 2013;

Maynard et al., 2015; Mumby and Kenneth, 2015; Gibbs and West, 2019). These patterns reflect zones of the high, medium, and low resilience, proposing the high zones as potentially conservable areas (Green et al., 2009; Davies et al., 2016). However, there is a great bias in developing recovery policies because we think that conserving high resilience areas is the solution to keep it in our seas, but only half of the solution. The other half is the management of factors in areas with intermediate and low resilience. In this sense, our study shows that resilience improvement in all zones is possible, as long as the maximum management restriction is applied.

We identified thirteen top resilient areas distributed heterogeneously in the five marine ecoregions. This finding represents that only 4.3% of all sampling points are top resilience areas. This is a very worrying fact because the presence of top resilience areas is anecdotal. Therefore, we must work actively in the field of management to increase the number of zones of maximum resilience in our seas. In protection scope, these areas are an inexcusable priority to safeguard for governments National, regional or municipal, if we want to preserve areas of top marine resilience of temperate rocky reefs. On the other hand, the necessity to identify areas of high resilience is a key step for their effective protection. For example, Green et al. (2009) identified the high resilience zones against climate change on coral reefs. Also, on coral reefs, Davies et al. (2016) detected priority resilience locations to preserve from a socio-ecological perspective. Or, Mumby and Kenneth, (2015) quantified and described the spatial trends in Caribbean coral resilience based on physical and biological variables. These studies are extremely important because they allow us to detect patterns and priority areas to preserve from various perspectives, but, once again, we are looking at only a fraction of reality. To avoid this study bias our work is in line with Maynard et al. (2010) and Sanabria-Fernandez et al. (2019), which integrates three dimensions that modulate marine resilience, i.e., biological, environmental, and management. This perspective allows a more integrative vision of community resilience supported by multiple dimensions. In other words, we ensure that these areas to be preserved are truly a treasure of our seas.

This study detected Top and Bottom resilient areas using 17 factors that modulate the marine resilience of temperate rocky reefs, which makes our index extremely robust. A potential improvement could be the inclusion of connectivity as a resilience factor in the IRIS calculation (Olds et al., 2012). In coral reef habitats, the contribution of larvae due to connectivity causes an increase in marine resilience. A second limitation of this study is that we built an IRIS Artificial under the scenario of maximum restrictions at the management level. For example, no fishing, no pollution, no access to the coast by the human population. But this scenario is extremely difficult to build because illegal fishing will always exist and even in areas of maximum protection (Edgar et al., 2014). Nevertheless, beyond these limitations, our study contributes to enhance and safeguard the resilience from a real and tangible lens.

This research sheds light on two potential pathways to safeguard (conserve) and increase (manage) the marine resilience of temperate rocky reefs. Also, the study includes management as a key tool, allowing the regulation of factors of anthropogenic origin. This fact has allowed us to know where and how much resilience can be improved. Also, this resilience management is dependent on the geographical scale studied, allowing us to know the needs of each ecoregion. Therefore, this work not only contributes to preserving a property that maintains the health of the oceans but also establishes priorities to build it. This fact allows us to elaborate on conservation and management policies focused on a geographical scale in each ecoregion and on each management factor.

5.5. Conclusions

Our research has shown that resilience does not show a homogeneous pattern in its distribution on rocky reefs habitats. Within this distribution, there are almost twice as many zones with low than with high resilience. Different management policies in the top and bottom resilient areas are needed. Due to the relevance and scarcity of top resilient areas, we propose them as priority zones to preserve. Conversely, the bottom resilient areas require management, i.e., urgent regulation of anthropogenic factors to increase their resilience. Fortunately and in general, resilience could be increased, up to 11% through management only. Also, this potential route to safeguard and recover resilience must be at the level of each ecoregion because each unit has its own management needs. In synthesis, this study has shown that resilience can be increased, provided that effective management measures are implemented. However, a high priority is needed for protection and resilience management strategies to be focused in the same direction. Otherwise, we would be missing the opportunity to safeguard resilience and building up a catastrophic scenario for the health of our seas and oceans.

General discussion

Picture: Underwater picture of *Scorpaena notata* from Melilla. Jose A. Sanabria-Fernandez took this picture during an INBIOMAR II 2020 research grant sampling trip.

Human beings depend on biodiversity in countless aspects (Wilson 1988; Millennium Ecosystem Assessment, 2005; Díaz et al., 2006). And yet, paradoxically, anthropogenic activities are the cause of the rapid loss of biodiversity that characterizes our current era (Morris, 2010; Ceballos et al., 2015). When biodiversity is negatively affected, ecosystem properties such as resilience are also eroded and lost (Gunderson and Holling, 2002; Folke et al., 2004; Gunderson et al., 2009). Resilience is a key property since it reports on the ecosystem recovery capacity (Holling, 1973; 1996; Peterson et al., 2008). Therefore, the study of resilience using biodiversity as a model is a challenge that could contribute to the efficient conservation of ecosystems (Walker, 1992, 1995; Peterson et al., 2008; Fischer et al., 2009).

This thesis comprised five chapters exploring the threats and problems affecting the biodiversity-resilience binomial and provides cutting-edge solutions to preserve them. In this regard, the first three chapters explore the impacts of different human activities on marine diversity. Chapter I addresses the impact of artificial reefs on biodiversity. To this end, I developed a new indicator (NAR indicator) that allowed quantification of the impact of artificial reefs on coastal marine biodiversity. Artificial structures hold a lower diversity of species with less ability to move (Sanabria-Fernandez et al., 2018). Chapter II developed a methodology to quantify the cost of recovery and degradation of biological communities. Using protected and unprotected areas, I found that the recovery of biological diversity is costlier than degradation, which has strong implications for the conservation of marine biodiversity. Chapter III addressed the study of the efficiency of marine reserves on certain biological properties of the fish community. I designed the Conservation Status Index to assess fish communities with a total of nine attributes associated with fish diversity, fish biomass, and other relevant factors of the fish community (Sanabria-Fernandez et al., 2019). Protection had a largely positive but unreliable impact on fish biomass as opposed to the reliable but minor positive effect of protection on biodiversity.

Resilience was one of the ecosystem properties that played an important role in explaining our results. Unfortunately, there is still very little empirical evidence to support a better understanding of resilience in temperate marine communities. Chapters IV and V contributed to the study of resilience from a broad perspective. In Chapter IV, I designed the Resilience Indicator of a Site (IRIS), allowing the quantification of resilience throughout the use of 17 factors known to regulate resilience (Sanabria-Fernandez et al., 2019). I found that resilience was determined by the intensity and not by the relevance of the factors that regulate resilience. This finding allowed me to simplify the quantification of resilience, providing an opportunity to establish baseline data to quantify spatial and temporal patterns of resilience in temperate rocky reefs. In Chapter V, I used the Resilience Indicator of a Site to identify the Top and Bottom Resilience areas of the Spanish littoral rocky reefs, along with the identification of management factors that can be modified to improve resilience. Efficient management can certainly increase the resilience of temperate rocky reefs and Chapter V allowed a quantitative estimate of the magnitude of the improvement in resilience with the proper management of identified factors.

This thesis actively contributed to the conservation of marine biodiversity from three different angles. First, through the development of ecologically-based indicators with a high degree of applicability. Second, through the establishment of baseline data to unlock spatial patterns and temporal trends. And third, through the identification of the management actions and spatial areas that can help maximize the resilience of our coastal areas.

Biodiversity

The sustained addition of artificial substrates on shallow rocky bottoms is causing fragmentation of natural habitats and enhancing diversity loss (Duarte et al., 2012; Firth et al., 2016). However, there is an unequal response of the biological community towards the impact caused by these artificial structures. My thesis investigated this impact at the species level, but at the same time allowed a broader evaluation of the whole community. Chapter I showed the importance of including features such as species density and mobility to understand the true impact of artificial reefs on biodiversity. This has allowed to learn that organisms with low density and mobility are absent from artificial substrates.

Marine biodiversity is being seriously affected by the addition of artificial substrates and its study requires further attention. The apparent homogeneity displayed by the most common and highly mobile species is an artifact that distorts the reality of the marine community. For example, the marine fish community showed higher fish population densities on artificial reefs than in natural ones (Granneman and Steele, 2015). In contrast, Rooker et al. (1997) confirmed that both substrates, artificial and natural, harbored similar fish population densities. Other biological groups, such as benthic macroinvertebrates, showed higher densities and diversity in natural substrates compared to artificial reefs (Badalamenti et al., 2002). On the other hand, plants and sessile organisms show very similar densities in natural and artificial substrates (Chapman and Clynick, 2006). In other words, the results are highly heterogeneous and the real impact that artificial reefs are having on marine diversity is unknown. Our approach aims at interpreting this reality through the mobility and density of each species. Regarding species with greater mobility and density, i.e. fish, our results are aligned with Chapman (2003), showing to be extremely abundant in both substrates. Conversely, the marine community comprising lower mobility and lower density species, i.e. sessile organisms, were absent in artificial reefs, as opposed to what was stated by Hunter and Sayer (2009) and Granneman and Steele (2015). The time that the artificial structure has been submerged is a key factor that can affect species density in different substrates (Perkol-Finkel et al., 2006; Burt et al., 2011). Perkol-Finkel and Beneyahu (2004, 2007) showed that it may take more than a decade for biological communities of natural and rocky reefs to become similar. However, our study showed no evidence that artificial substrates will end up resembling their natural counterparts over the 50 year-period span of the artificial reefs. This study unveils an alternative reality to the one known until now from the traditional artificial reefs and it is likely to illustrate in a more balanced way the true impact of artificial structures on marine biodiversity. Furthermore, this chapter brings to light an unknown scenario in great need of management.

There is a lack of understanding of the dimensions of the fish community that are disturbed by the presence of artificial reefs. There are very few studies comparing the different metrics of the fish community in artificial and natural substrates (Carr and Hixon, 1997; Clynick et al., 2008). Thus, we are still a long way from knowing the impact that artificial substrates have on the various aspects of the fish community. In Chapter III, we developed the Conservation Status index (CSI), which could become a potential tool for clarifying what features of the fish community are being disturbed by artificial reefs. Although the CSI was developed and applied in the assessment of the efficiency of marine reserves (Sanabria-Fernandez et al., 2019), it proved to be an ideal tool for this scenario.

The protection of marine areas requires scientific tools to help develop effective conservation policies. We have guidelines for establishing Marine Protected Areas (Day et al., 2019), which specify certain biological requirements for a marine area to be officially protected. Furthermore, we know the five key factors that ensure a marine reserve preserves its biodiversity (Edgar et al., 2014). However, methodologies aimed at detecting potential protected areas are extremely diverse. Selig et al. (2014) proposed a methodology for the detection of priority areas to be preserved and included the biological dimension through species richness and human pressure. On the other hand, Abdulla et al. (2009) suggested previous identification of cultural factors, trophic relationships, and areas with a high level of predators before the introduction of marine reserves in the Mediterranean Sea. Finally, Baley and Thompson (2009) proposed the establishment of marine reserves according to the population density of marine mammals and the environmental factors that determine their presence. Another study suggests conservation categories based on resilience, connectivity, and special reproduction areas (Mcleod et al., 2019). In chapter II, we design a methodology that allows us to measure the cost of recovery in biological terms. This approach has high applicability in conservation science because it allows the identification of areas with high resilience before they are protected. Unlike others (Abdulla et al., 2009, Baley and Thompson, 2009, Selig et al., 2014) our approach is entirely based on the biological community, i.e., the population density of all fish, invertebrates, and algal species. Community-based studies, such as ours, provide more robust and comprehensive information on the cost of recovery. However, applying this methodology requires having access to a rich data bank at the community level and a sampling design with high spatial resolution. Although it can be applied to certain specific communities, for example, the fish or invertebrate community only, conclusions are not as robust as if the whole marine community was considered. This approach is the exact opposite of the conservation policies being pursued today (Day et al., 2019). Therefore, I believe that this approach, based on multiple biological dimensions, combined with the five factors for effective marine reserves (Edgar et al., 2014), is the most beneficial approach for the conservation of marine diversity.

Marine protection brings numerous benefits to marine biodiversity (Edgar et al., 2004; Campbell et al., 2017). The efficiency of the levels of protection informs us of how much or how little we are protecting our ecosystems. Knowing the (in)efficiency of certain protection forms is an unprecedented contribution to conservation because it helps us to reformulate management actions and to maximize conservation objectives, as it could be redirecting inefficient management strategies in marine reserves. Currently, there are many studies on the benefits of marine protected areas based on diversity (), biomass (Aburto-Oropeza et al., 2001, Micheli et al., 2012), endangered species (Harmelin-Vivien et al., 2015), trophic cascades (Edgar et. al., 2017), from single species up to fish and invertebrates' communities. In contrast, efficiency studies based on the benefits of marine protection forms are scarce and geographically isolated. Chapter III assessed the (in)efficiency of marine protection, covering different dimensions of the marine fish community, through the Conservation Status Index (CSI). Our results showed that marine protection was inconsistently very efficient in increasing biomass (60.01%), and consistently inefficient in increasing diversity (14.41%). Biomass results are in line with Harmelin-Vivien et al. (2015), who found higher biomass of *Sciaena umbra* (vulnerable species) within marine reserves of Corsica. In terms of diversity, Villamor & Becerro (2012) found an absence of differences in five Mediterranean marine reserves in terms of species richness, which reinforces our findings on the relative inefficiency of protecting diversity. Diversity was the second most important beneficiary of marine protection. When we looked at the efficiency of each of the nine individual indicators that make up the CSI, the indicator that reflected the highest efficiency was the biomass of species in the IUCN red list, which accounted for 48.7% of the protection benefits. This result agrees with findings from Brazil's marine reserves (Rolim et al., 2019). To assess the efficiency of marine reserves, the Conservation Status Index is a tool that contributes and provides comprehensive and robust information from a community point of view, going one step beyond the traditional indexes previously applied (Villamor and Becerro, 2012, Micheli et al., 2012, Harmelin-Vivien et al., 2015). Furthermore, the CSI can be applied on a temporal scale as long as it is based on community data. Applying this index reflects the dynamics of the fish community dimensions over time, revealing, from a temporal point of view, the efficiency of management actions in marine reserves.

Resilience

Biodiversity regulates resilience, the capacity of the natural systems to recover from disturbance (Gunderson et al., 2009; Oliver et al., 2015). Resilience is high in high diversity biological communities (Elmqvist et al., 2003). Diversity and resilience depend on anthropogenic and climatic pressures and threats to which they are exposed to (Gunderson and Holling, 2002; Gunderson et al., 2009; Mumby and Anthony, 2015). To obtain a global and more comprehensive perspective of marine resilience, some studies include several biological components and the pressures acting upon them (Maynard et al., 2010, Ladd and Collado 2011, McClanahan et al., 2012). In this regard, Maynard et al. (2010) integrated multiple biological indices along with various anthropogenic and climate pressure factors. The authors classified the factors according to their relevance and assessed the resilience of the coral communities in the Great Barrier Reef and Guam (Maynard et al., 2015). Ladd and Collado (2011) adapted the methodology described by Maynard et al. (2010) and measured the resilience of coral reefs in the Caribbean Sea. In this thesis, I have followed their approach due to its capacity for integrating multiple factors and for the possibility of scaling up spatially and temporally beyond coral reef environments. However, we developed a new mathematical formulation of the index proposed by Maynard et al. (2010) and adapted it to the temperate rocky reefs. I found that the apparent relevance of the different factors that modulate resilience is irrelevant, providing an important simplification to calculate the index. My study proved that the resilience indicator provided the same information and draw the same conclusions with or without considering the relevance of the different factors. Although it may seem that factors such as overfishing, pollution, ocean warming, among others, have different importance on resilience (Maynard et al., 2010; Ladd and Collado, 2011; McClanahan et al., 2012; Maynard et al., 2015), the results are similar either applying or ignoring the quantitative estimate of their relevance (Sanabria-Fernandez et al., 2019). For this reason, our resilience indicator (IRIS) does not include factor relevance in the computations. This implies a simplification in the quantification of resilience and facilitates the study of chronological trends and spatial patterns in temperate seas.

Management is a key tool to increase and preserve resilience (Folke et al., 2004). The efficient regulation of factors that modulate resilience, such as overfishing and pollution, makes it possible not only to stop its loss but also to reverse it (Williams et al., 2016; Bejarano et al., 2019). Unfortunately, for this management to be efficient, it must be applied at the appropriate geographical scale and each factor must be specifically managed (Gunderson et al., 2009; Folke et al., 2004). I addressed these issues in chapter V, where I used resilience to identify priority geographic areas for conservation, including areas where specific management actions can result in improved resilience. There are important studies that select highly resilient areas, as it is the case with Green et al. (2009). They developed a network of marine reserves in the face of climate change to preserve resilience based on biological and socio-economic factors in Papua New Guinea. Maynard et al. (2015) identified areas with different resilience values and studied the factors that foster resilience, specifically in highly resilient areas. But in Chapter V, I explored beyond the identification of top and low resilience zones. I identified the geographic areas where resilience can be increased through appropriate management measures. This approach is not only new. It is extremely important for management because it provides insights into the capacity to improve resilience through management. The method described in Chapter V identifies the management factors that should be considered and where they should be considered. It also provides an estimation of how much we would increase the system's resilience through management. Our results showed that the management of anthropogenic factors that modulate resilience depended on the area studied. For example, from an herbivorous fish fisheries perspective, Chung et al. (2019) showed that fisheries should be managed (minimized) at a given geographic level to preserve the resilience of Hawaii's coral reefs. At the multi-factor level, Maynard et al. (2015), made it clear that factors held different importance on each island studied. Our results at the marine ecoregion level agreed with these results. Fortunately, we now know how much resilience can be increased if we manage these factors efficiently. This is a challenge in the development of real and tangible guidelines that seek to safeguard the resilience of rocky reefs in temperate seas.

So, what's next?

This thesis provided new tools for the management of biodiversity. It allowed me to unmask and learn about the impact that human actions have on marine biodiversity. On the other hand, it sought to actively increase the resilience of rocky reefs in temperate seas through the management of the biodiversity threats. But there is a long way to go, for example in the field of artificial reefs, it would be interesting to learn what dimensions of the fish community are the ones affected, either diversity, biomass, or other aspects such as fish vulnerability. It is totally necessary to go deeper into how marine reserves benefit diversity, and so it is important to study the different biological dimensions in marine reserves with different numbers of NEOLIS (Edgar et al., 2014). By doing so, I will be able to know what dimensions of the fish community benefit from the number of NEOLIS. In terms of resilience, it becomes crucial to conduct studies at a chronological level, that is, to study how resilience on temperate rocky reefs evolves over the years from an integrative point of view. This would show whether the management being implemented is truly efficient and the resilience of our seas and oceans preserved.

Conclusions

Picture: Underwater picture from Isla de Mar, Alhucemas Archipelago (Spanish territories in the African continent). In the picture you can see specimens of *Eunicella singularis*, *Paracentrotus lividus*, and *Arbacia lixula*. Jose A. Sanabria-Fernandez took this picture during an INBIOMAR II 2020 research grant sampling trip.

Chapter I

Ocean sprawl shows us a scenario where species with low mobility and density were practically non-existent, i.e., we are fueling the disappearance of marine species from shallow rocky reefs.

Chapter II

Unprotected marine areas are more resistant to recover their biodiversity than partially protected areas. Besides, the resistance to recovery depends on each biological group, i.e., fish, invertebrates, and algae.

Chapter III

Marine protection did not equitably protect the different dimensions of the fish community. Specifically, biomass was the dimension that presented the greatest benefit under protection, even more than diversity.

Chapter IV

The relevance of the factors that modulates marine resilience was irrelevant to the quantification of resilience patterns. Conversely, the intensity of the factors was vital for computing resilience and establishing patterns and trends.

Chapter V

Marine resilience was heterogeneously distributed along the Spanish coast. Also, proper management can increase marine resilience trough the regulation of anthropogenic factors.

Thesis

This thesis contributed to novel approaches applied to different scenarios to know the conservation state of marine diversity and to search for solutions to stop the loss of diversity that our seas are suffering.

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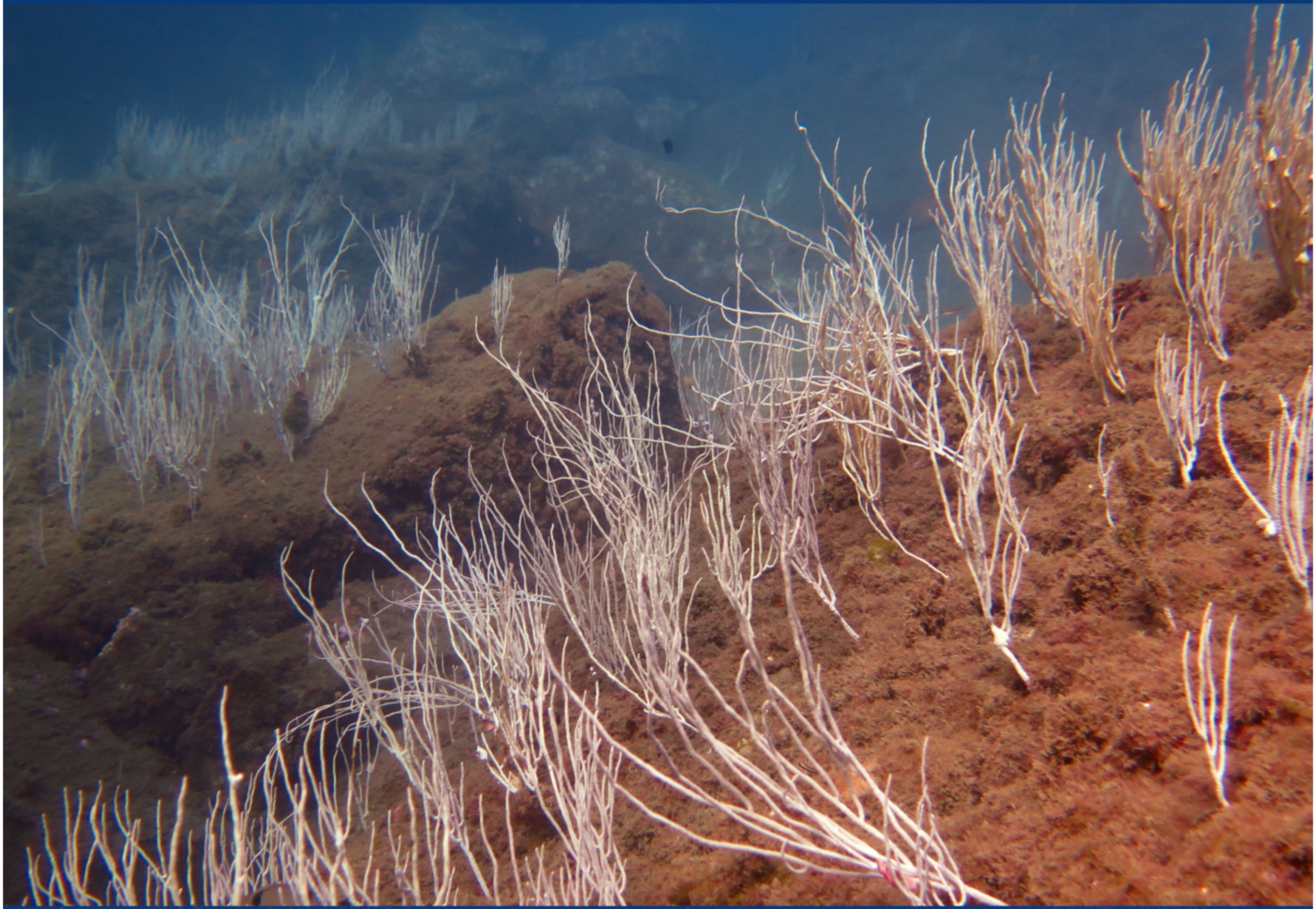

Picture: Underwater seascape from Alhucemas Island, Alhucemas Archipelago (Spanish territories in the African continent). In the picture you can see specimens of *Eunicella singularis* on rocky reefs. Jose A. Sanabria-Fernandez took this picture during an INBIOMAR 2019 research grant sampling trip.

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Appendix

Chromis chromis, Coris julis, and Thalassoma pavo. Jose A. Sanabria-Fernandez took this picture during the sampling trip of INBIOMAR II research grant in 2020.

Appendix Chapter I

Appendix 1. List of the fish, invertebrate, and algal species identified in our study and categorized in their corresponding class of mobility (high, medium, and low) and occupancy (high, medium, and low).

Group	*Species*	*Mobility*	*Occupancy*
Fish species	*Abudefduf luridus*	High	High
	Apogon imberbis	Medium	Low
	Atherina presbyter	High	Low
	Aulostomus strigosus	High	High
	Boops boops	High	High
	Bothus podas	High	Low
	Canthigaster capistrata	High	High
	Chelon aurata	High	Low
	Chelon labrosus	High	Low
	Chromis limbata	High	High
	Diplodus cervinus	High	Medium
	Diplodus sargus	High	High
	Diplodus vulgaris	High	Medium
	Epinephelus marginatus	High	Low
	Gnatholepis thompsoni	Medium	High
	Gymnothorax unicolor	Medium	Low
	Heteropriacanthus cruentatus	High	Low
	Kyphosus sectatrix	High	Low
	Labrisomus nuchipinnis	Medium	Low
	Lepadogaster candolii	Medium	Low
	Mauligobius maderensis	Medium	Low
	Mullus surmuletus	High	Low
	Muraena augusti	Medium	Low
	Mycteroperca fusca	High	Medium
	Myliobatis aquila	High	Low
	Oblada melanura	High	Medium
	Ophioblennius atlanticus	Medium	Medium
	Pagellus acarne	High	Low
	Pagrus auriga	High	Low
	Parapristipoma octolineatum	High	Low
	Pomadasys incisus	High	Low
	Pseudocaranx dentex	High	Medium
	Sarpa salpa	High	High
	Scorpaena canariensis	Medium	Medium
	Scorpaena maderensis	Medium	Medium
	Scorpaena notata	Medium	Low
	Scorpaena porcus	Medium	High
	Seriola rivoliana	High	Low
	Serranus atricauda	High	Medium
	Serranus scriba	High	Low
	Sparisoma cretense	High	High
	Sphoeroides marmoratus	High	Medium
	Sphyraena viridensis	High	Low
	Spondyliosoma cantharus	High	Medium
	Symphodus trutta	High	Medium
	Synodus saurus	High	Low

	Synodus synodus	Medium	High
	Taeniura grabata	Medium	Medium
	Thalassoma pavo	High	High
	Tripterygion delaisi	Medium	Low
Invertebrate species	*Aplysina aerophoba*	Low	Low
	Arbacia lixula	Medium	Medium
	Calcinus tubularis	Medium	High
	Cerithium vulgatum	Medium	High
	Charonia lampas	Medium	Low
	Clibanarius aequabilis	Medium	Low
	Coscinasterias tenuispina	Medium	Low
	Crambe crambe	Low	Low
	Dardanus calidus	Medium	Medium
	Diadema africanum	Medium	Low
	Felimare picta	Medium	Low
	Haliotis tuberculata	Medium	Low
	Holothuria (Platyperona) sanctori	Medium	Medium
	Holothuria (Roweothuria) arguinensis	Medium	High
	Hydroidea spp.	Low	Low
	Marthasterias glacialis	Medium	Low
	Mollusca spp.	Medium	Low
	Octopus vulgaris	Medium	Low
	Pagurus anachoretus	Medium	High
	Paracentrotus lividus	Medium	Medium
	Percnon gibbesi	Medium	High
	Pinna rudis	Medium	High
	Plesionika narval	Medium	Low
	Porifera spp.	Low	Low
	Sarcotragus foetidus	Low	Low
	Sarcotragus spinosulus	Low	Low
	Sphaerechinus granularis	Medium	Low
	Stenorhynchus lanceolatus	Medium	Low
	Stramonita haemastoma	Medium	Medium
Algal species	*Aphanocladia stichidiosa*	Low	Low
	Asparagopsis taxiformis	Low	Medium
	Caespitose brown algae spp.	Low	Medium
	Caespitose green algae spp.	Low	High
	Caespitose red algae spp.	Low	Medium
	Calcareous algae spp.	Low	Medium
	Codium adhaerens	Low	Low
	Colpomenia sinuosa	Low	Low
	Crustose brown algae spp.	Low	Low
	Crustose green algae spp.	Low	Low
	Crustose red algae spp.	Low	Low
	Cystoseira compressa	Low	Low
	Dasycladus vermicularis	Low	Low
	Dictyota dichotoma	Low	Medium
	Ellisolandia elongata	Low	Low
	Ganonema farinosum	Low	Low
	Jania rubens	Low	Low
	Jania virgata	Low	Low
	Lobophora variegata	Low	Medium
	Lophocladia trichoclados	Low	Low

	Neogoniolithon brassica-florida	Low	Medium
	Neogoniolithon mamillosum	Low	Low
	Padina pavonica	Low	Low
	Phaeophyceae spp.	Low	Low
	Polysiphonia subulifera	Low	Low
	Pseudolithoderma adriaticum	Low	High
	Spatoglossum solieri	Low	Low
	Wrangelia argus	Low	Low

Appendix Chapter III

Table S1. Average values of the four Conservation Status Indices in each protected and unprotected area. Unprotected areas represent the average value of each marine ecoregion. For more details see Table 1 and Map 1.

Map code	Marine ecoregion	Protected & unprotected areas	$CSI_{diversity}$	$CSI_{biomass}$	$CSI_{relevant}$	CSI_{global}
1	South European Atlantic Shelf	Islas Cíes	0.56	0.81	1.53	2.91
2	South European Atlantic Shelf	Archipielago de las Berlengas	0.58	0.60	0.61	1.79
3	South European Atlantic Shelf	Da Arrabida	0.89	0.63	1.14	2.66
A	South European Atlantic Shelf	Unprotected area	0.48	0.56	0.80	1.84
4	Azores, Madeira and Canary Is.	Punta de la Restinga - Mar de las Calmas	1.24	2.07	2.18	5.49
5	Azores, Madeira and Canary Is.	Isla de la Palma	0.95	1.94	1.07	3.96
6	Azores, Madeira and Canary Is.	Isla de la Graciosa e islotes del Norte de Lanzarote	0.99	1.70	0.96	3.65
B	Azores, Madeira and Canary Is.	Unprotected area	0.99	0.88	0.84	2.71
7	Alboran Sea	Peñón de Vélez de la Gomera	0.57	1.45	0.70	2.72
8	Alboran Sea	Islas Alhucemas	0.68	2.08	1.47	4.23
9	Alboran Sea	Isla de Alboran	0.88	1.83	1.18	3.89
10	Alboran Sea	Islas Chafarinas	0.65	1.30	0.62	2.57
11	Alboran Sea	Maro Cerro Gordo	0.74	0.96	1.36	3.06
12	Alboran Sea	Cabo de Gata-Níjar	0.86	0.83	0.63	2.32
C	Alboran Sea	Unprotected area	0.78	0.66	0.84	2.28
13	Western Mediterranean	Cabo de Palos e Islas Hormigas	0.66	1.07	0.87	2.60
14	Western Mediterranean	Isla de Tabarca	1.16	1.23	1.81	4.20
15	Western Mediterranean	Freus de Ibiza y Formentera	1.01	1.31	0.44	2.76
16	Western Mediterranean	Archipielago de Cabrera	0.83	1.92	1.42	4.17
17	Western Mediterranean	Migjorn de Mallorca	0.95	1.08	0.54	2.57

18	Western Mediterranean	Cala Rajada	1.06	0.58	0.65	2.29
19	Western Mediterranean	Bahía de Palma	1.15	0.55	0.56	2.26
20	Western Mediterranean	Islas Columbretes	0.97	1.90	0.51	3.38
21	Western Mediterranean	Islas Medas	0.98	1.29	1.09	3.36
22	Western Mediterranean	Cabo de Creus	0.88	0.47	0.52	1.87
D	Western Mediterranean	Unprotected area	0.82	0.56	0.49	1.87

Appendix Chapter IV

Supplementary Table 1. List of the fish species quantified in our study that are known to feed on sea urchins at some point of their life cycle. Alphabetically ordered.

Fish species (Scientific name)
1. *Balistes capriscus*
2. *Canthidermis sufflamen*
3. *Coris julis*
4. *Diplodus cervinus cervinus*
5. *Diplodus sargus sargus*
6. *Diplodus vulgaris*
7. *Pagrus auriga*
8. *Thalassoma pavo*

Supplementary Table 2. List of the fish species quantified in our study that are considered top predators. Alphabetically ordered.

Fish species (Scientific name)
1. *Auxis rochei rochei*
2. *Belone belone*
3. *Dicentrarchus labrax*
4. *Dentex dentex*
5. *Epinephelus costae*
6. *Epinephelus marginatus*
7. *Mycteroperca rubra*
8. *Phycis phycis*
9. *Plectorhinchus mediterraneus*
10. *Scorpaena porcus*
11. *Scorpaena scrofa*
12. *Seriola dumerili*
13. *Serranus atricauda*
14. *Sphyraena viridensis*
15. *Trachinus draco*
16. *Trachurus mediterraneus*

Supplementary Table 3. Classification of the fish species quantified in our study as benthic invertivore, browsing invertivore, higher carnivore, and planktivore. Information on trophic level from FishBase (www.fishbase.org). Alphabetically ordered.

Benthic invertivore

1. *Apogon imberbis*
2. *Boops boops*
3. *Canthidermis sufflamen*
4. *Centrolabrus exoletus*
5. *Coris julis*
6. *Ctenolabrus rupestris*
7. *Diplodus annularis*
8. *Diplodus cervinus cervinus*
9. *Diplodus sargus sargus*
10. *Diplodus vulgaris*
11. *Gobius geniporus*
12. *Labrus merula*
13. *Labrus viridis*
14. *Lithognathus mormyrus*
15. *Mullus surmuletus*
16. *Muraena helena*
17. *Oblada melanura*
18. *Pagellus acarne*
19. *Pagellus erythrinus*
20. *Pagrus pagrus*
21. *Parapristipoma octolineatum*
22. *Pomadasys incisus*
23. *Serranus cabrilla*
24. *Serranus scriba*
25. *Spicara maena*
26. *Spondyliosoma cantharus*
27. *Symphodus doderleini*
28. *Symphodus mediterraneus*
29. *Symphodus melanocercus*
30. *Symphodus melops*
31. *Symphodus ocellatus*
32. *Symphodus roissali*
33. *Symphodus rostratus*
34. *Symphodus tinca*
35. *Thalassoma pavo*
36. *Tripterygion delaisi*

Browsing herbivore

1. *Chelon labrosus*
2. *Diplodus puntazzo*
3. *Gobius bucchichi*
4. *Gobius xanthocephalus*
5. *Liza aurata*
6. *Liza ramada*
7. *Mugil cephalus*
8. *Parablennius incognitus*
9. *Parablennius pilicornis*
10. *Parablennius rouxi*
11. *Parablennius sanguinolentus*
12. *Sarpa salpa*

Higher carnivore

1. *Auxis rochei rochei*
2. *Belone belone*
3. *Dentex dentex*
4. *Dicentrarchus labrax*
5. *Epinephelus costae*
6. *Epinephelus marginatus*
7. *Mycteroperca rubra*
8. *Phycis phycis*
9. *Plectorhinchus mediterraneus*
10. *Scorpaena porcus*
11. *Scorpaena scrofa*
12. *Seriola dumerili*
13. *Serranus atricauda*
14. *Sphyraena viridensis*
15. *Trachinus draco*
16. *Trachurus mediterraneus*

Planktivore

1. *Anthias anthias*
2. *Atherina boyeri*
5. *Chromis chromis*
6. *Engraulis encrasicolus*

3. *Atherina hepsetus*
4. *Boops boops*
7. *Spicara smaris*
8. *Syngnathus abaster*

Articles published

Picture: Underwater picture from Fuerteventura Island (Canary Islands). In the picture you can see specimens of *Salpa sarpa*, *Trachinotus ovatus*, *Chelon auratus,* and *Diplodus sargus*. Jose A. Sanabria-Fernandez took this picture in 2017.

Marine Environmental Research 140 (2018) 190–199

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Building up marine biodiversity loss: Artificial substrates hold lower number and abundance of low occupancy benthic and sessile species

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ARTICLE INFO

Keywords:
Abundance based index
Anthropogenization
Artificial substrates
Biodiversity
Common and rare species
Marine ecology
Ocean sprawl
Rocky reef communities

ABSTRACT

Ocean sprawl is replacing natural substrates with artificial alternatives. We hypothesized that, after submersion, high occupancy, high mobility species colonize artificial substrates faster than low occupancy, low mobility species, a biodiversity divergence that will slowly fade out with time. Using quantitative visual census of species in 10 artificial and their adjacent natural substrates, we tested for the existence and temporal evolution of this divergence. Assigning species to one of three occupancy and one of three mobility categories, we found that artificial substrates increased the performance of high mobility, high occupancy species while decreased the performance of low occupancy species with medium and low mobility. This biodiversity divergence remained unchanged over the 50-year underwater timespan of the artificial substrates investigated. Our results suggest that proliferation of artificial substrates is building up a biodiversity loss driven by the least conspicuous and uncommon benthic and sessile species that is undermining coastal marine biodiversity.

1. Introduction

Coastal environments are critical components of the Earth support system. They provide us with goods and services that surpass those provided by any terrestrial ecosystem (Costanza et al., 1997). The relevance of coastal systems stems from their specific biological and environmental traits. Coastal waters up to 200 m deep are about 5–10% of the world surface, yet they account for 25% of the primary production of the oceans, 79% of marine fish species, and 90% of marine exploitation (Barnabé and Barnabé-Quet, 2000; Ray and McCormick-Ray, 2009). In short, coastal waters hold the greatest variety and abundance of marine species (Gray, 1997) but they also are among the most threatened by anthropogenic stressors (Halpern et al., 2007).

Demographic pressures on coastal ecosystems are steadily increasing as coastal zones are home to a large and growing proportion of the world's population, which could rise by more than 50% between 2000 and 2030 (Neumann et al., 2015). Human-induced changes of the coastal environment occur through a variety of activities such as overfishing, pollution, or habitat destruction. Habitat degradation, fragmentation, and loss are major threats to biodiversity (Sih et al., 2000). These are widespread phenomena in coastal areas with over 50% of the world and 86% of Europe's coasts at moderate or high risk of degradation (Bryant et al., 1995). Given the high value of the coastal services to humans, coastal degradation may cause a great environmental burden with important implications to our society (Costanza et al., 2014). A better understanding of the effect of human alterations on the marine coastal diversity will certainly help minimize the negative consequences of coastal development and promote more efficient biodiversity conservation and management.

Ocean sprawl, the proliferation of artificial structures in the sea, is an important component of coastal degradation in marine environments (Duarte et al., 2012; Firth et al., 2016). Breakwaters, dykes, coastal defense structures, and other human-made constructions are increasingly present in coastal areas to meet the growing demand for commercial, touristic, and residential activities of the last decades (Bulleri and Chapman, 2010; Firth et al., 2016). Artificial structures are becoming a significant habitat for marine organisms in detriment of their natural counterparts (Airoldi and Beck, 2007; Dugan et al., 2011; Duarte et al., 2012; Bishop et al., 2017). Beyond some striking examples of ocean sprawl scattered over the world (e.g., Dubai or Qatar in the Persian Gulf, Penang Is or Singapore in the Malay Peninsula, Firth et al., 2016; Chee et al., 2017), the phenomenon is truly widespread and a cause of environmental concern. The Mediterranean coasts of France, Italy, and Spain have over 1500 km of artificial structures (Airoldi and

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https://doi.org/10.1016/j.marenvres.2018.06.010
Received 21 January 2018; Received in revised form 30 May 2018; Accepted 13 June 2018

Beck, 2007), which represents about 15% of their coastline. Ocean sprawl causes loss of coastal habitats (e.g., Airoldi and Beck, 2007) and shifts in species abundance and distribution (Clynick et al., 2008; Airoldi and Bulleri, 2011; Burt et al., 2011; Heery et al., 2017). Yet, we are far to understand the ecological importance of artificial habitats and whether, given enough time, artificial substrates will have the capacity to hold communities equivalent to those on natural substrates.

Artificial habitats may add new variables and habitat types (e.g., material, rugosity, or dark sciaphilic habitats in shallow communities) with important implications in community organization and functioning (Chapman, 2003; Bulleri and Chapman, 2010; Ponti et al., 2015). High mobility species such as fish may colonize new habitats sooner than species with more limited mobility such as mobile invertebrates or sessile organisms, which may rely more strongly on reproductive traits (Kinlan and Gaines, 2003; Perkol-Finkel and Benayahu, 2007; Lin et al., 2008; Miller et al., 2009; Gothland et al., 2014). Species abundance and size of the organisms may also determine their capacity to colonize new habitats, with common (i.e., abundant) species having numerical advantage over uncommon species in terms of space occupation (MacKenzie et al., 2003; Strain et al., 2017). Similarly, widely distributed species that inhabit numerous locations (frequent, high occupancy species) are more likely to colonize artificial habitats because surrounding natural reefs may act as a "pool source" (Svane and Petersen, 2001). On the other hand, irregularly distributed species inhabiting few locations (infrequent, low occupancy species) may need longer time periods to colonize artificial habitats, underpinning a secondary successional diversity (Tilman, 1988). Colonization of artificial habitats by common and high occupancy species may create a false state of similarity with natural substrates because the less conspicuous species (uncommon and low occupancy species) are easier to overlook. Yet, the less conspicuous species are bond to represent a significant percentage of the overall biodiversity (Whittaker, 1965) and play critical roles in ecosystem functioning (Grime, 1998), so their absence in artificial habitats would tone down biodiversity severely.

It is unclear whether artificial habitats deviate significantly from natural substrates or they can function as their natural counterparts given enough time (Carr and Hixon, 1997; Glasby and Connell, 2001; Perkol-Finkel et al., 2006). We herein hypothesized that species composition and abundance in artificial habitats deviate from natural reefs. Artificial substrates will favor some species and disfavor others, resulting in significant community differences between natural and artificial habitats. These differences, however, may decrease over the long term making artificial substrates suitable environments to maintain current levels of marine biodiversity. In our study, we selected 10 artificial substrates that have been underwater from 0 to 54 years and tested whether the number and abundance of species differed with their associated natural reefs.

2. Material and methods

We quantified species composition and abundance in 10 locations in Tenerife, Canary Islands (Fig. 1, Table 1). At each location, we surveyed hard bottom habitats with either artificial or natural substrates. All artificial structures in our study were breakwaters, mostly built to provide shelter for boats. None of the artificial structures investigated in our study aimed to enhance species, to restore habitats, to prevent areas from trawling or fishing, or to promote recreational fishing or diving. In this regard, all the artificial substrates investigated were located in the seaward site of the breakwaters, had similar exposure, orientation, slopes, and depths than their natural counterparts and resembled their nearby rocky reefs but with big quarry rocks or concrete boulders added to provide coastal defense (Table 1). The artificial boulders did provide a sciaphilic habitat mostly missing in the natural reefs of our study due to the large number of dark spaces created by the three-dimensional artificial structures. We obtained from official sources (Cabildo de Tenerife, Autoridad Portuaria de Tenerife, and City Councils) the year of construction of each artificial structure to calculate the number of years they have been underwater until we surveyed them. At each site, we ran three visual censuses that quantified fish, invertebrate, and sessile species using the Reef Life Survey methodology (Edgar and Stuart-Smith, 2014) during summer 2012 (June–-September). Briefly, the first visual census quantified number and abundance of demersal fish species in an area of 50 × 10 m. The second visual census quantified macro invertebrate and cryptic fish species in a 50 × 2 m. Finally, to quantify sessile species, we took 25 × 25 cm photoquadrat (PQ) every 2.5 m along the 50 m long transect, for a total of 20 PQs. Then, for each PQ, we generated 20 random points with the software CPCe V. 4.1 (Kohler and Gill, 2006) to quantify the percent cover of sessile species. These three methods also represent degree of mobility, as the first method targets the highly mobile, swimming, demersal fish community (high mobility), the second method targets the benthic invertebrate and cryptic fish community (medium mobility), and the third method targets the fixed-to-the-substrate invertebrate and algal sessile community with highly restricted or no mobility as adults (low mobility).

Because we quantified species abundances in artificial substrates and adjacent natural reefs, we "paired" for every species in our study the abundance data in each artificial substrate to its natural counterpart using the following abundance based index:

$$NAR = \frac{Natural - Artificial}{\max(Natural,\ Artificial)}$$

where *Natural* is the number of specimens of a single species present in the natural substrate, *Artificial* is the number of specimens of the same species present in the artificial substrate, and max (*Natural, Artificial*) is the largest of these abundances. NAR computation for sessile species, quantified through the use of PQs, was identical except for the use of percent cover instead of abundance.

For every species, *NAR* (*Natural-Artificial Ratio*) is the proportion of change in the number of specimens (or percent cover) found in artificial as compared to natural substrates. *NAR* values range between 1 and -1, with positive values when the species is more abundant in the natural substrate and negative values when the species is more abundant in the artificial substrate. Therefore, a *NAR* value of 0.75 represents a situation where the abundance of one species in the artificial substrate is 75% less than that in the natural reef, while the opposite is true for a *NAR* value of -0.75 (i.e., abundance in the natural substrate is 75% less than that in the artificial substrate). For any given species, *NAR* equals 0 when the number of specimens in both substrates is identical.

Finally, we also categorized species as low, medium, or high occupancy species based on the number of locations (including both substrate types) where every species was found. Out of the 10 locations we sampled, we defined low occupancy species as those that occurred in 3 or less locations, high occupancy species as those that occurred in 8 or more locations, and medium occupancy species as those that occurred in 4–7 locations. It is important to note that these three categories classified species independently of the actual number of specimens quantified for each species. For example, a high occupancy species may have a very small number of specimens, being considered "rare" under an abundance criterion. Similar, a low occupancy species could be present in very large numbers and be considered common or frequent. For this reason, and to avoid misinterpretation, in this study we avoid the terms "frequent, common, and rare" and refer to high, medium, and low occupancy species to unambiguously state that these categories do not refer to abundance but to the small-scale geographic distribution in our study.

We used five analytical approaches to test for a number of hypotheses. First, we ran paired t-tests to test for differences in richness (number of species), diversity (Shannon Diversity Index), abundance (number of specimens), and number of exclusive species between artificial and natural substrates. We defined exclusive species as those that, for every location, were present in either the natural or the

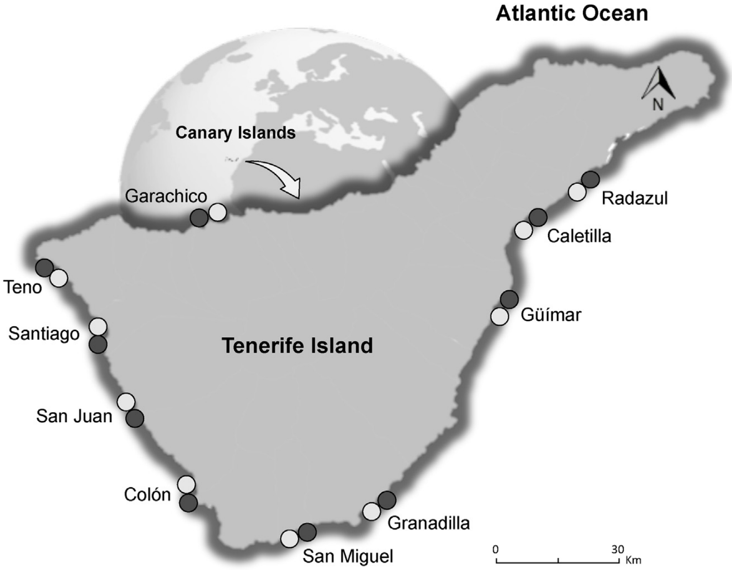

Fig. 1. Sampled artificial (dark circles) and adjacent natural substrates (light circles) scattered along the coast of Tenerife, Canary Islands. See Table 1 for additional site information.

artificial substrate, but not in both. It is possible that the same taxonomic species contributes multiple times as an exclusive species, regardless substrate type. For example, species "A" could be present exclusively in the natural substrate in one location and exclusively in the artificial substrate in another location, contributing as an exclusive species in both locations. Regardless the variable, all paired t-tests had 10 replicates, i.e., one natural and one artificial value for location. A second analytical approach used log-linear models to test for differences in richness, abundance, and number of exclusive species as a function of substrate type, species occupancy, and species mobility. Because log-linear models are a type of multiway frequency table analysis, data for each cell in the table was a single value with the total number of species, total abundance, or total number of exclusive species under each respective category. Log-linear models were run with the three variables of interest (substrate type, species occupancy, and species mobility) and their two-way interactions. Third, we also tested for differences in richness, diversity, abundance, and number of exclusive species (all variables rank-transformed because of lack of assumptions) between artificial and natural substrates with a threeway analysis of variance applying "*aov*" function of the vegan package in R (Oksanen et al., 2016) with substrate type, species occupancy, and mobility as fully orthogonal, fixed factors (i.e., 180 data points for each variable; 3 levels of mobility x 3 levels of occupancy x 2 substrate types x 10 locations). We used a fourth analytical approach to test whether artificial substrates increasingly resembled their natural counterparts with time. To do so, we ran an analysis of covariance on the rank-transformed *NAR* using species occupancy and mobility as fixed factors and age of the artificial substrates as covariate. Because *NAR* was calculated for each species in our data set and many occurred in multiple locations, the total number of data points in this analysis was 492, i.e., there were

Table 1
Sampling locations (and numbers for their identification in Fig. 1) with average depth (m), latitude and longitude for both natural and artificial substrates, age of the artificial substrate (in years from submersion to sampling time) and type of material used for the construction of the breakwaters, i.e., material of artificial substrates.

Number	Location	Natural Substrate (NS)	Depth NS	Artificial Substrate (AS)	Depth AS	Age AS	Material AS
1	Garachico	28°22′17.38″ N 16°45′10.33″ W	5	28°22′24.13″ N 16°45′09.62″ W	2.5	0	Concrete
2	Teno	28°20′32.78″ N 16°55′06.98″ W	4.6	28°20′30.86″ N 16°55′11.27″ W	5.4	34	Concrete
3	Santiago	28°16′06.98″ N 16°51′05.11″ W	6.8	28°14′54.31″ N 16°50′34.74″ W	8.8	35	Concrete
4	San Juan	28°10′46.50″ N 16°49′10.26″ W	6.2	28°10′46.03″ N 16°48′57.61″ W	6.6	24	Concrete
5	Colón	28°06′00.46″ N 16°45′20.83″ W	7.9	28°04′47.04″ N 16°44′17.59″ W	7	27	Concrete
6	San Miguel	28°01′21.15″ N 16°36′33.25″ W	3.7	28°01′17.96″ N 16°36′36.42″ W	4.7	8	Concrete
7	Granadilla	28°05′16.07″ N 16°29′25.39″ W	6.5	28°05′14.39″ N 16°36′37.25″ W	3.3	18	Concrete
8	Güímar	28°17′42.79″ N 16°22′21.10″ W	3.8	28°17′16.32″ N 16°22′42.67″ W	3.2	4	Quarry rock
9	Caletillas	28°23′02.74″ N 16°21′11.87″ W	3.6	28°22′54.29″ N 16°21′21.81″ W	5.9	54	Concrete
10	Radazul	28°24′07.77″ N 16°19′39.77″ W	6	28°24′05.50″ N 16°19′35.72″ W	5.8	4	Quarry rock

multiple *NAR* values (multiple species) for each of the 10 age values (one for each location). Regressions in the analysis of covariance were highly replicated (between 32 and 93 data points depending on the mobility x occupancy combination). Finally, we also ran a permutational analysis of variance (PERMANOVA) of square-root transformed species abundance data to test for community level differences between natural and artificial substrates. We used a resemblance matrix based on Bray-Curtis distance and the "*Adonis"* function of vegan package (R Development Core Team, 2013; Oksanen et al., 2016) with 999 permutations.

3. Results

We found none non-indigenous or invasive species out of the 107 identified species quantified in our study (Appendix 1). Overall, seven out of the 10 natural substrates had more species than their artificial counterparts, yet the total number of species failed to statistically differ between natural and artificial substrates (paired *t*-test, $T = -0.918$, $df = 9$, $p = 0.382$). The log-linear model fit well with the total number of species found in natural and artificial substrates (Likelihood Ratio $\chi^2 = 3.429$, $df = 4$, $p = 0.489$). The same model without occupancy had a poor fit ($\chi^2 = 18.548$, $df = 6$, $p = 0.005$), causing a significant change in the model ($\chi^2 = 15.119$, $df = 2$, $p = 0.001$). The number of low occupancy species with medium and low mobility in natural substrates doubled and tripled those found in artificial substrates (Fig. 2a). We also found that the average number of species found in natural and artificial substrates might vary as a function of species occupancy and mobility (three-way ANOVA, see probability of three-way interaction term between substrate type, occupancy, and mobility, and probability of substrate type in Table 2a).

Similarly, eight out of 10 natural substrates had higher Shannon Diversity Index than their artificial counterparts, yet diversity failed to statistically differ between natural and artificial substrates (paired *t*-test, $T = -1.983$, $df = 9$, $p = 0.079$). We found that the average Shannon Diversity Index found in natural substrates was significantly larger than in artificial substrates (three-way ANOVA, significant substrate type, Table 2b), driven by the higher diversity values in natural than in artificial substrates for the low occupancy species with medium and low mobility (Fig. 3).

Seven out of the 10 natural substrates had more exclusive species than their artificial counterparts, yet the total number of exclusive species failed to statistically differ between natural and artificial substrates (paired *t*-test, $T = -0.918$, $df = 9$, $p = 0.382$). The total number of exclusive species that were found in either natural or artificial substrates varied as a function of occupancy and mobility (Fig. 2b, $\chi^2 = 9.886$, $df = 2$, $p = 0.007$). High occupancy species with high mobility were more often seen exclusively in artificial than in natural substrates (56 *vs.* 42) while the opposite was true for low occupancy species with medium (36 *vs.* 56) and low (19 *vs.* 37) mobility (Fig. 2b). Substrate type also had an effect on the average number of exclusive species, although its effect varied as a function of mobility and occupancy (three-way ANOVA, significant substrate type effect and its interaction with occupancy and mobility, Table 2c).

The total number of specimens also failed to statistically differ between natural and artificial substrates (paired *t*-test, $T = 1.151$, $df = 9$, $p = 0.280$). Yet, the total number of specimens in natural and artificial substrates varied as a function of occupancy and mobility (Fig. 2c, $\chi^2 = 512.786$, $df = 4$, $p < 0.001$). High occupancy species with high mobility were more abundant in artificial than in natural substrates (25.4 *vs.* 9.2) while the opposite was true for low occupancy species with medium (17 *vs.* 56) and low (600 *vs.* 893) mobility (Fig. 2c). We also found that the average number of specimens found in natural and artificial substrates varied as a function of species occupancy and mobility (three-way ANOVA, significant interaction term between substrate type, occupancy, and mobility, Table 2d).

NAR varied as a function of species occupancy, species mobility, and their interaction ($p = 0.005$, $p < 0.001$, and $p = 0.005$, respectively, Table 3). Age had no effect on *NAR*, either directly ($p = 0.436$, Table 3) or through its interaction with species occupancy and mobility ($p = 0.121$, Table 3). Low occupancy species with medium and low mobility were more abundant in natural than in artificial substrates (Fig. 4). High mobility species showed negative *NAR* values regardless their occupancy (Fig. 4). Permutational analysis of variance (PERMANOVA) failed to detect differences in species abundances between natural and artificial substrates (Pseudo-F = 1.064, $df = 1$, $p = 0.354$, Fig. 5).

4. Discussion

Human alteration of coastal ecosystems is widespread and artificial substrates are becoming a significant habitat in shallow rocky communities (Airoldi and Beck, 2007). The proliferation of artificial

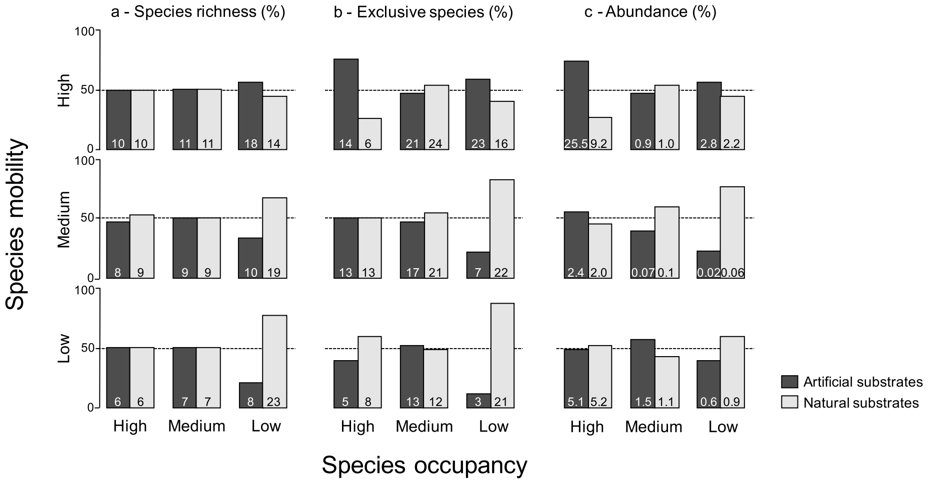

Fig. 2. Percentage of a) species richness, b) exclusive species, and c) total species abundance found in artificial (dark bars) and natural (light bars) substrates. Numbers within bars are a) total number of species, b) total number of exclusive species, and c) total abundance ($x10^3$) pooled across substrates as a function of species occupancy (high, medium, and low occupancy, x-axis) and mobility (high, medium, and low mobility, y-axis).

Table 2

Summary of the three-way analysis of variance on a) species richness, b) Shannon diversity index, c) number of exclusive species, and d) total abundance of specimens with substrate type, species mobility, and species occupancy as fixed factors.

Variable	Factors	df	SS	MS	F	p
Richness	Substrate	1	3234	3234	3.46	0.064
	Mobility	2	11,193	5596	5.99	0.003
	Occupancy	2	287,973	143,987	154.22	< 0.001
	Substrate*Mobility	2	2873	1436	1.53	0.217
	Substrate*Occupancy	2	4024	2012	2.15	0.119
	Mobility*Occupancy	4	1,0408	2602	2.78	0.028
	Substrate*Mobility*Occupancy	4	8801	2200	2.35	0.055
	Residuals	162	151,245	934		
Diversity	Substrate	1	7618	7618	5.27	0.022
	Mobility	2	6210	3105	2.14	0.119
	Occupancy	2	200,250	100,125	69.31	< 0.001
	Substrate*Mobility	2	1855	928	0.64	0.527
	Substrate*Occupancy	2	5064	2532	1.75	0.176
	Mobility*Occupancy	4	14,217	3554	2.46	0.047
	Substrate*Mobility*Occupancy	4	11,800	2950	2.04	0.09
	Residuals	162	234,025	1445		
Exclusive species	Substrate	1	12,103	12,103	5.71	0.017
	Mobility	2	16,201	8100	3.82	0.023
	Occupancy	2	20,717	10,359	4.89	0.008
	Substrate*Mobility	2	8423	4211	1.98	0.14
	Substrate*Occupancy	2	20,099	10,050	4.74	0.009
	Mobility*Occupancy	4	9851	2463	1.16	0.329
	Substrate*Mobility*Occupancy	4	21,138	5284	2.49	0.044
	Residuals	162	343,088	2118		
Abundance	Substrate	1	149	149	0.17	0.677
	Mobility	2	276,597	138,299	160.2	< 0.001
	Occupancy	2	45,298	22,649	26.23	< 0.001
	Substrate*Mobility	2	958	479	0.55	0.575
	Substrate*Occupancy	2	1904	952	1.1	0.334
	Mobility*Occupancy	4	10,771	2693	3.11	0.016
	Substrate*Mobility*Occupancy	4	9928	2482	2.87	0.024
	Residuals	162	139,847	863		

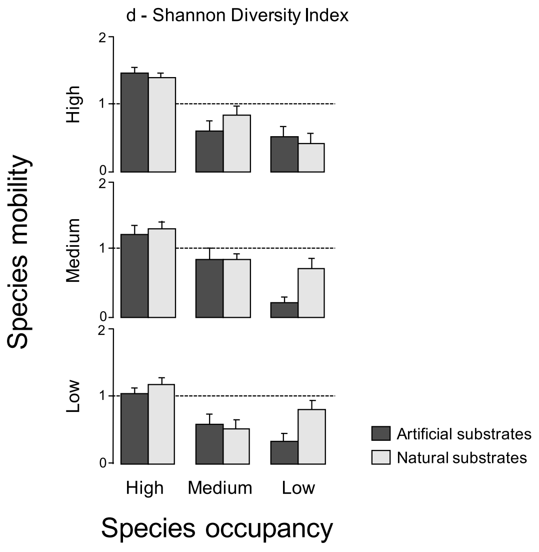

Fig. 3. Mean (± 1SE) Shannon diversity index of the species found in the 10 artificial (dark bars) and adjacent natural (light bars) substrates as a function of species occupancy (high, medium, and low occupancy, x-axis) and mobility (high, medium, and low mobility, y-axis).

Table 3

Summary of the two-way analysis of covariance on the *Natural-Artificial Ratio* (*NAR*) using species mobility and occupancy as factors and age of the artificial substrates as covariate.

Factors	df	SS	MS	F	p
Occupancy	2	194,601.6	97,300.8	5.281	0.005
Mobility	2	290,674.5	145,337.2	7.888	0.000
Age	1	11,182.5	11,182.5	0.607	0.436
Mobility*Occupancy	4	278,698.1	69,674.5	3.781	0.005
Mobility*Occupancy*Age	4	135,015.3	33,753.4	1.832	0.121
Error	478	8,807,322.7	18,425.3		

structures in the sea, referred to as ocean sprawl (Firth et al., 2016), is a cause of concern because artificial substrates may not function as the natural substrates they often replace (Carr and Hixon, 1997; Airoldi and Beck, 2007; Burt et al., 2009). Many studies have evaluated whether communities in natural and artificial substrates differ, yet evidence is somehow contradictory and incomplete. For example, fish populations in artificial structures can be either larger (Jessee et al., 1985; Rilov and Benayahu, 2000; Granneman and Steele, 2015), similar (Santos et al., 2013; Ross et al., 2016), or smaller (Carr and Hixon, 1997; Rooker et al., 1997) than in natural reefs. Differences between natural and artificial substrates may vary depending on the variable recorded (e.g., species richness, species abundance, species diversity), the location investigated, the species quantified, or the complexity of the artificial structures, among others (Hunter and Sayer, 2009; Granneman and Steele, 2015). Our results showed biodiversity differences between adjacent natural and artificial substrates. These differences were majorly driven by the larger diversity of low occupancy species with medium or low mobility (i.e., rare benthic and sessile species) in natural substrates and the larger abundance of high occupancy and high mobility species in artificial substrates (i.e., common demersal fish species). Occupancy and mobility were, therefore, critical species traits to explain differences between substrate types. Failure to include these species traits resulted in non-significant differences between both substrate types. Our results suggest that the more common and mobile species create an illusion of natural communities in artificial substrates,

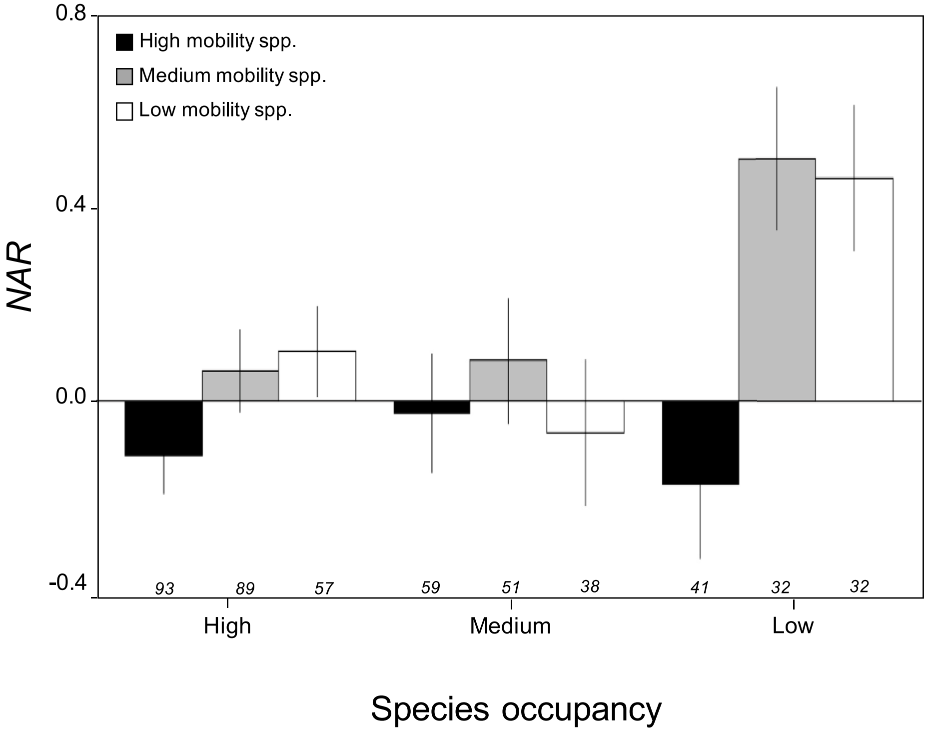

Fig. 4. Mean (± 1SE) *Natural-Artificial Ratio* (*NAR, y-axis*) of the species found in the 10 artificial and adjacent natural substrates as a function of species occupancy and mobility (x-axis). Positive *NAR* values are obtained with larger species abundance in natural than in artificial substrates, while negative *NAR* values are obtained with larger species abundance in artificial than in natural substrates. Numbers below bars are the number of NAR values (i.e., species) contributing to each occupancy*mobility combination. See Materials and methods for additional details.

by homogenizing both habitats and masking the negative effect that artificial substrates have in a large proportion of species. We found no evidence to support that these differences decreased over time, suggesting that artificial substrates are bad surrogates of their natural counterparts, at least over the 54-yr span investigated in our study.

There are reasons to expect that artificial substrates can mimic or surpass the biodiversity found in natural substrates (Baine, 2001). Artificial structures may provide additional habitats and refuge to those available in natural reefs, which could result in increased species richness, abundance, or diversity (Menge, 1976; Jessee et al., 1985; Granneman and Steele, 2015). Out of the many possible artificial structures deployed in the ocean, artificial reefs have been widely used as a tool to help mitigate undesired trends such as habitat loss (Pickering and Whitmarsh, 1997) or to help preserve, restore, or enhance desired ecological functions such as diversity and production (Perkol-Finkel and Benayahu, 2005) or fisheries (Baine, 2001).

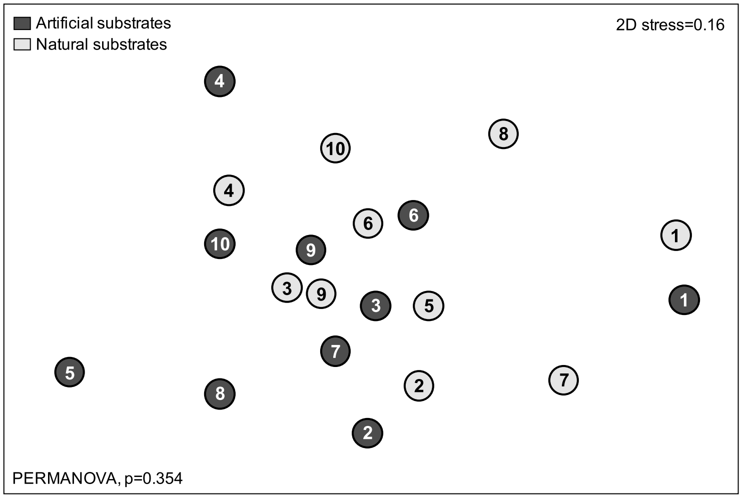

Fig. 5. Non-metric multidimensional scaling (MDS) based on Bray-Curtis distance similarity matrix calculated from square-root transformed abundances of all species found in artificial (dark) and natural (light) substrates. Numbers within circles indicate locations as specified in Table 1. P value provided by permutational analysis of variance to test for differences between artificial and natural substrates. See text for additional details.

Artificial reefs built with concrete blocks seem to increase both fish species and fish biomass (Pickering and Whitmarsh, 1997) as compared to artificial reefs built with pipes or natural reefs (Brock and Norris, 1989). Compared to natural reefs, the smaller size of artificial reefs can also explain higher species densities due to increase reef perimeter/area ratio (Jessee et al., 1985; DeMartini et al., 1989; Bohnsack et al., 1994). Most evidence for enhanced biodiversity (in a broad sense) by artificial reefs stem from fish data (Svane and Petersen, 2001), but increased invertebrate and algal populations have also been reported (Hunter and Sayer, 2009; Granneman and Steele, 2015). Whether the increased abundance, biomass, or diversity (in a broad sense) found in artificial reefs is due to increased production in the artificial structure or to attraction from surrounding environments, i.e., the production vs attraction debate (Pickering and Whitmarsh, 1997), remains unresolved.

Yet marine artificial structures can be deployed with no ecological/conservational goals in mind, for example, to provide shelter for boats as the breakwaters investigated in our study. These type of structures can show trends that diverge from those found in artificial reefs, with decreased biodiversity (in a broad sense) on artificial structures (Chapman, 2003; Airoldi et al., 2015). Our results provided evidence that the effect of artificial substrates varied as a function of the variable and species (or species group) investigated. Three set of data supported evidence for increased performance of artificial over natural substrates in our study. First, average *NAR* (*Natural-Artificial Ratio*) for high mobility species was negative, providing evidence for larger abundance of high mobility species in artificial than in natural substrates. Because *NAR* was calculated for every species in our study, the negative average values suggest that the larger abundance of high mobility species found in artificial substrates was a general pattern driven by many species. In fact, 80% of the high occupancy and 45% the low occupancy species with high mobility were more abundant in artificial substrates (as opposed to only 20% and 30% that were more abundant in natural substrates). Second, total and average abundance of high occupancy species were higher in artificial than in natural substrates. Third, the number of exclusive high mobility species with high occupancy found in artificial substrates doubled those found in natural substrates. Our results might suggest that the success of these species stem from their capacity to inhabit a variety of habitats (high occupancy) and to occupy new habitats as they become available (high mobility). All high mobility species in our study were demersal fish, so our study supports for the increased fish abundance and biomass found in many artificial reefs (Chapman, 2003), often deployed with specific conservation goals (as opposed to the coastal protection goals of the breakwaters investigated in our study). Increased fish abundance is a sought-after effect that can bring benefits to multiple stakeholders, including recreational and commercial fishing (Whitmarsh et al., 2008) or diving industry (van Treeck and Schuhmacher, 1999; Crabbe and McClanahan, 2006; Kirkbride-Smith et al., 2013), among others. Given that only high mobility species showed increased performance in the artificial substrates, our results could support for a stronger attraction than production effect in the attraction vs production debate (Pickering and Whitmarsh, 1997).

Our data showed stronger evidence for decreased performance of artificial over natural substrates, which was driven by low occupancy species with medium and low mobility. In our study, medium mobility species included multiple invertebrates and cryptic fish species. Adult organisms of these species are clearly more attached to the substrate than demersal fish and have a somehow reduced mobility. In our study, low mobility species included any sessile organism permanently attached to the substrate and, therefore, with highly restricted (i.e., nil) mobility. Other studies have also reported decreased artificial reef performance associated with sessile species, i.e., higher coral richness and diversity in natural habitats than in artificial reefs (Perkol-Finkel and Benayahu, 2004; Perkol-Finkel et al., 2005, 2006; Burt et al., 2009). Our data also showed that artificial substrates had lower numbers of low occupancy benthic and sessile species that were observed exclusively in either the natural or the artificial substrate, giving additional evidence for the decreased performance of artificial substrates in species richness. Yet, abundance of sessile species may be higher in artificial than natural reefs (Hunter and Sayer, 2009; Granneman and Steele, 2015). Even more, artificial reefs can be less diverse but, at the same time, hold higher abundance than natural reefs (Burt et al., 2009). We found the opposite, i.e., larger total abundance per species and larger average *NAR* of low occupancy benthic and sessile species on natural reefs, providing evidence for higher species density in natural than in artificial substrates. Because only medium and low mobility species with low occupancy showed decreased performance in the artificial substrates, these results could support for a weaker production than attraction effect in the attraction vs production debate (Pickering and Whitmarsh, 1997). If our data can be interpreted within this debate, our study might provide greater support for the attraction (improved performance of demersal fish, i.e., associated with the attraction effect) over the production effect (reduced performance of sessile species, i.e., associated with production effect) of the debate. Information on the size distribution of species in both substrate types (not analyzed in our study) could help shed more light into this unresolved debate.

Overall, and beyond the specific results, our findings suggest that artificial substrates missed an important component of biodiversity, the least widely distributed benthic and sessile species. Despite their scarcity, these species were 40% of the total number of species in our study, representing a significant part of the biodiversity of the rocky littoral bottoms. Yet, because the species missing in our artificial substrates were the least apparent species in the community, artificial substrates gave an illusion of natural-like substrates driven by the most conspicuous species. In fact, and for all variables analyzed in our study, natural and artificial substrates failed to differ statistically unless we considered species occupancy and mobility. These species traits were, therefore, critical to find differences between natural and artificial substrates and provided evidence for the big impact that common species have at the community level, both statistically and at an observational, landscape scale. The large influence of common species at the community level exceeds biodiversity implications *per se*, linking biodiversity with ecosystem functioning (Grime, 1998). While common species are responsible for immediate effects, the filter and founder effects of the not-so-common species may become apparent at longer time scales and cannot be neglected (Grime, 1998).

Long-term data on the composition and abundance of species inhabiting artificial reefs is scarce, particularly with proper comparisons with natural reefs. In a 15-year study of artificial reefs off Rio de Janeiro, fish species richness, abundance, and biomass increased up to the 6–7th year to decrease thereafter although, unfortunately, no data is available from adjacent natural reefs (Neves dos Santos and Zalmon, 2015). Other studies have comparisons with natural reefs, but the artificial reefs have been few years underwater. Fish populations in young artificial reefs seem to be larger than in natural reefs (Bohnsack et al., 1994; Clark and Edwards, 1999; Chapman and Clynick, 2006) although fish assemblages may (Bohnsack et al., 1994; Clark and Edwards, 1999) or may not (Tupper and Hunte, 1998) differ. Data for mollusks showed an opposite pattern with lower diversity, richness, and evenness but larger number of specimens and dominance in artificial than natural reefs (Badalamenti et al., 2002). However, their natural and artificial reefs were associated with clear and turbid waters, which could act as a confounding factor (Badalamenti et al., 2002). Besides fish, Chapman and Clynick (2006) also quantified the algal and sessile invertebrate populations on their natural and artificial reefs, which were both similar.

At the other side of the age spectrum, data from a single 119-year old shipwreck and the adjacent reef where it sunk showed that natural-like communities developed only where the structure of the wreck matched the reef structure (Perkol-Finkel et al., 2006). Despite being underwater for over a century, wreck sections that differed structurally from natural reefs also differed ecologically (Perkol-Finkel et al., 2006).

Likewise, sessile communities in natural reefs differed with those from breakwaters of varying age, even after 31 years underwater (Burt et al., 2011). Similarity between natural and breakwater communities increased with time (Burt et al., 2011), which could be interpreted as an example of directional replacement of species. In fact, turf algae dominated breakwaters until 1.5 years, followed by a peak in bivalves on the 3.5 to 5.5-year-old reefs, and then coral cover gradually increased with reef age (Burt et al., 2011). These transitions from short-lived, fast-growing, opportunistic species to long-lived, slow-growing, competitively superior species agrees with the directional replacement of species in classic succession although it does not guarantee stable communities equivalent to those found in surrounded natural reefs (Svane and Petersen, 2001). Other studies have shown that artificial reef communities may take over a decade to resemble those in natural reefs (Aseltine-Neilson et al., 1999; Abelson and Shlesinger, 2002; Perkol-Finkel and Beneyahu, 2004, 2007), but the resulting community may not be natural-like (Perkol-Finkel et al., 2006).

Our study is a snapshot comparison of multiple artificial substrates and their adjacent natural counterparts. For each location, natural and artificial substrates were equivalent in terms of orientation, wave exposure, depth, and slope. The artificial substrates we investigated differed in ecological conditions and spanned from 0 to 54 years underwater. We observed no major, community-level temporal trend in the presence and abundance of species. In the 20 reefs studied, we quantified presence and abundance of a total of 107 species. Detailed analyses at the species level or species-specific patterns along the 50-year timespan of our study are beyond the scope of this study. Our goal was to test whether communities inhabiting artificial substrates were equivalent to those found in natural substrates of the same area. As discussed previously, there are multitude examples with varying results often leading to contrasting conclusions. Our approach focused on many species to maximize ecological patterns over species specific responses, paired every artificial substrate with its adjacent natural reef to minimize community differences due to distinct geographic and environmental conditions, and used artificial substrates with varying numbers of years underwater to test for temporal trends in community organization. Overall, i.e., without considering species mobility and occupancy in our models, we found no statistical differences in diversity (broadly defined) between artificial and natural substrates. They seemed to be equivalent. These results were driven by the strong influence of common species, which minimized the large differences in low occupancy species with medium and low mobility. These benthic and sessile species were 40% of the species in our study and they were significantly less represented, both in terms of species number and abundance, in artificial substrates. Inclusion of species mobility and occupancy was therefore critical to describe the biodiversity loss associated with the artificial communities. Contrary to our expectations, age played no significant role to explain differences between natural and artificial substrates. Our results suggest that, regardless of directional replacement of species, communities developing in artificial substrates need not match their natural counterparts, as previously reported (Perkol-Finkel et al., 2006). This output agrees with the ecological succession following non-catastrophic disturbances, despite artificial substrates do offer a denuded substrate for primary succession (Platt and Connell, 2003). Given the current proliferation of artificial structures in our shallow marine environments, we might be building up a large biodiversity loss in shallow water marine communities around the globe. This unintentional loss is hard to detect as it seems to target the least conspicuous and less investigated benthic and sessile species. Fish species, the main target of many studies, seem to thrive in artificial substrates both in terms of number and abundance of species. Since communities inhabiting artificial substrates deviate from natural communities, artificial structures could lead to an increase of regional diversity (Connell and Glasby, 1999). Our results suggest otherwise that artificial substrates are not surrogates for natural communities (Burt et al., 2011). Understanding the strengths and weaknesses of artificial structures will sure lead to a more effective use of these habitats. Should we aim to minimize biodiversity loss and promote its conservation, reliance on artificial substrates as surrogates of natural reefs looks dubious. Strategies that lessen habitat destruction combined with alternative protection and restoration measures may provide more efficient mechanisms for biodiversity conservation (Abelson et al., 2016; Geist and Hawkins, 2016; Kollmann et al., 2016).

Acknowledgments

We sincerely appreciate the unconditional support of Carlos Ceballos, from the Club Actividades Subacuáticas BIOSUB (www.biosub.es), and The Hotel Rural Casa Amarilla (www.fincacasamarilla.com) to our field activities. We also thank the Reef Life Survey Spain diver community for their help during field surveys and special thanks to Daniel Hernández for his contribution in the field work. This work was supported by the Spanish Ministry of Economy grant MARINERES [grant number CGL2013-49122-C3-1-R]. We deeply appreciate the constructive comments from Dr. Louise Firth and other anonymous reviewers that helped improve the quality of our study.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.06.010.

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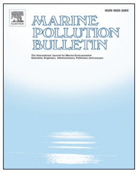
Marine Pollution Bulletin 143 (2019) 24–32

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul



Marine protected areas are more effective but less reliable in protecting fish biomass than fish diversity

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ARTICLE INFO

Keywords:
MPA efficiency
Higher carnivores
IUCN Red List
Protection benefits
Threatened species
Vulnerability

ABSTRACT

Marine protected areas (MPAs) provide multiple conservation benefits, thus raising the question of how good and consistent they are at their roles. Here, we quantified three components, namely, diversity, biomass, and other relevant variables, in numerous protected and unprotected areas across four marine ecoregions in southwestern Europe. We created a “global conservation status index” ($\mathrm{CSI}_{\mathrm{global}}$) as the sum of $\mathrm{CSI}_{\mathrm{diversity}}$, $\mathrm{CSI}_{\mathrm{biomass}}$, and $\mathrm{CSI}_{\mathrm{relevant}}$. We then tested whether CSI and its three components varied as a function of protection and marine ecoregion. MPA efficiency, defined as the effect size of protection on $\mathrm{CSI}_{\mathrm{global}}$, was unreliable and varied with geography. $\mathrm{CSI}_{\mathrm{biomass}}$ and $\mathrm{CSI}_{\mathrm{relevant}}$ contributed to the unreliability of MPA efficiency, while $\mathrm{CSI}_{\mathrm{diversity}}$ was reliable. $\mathrm{CSI}_{\mathrm{biomass}}$ showed the major efficiency in protected areas (60%). Biomass of threatened species was the single largest variable that contributed to MPA efficiency. Our easy-to-use approach can identify high- and low-efficient MPAs and help to clarify their actual roles.

1. Introduction

Marine protected areas (MPAs) are one of the main management tools for the current human-driven biodiversity crisis. With increasing anthropogenic pressures, MPAs are essential to preserve natural resources, biodiversity, and ecosystem properties (Micheli et al., 2012; Hilborn, 2016; Campbell et al., 2017). MPAs have steadily increased in the last decades to > 5% of coastal areas under national jurisdictions and < 1% of the high seas (Spalding et al., 2013) figures that keep on increasing with the establishment of some large MPAs, particularly in tropical waters (Devillers et al., 2015). MPAs are pivotal tools for coastal fisheries management and biodiversity conservation (Edgar et al., 2014). Yet, only 10% of the MPA surfaces are no-take zones, free of extraction, or habitat alteration activities, while 94% of MPAs allow fishing and other activities (Thomas et al., 2014; Costello and Ballantine, 2015; Campbell et al., 2017). Certainly, MPAs include a high range of areas, designs, uses, and management goals (Al-Abdulrazzak and Trombulak, 2012; Edgar et al., 2014; Pérez-Ruzafa et al., 2017), which could result in many benefits and varying degrees of protection efficiencies.

Besides MPAs, additional protection measures have been taken to contribute to biodiversity conservation, protection of threatened species, and restoration of fish stocks, including national parks, marine sanctuaries, natural parks, or natural monuments (Al-Abdulrazzak and Trombulak, 2012). Moreover, areas such as military zones can offer protection because of strong surveillance, highly restrictive access, and ban of extractive activities. All these protection measures can lead to the recovery of natural resources and other positive effects on natural communities (Russ et al., 2005; Weeks et al., 2010; Campbell et al., 2017).

The benefits of protection in marine communities are abundant, mostly focused on traits associated with diversity, biomass, or other relevant aspects related to protection. Protected areas are associated with larger species richness (Wantiez et al., 1997; Ciriaco et al., 1998; Edgar and Barrett, 1999; Barrett et al., 2007), larger trophic diversity (Shears and Babcock, 2003; Harmelin-Vivien et al., 2015), and larger functional diversity (Stelzenmüller et al., 2009; Villamor and Becerro, 2012; Guilhaumon et al., 2015) than unprotected areas. Protection also

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https://doi.org/10.1016/j.marpolbul.2019.04.015
Received 29 May 2018; Received in revised form 26 March 2019; Accepted 3 April 2019

triggers an increase in fish biomass, particularly of commercial fish species (Barrett et al., 2007; Fenberg et al., 2012; Parravicini et al., 2014; Pérez-Ruzafa et al., 2017), likely as a result of decreased fishing pressures (e.g., larger biomass of fish over 20 cm; Edgar and Barrett, 1999; Barrett et al., 2007; Stuart-Smith et al., 2017). However, the biomass of other groups of species such as fish species in the IUCN Red List (Nieto et al., 2015) has received less attention (Willis et al., 2003; Afonso et al., 2011; Harmelin-Vivien et al., 2015). Other relevant variables unevenly used to assess the effects of marine protection include abundance of higher carnivores (Cole, 1994; Harmelin et al., 1995), vulnerability of fish community (Cheung et al., 2007; Stuart-Smith et al., 2017; Vasconcelos et al., 2017), and fish size (Shears and Babcock, 2003; Sciberras et al., 2013). Overall, most available evidence supports for a positive effect of protection on all these traits, providing ample MPA benefits in terms of fish diversity, fish biomass, and relevant traits of the fish community.

The variability in MPA traits and benefits also points toward the possibility that MPAs may be inconsistent in their multiple roles, leading to varying degrees and contrasting levels of efficiency (Dichmont et al., 2013; White et al., 2014). In fact, the positive effects of protection are unevenly spread across MPAs, and numerous studies fail to provide evidence for the expected beneficial effects of protection. Literature on the so-called paper parks provides ample evidence that MPAs can be inefficient (Bustamante et al., 2014; Gallacher et al., 2016) due to multiple factors (Rife et al., 2013; Edgar et al., 2014). Often, the protection effects of MPAs, e.g., increase in species richness or abundance, are noticeable after sufficiently long periods together with suitable control sites (Stobart et al., 2009; Chirico et al., 2017). Moreover, many studies that assessed MPA efficiency have focused on one rather than several benefits (McClanahan et al., 1999; Vanderklift et al., 2013), which could account for differences associated with the specifics of each benefit, MPA, or geographic region investigated (Caveen et al., 2015; Fletcher et al., 2015; Hughes et al., 2016).

Studies examining the effects of protection on multiple benefits over large geographic scales can provide opportunities to advance our understanding on how good MPAs are at achieving their multiple benefits and how reliable MPAs are at providing such benefits. In this study, we followed this approach to shed some light on the relationship between protection and their benefits. We used fish communities across southwestern Europe to investigate how fish diversity, fish biomass, and other relevant protection-related benefits contributed to the overall differences between fish communities in protected and unprotected areas and tested whether these benefits were consistent or varied as a function of geography. We investigated > 20 protected sites distributed in four marine ecoregions of the world (Spalding et al., 2007) in the Atlantic-Mediterranean confluence area. We used species richness, trophic diversity, and functional diversity to evaluate MPA benefits on fish diversity; biomass of commercial fish, biomass of large fish, and biomass of threatened fish species to evaluate MPA benefits on fish biomass; and fish vulnerability, fish size, and abundance of higher carnivores as other MPA benefits on fish communities. Our results showed evidence for a small but consistent protection effect on fish diversity as opposed to larger and geographically variable protection effects on biomass and other relevant variables that resulted in unreliable MPA efficiency in our study area.

2. Material and methods

2.1. Study area and field survey

We sampled a total of 372 sites that are mostly scattered along, but not limited to, the coast of Spain, Portugal, and North Africa (Fig. 1). The locations included 22 MPAs from four marine ecoregions (Alboran Sea; Azores Canaries Madeira, hereafter Canary Is.; South European Atlantic Shelf, hereafter Atlantic; and Western Mediterranean) defined by Spalding et al. (2007) as “areas of relatively homogeneous species composition, clearly distinct from adjacent systems.” The species composition of each ecoregion is likely to be determined by the predominance of a small number of ecosystems or a distinct suite of oceanographic or topographic features (Spalding et al., 2007, Table 1). In this paper, we define MPA broadly to accommodate for the multiple protection measures available in our study area, including marine reserves, national parks, natural parks, and no-access military zones with strong enforcement. Specific goals of these 22 MPAs include biodiversity conservation (17 MPAs), fish stock restoration (12 MPAs), national defense (4 MPAs), and protection of endangered species (1 MPA). Our sampling design covered many protected and unprotected sites in each of the four ecoregions investigated, providing a good representation of both factors. All sampling was conducted in the summers of 2014, 2015, and 2016.

We used the Reef Life Survey protocol (Edgar and Stuart-Smith, 2014) to quantify the number, abundance, and size distribution of the fish community at each site. Briefly, in each sampled site, we took at least two underwater visual surveys along 50-m long × 10-m wide transects (Edgar and Stuart-Smith, 2014), with all conspicuous fish (> 25 mm size) identified and their abundances and sizes estimated. We restricted sampling between 6- and 15-m deep to minimize the influence of depth on fish communities.

2.2. Conservation status index (CSI)

Our quantitative data allowed us to calculate multiple variables from which we selected nine mostly unrelated traits to characterize fish communities (Table 2). These selected variables provided quantitative information on the status of each fish community in terms of diversity (species richness, trophic diversity, and functional diversity), biomass (biomass of commercial species, biomass of large specimens, and biomass of threatened species), and relevant traits (vulnerability, size community, and abundance of higher carnivores; Fig. 2). We calculated species richness as the total number of fish species in each transect. To calculate trophic diversity, we categorized every fish specimen into its respective trophic group, i.e., benthic invertivore, browsing herbivore, higher carnivore, planktivore, or scraping herbivore, and we computed the Shannon-Weaver diversity index as natural logarithm on the abundance of these trophic groups. To calculate functional diversity, we assigned all fish specimens to their corresponding levels of eight functional traits (water column position, preferred substrate, trophic group, dial activity pattern, habitat complexity, gregariousness, trophic breadth, and maximum length) and calculated Rao-Q following Stuart-Smith et al. (2013). Information on the trophic groups and functional traits of every fish species is available in FishBase (www.fishbase.com), (Froese and Pauly, 2000).

We used our observed abundance of fish size groups to estimate biomass of fish species (Ln transformed) based on species-specific length-weight relationships available in FishBase (Froese and Pauly, 2000). We defined large specimens as fish individuals larger than 200 mm length (hereafter biomass > 200 mm). We used Spanish Commercial List of Marine Fishes (http://www.mapama.gob.es/es/pesca/temas/mercados-economia-pesquera/fichas_sp_comerciales.aspx) to assign fish species to the commercially interesting species group and the European Red List of Marine Fishes of the International Union for Conservation of Nature (IUCN) to assign fish species to the threatened species group (Nieto et al., 2015).

We also used FishBase information (Froese and Pauly, 2000) to quantify the abundance of higher carnivores (log transformed) and to assign vulnerability values to every fish specimen in our data set. Then, we used the community-weighted mean as a vulnerability index. We calculated fish size as the community-weighted mean of the total length of the observed fish specimens in each site.

We defined the global conservation status index (CSI_{global}) as the sum of the nine variables investigated, which were standardized between 0 and 100 to give equal possible weight to their contribution to

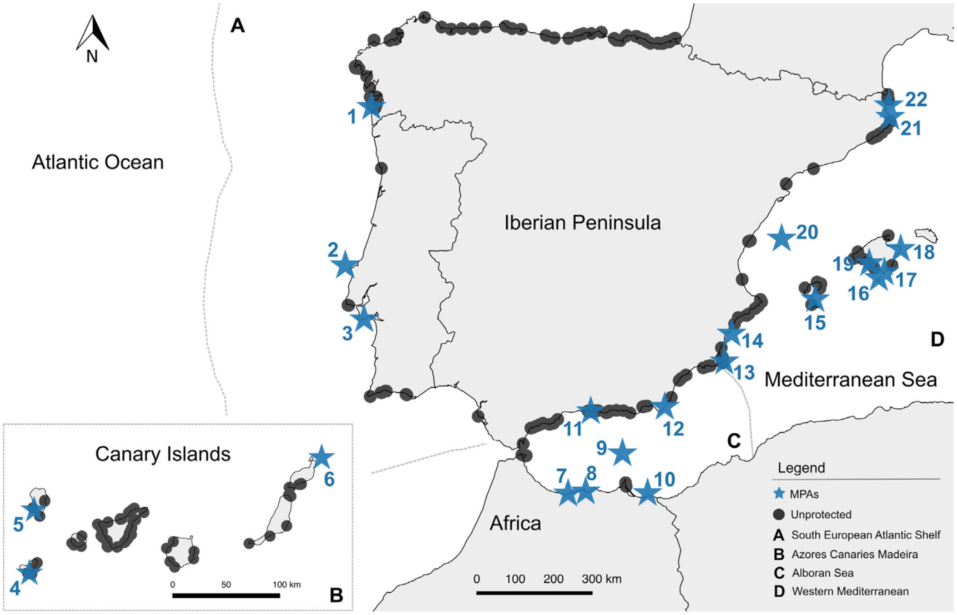

Fig. 1. Location of the 22 marine protected areas (stars) and hundreds of localities (circles) investigated in our study, spanning in four marine ecoregions of the world (A, B, C, and D; Spalding et al., 2007). See Table 1 for details.

Table 1
Marine protected areas investigated in our study, showing the code to find its location in Fig. 1, marine ecoregion, protected area name, protection status, and goals as specified in their official sites.

Map code	Marine ecoregion	Protected area	Protection status	Goals
1	South European Atlantic Shelf	Islas Cíes	National Park	Biodiversity conservation
2	South European Atlantic Shelf	Archipiélago de las Berlengas	Marine Reserve	Biodiversity conservation Fish stock restoration
3	South European Atlantic Shelf	Da Arrabida	Natural Park	Biodiversity conservation
4	Azores Canaries Madeira	Punta de la Restinga - Mar de las Calmas	Marine Reserve	Biodiversity conservation Fish stock restoration
5	Azores Canaries Madeira	Isla de la Palma	Marine Reserve	Biodiversity conservation Fish stock restoration
6	Azores Canaries Madeira	Isla de la Graciosa e islotes del Norte de Lanzarote	Marine Reserve	Biodiversity conservation Fish stock restoration
7	Alboran Sea	Peñón de Vélez de la Gomera	Military Area	National defense
8	Alboran Sea	Archipiélago de Alhucemas	Military Area	National defense
9	Alboran Sea	Isla de Alborán	Military Area and Marine Reserve	Biodiversity conservation Fish stock restoration National defense
10	Alboran Sea	Islas Chafarinas	Military Area	Biodiversity conservation National defense
11	Alboran Sea	Maro-Cerro Gordo	Natural Park	Biodiversity conservation
12	Alboran Sea	Cabo de Gata-Níjar	Marine Reserve	Biodiversity conservation Fish stock restoration
13	Western Mediterranean	Cabo de Palos e Islas Hormigas	Marine Reserve	Biodiversity conservation Fish stock restoration
14	Western Mediterranean	Isla de Tabarca	Marine Reserve	Biodiversity conservation Fish stock restoration
15	Western Mediterranean	Freus de Ibiza y Formentera	Marine Reserve	Biodiversity conservation Fish stock restoration
16	Western Mediterranean	Archipiélago de Cabrera	National Park	Biodiversity conservation
17	Western Mediterranean	Migjorn de Mallorca	Marine Reserve	Biodiversity conservation Fish stock restoration
18	Western Mediterranean	Cala Ratjada	Marine Reserve	Biodiversity conservation
19	Western Mediterranean	Bahía de Palma	Marine Reserve	Biodiversity conservation
20	Western Mediterranean	Islas Columbretes	Marine Reserve	Biodiversity conservation Fish stock restoration
21	Western Mediterranean	Islas Medas	Natural Park	Biodiversity conservation
22	Western Mediterranean	Cabo de Creus	Natural Park	Endangered species protection

Table 2
Correlation matrix showing the strength of the association (coefficient of determination) between the nine variables investigated in our study. * indicates significant correlations ($p < 0.05$).

	1	2	3	4	5	6	7	8	9
Biomass threatened species (1)	1								
Abundance of higher carnivores (2)	0.19*	1							
Biomass > 200 mm (3)	0.09*	0.12*	1						
Trophic diversity (4)	0.09*	0.04*	0.00	1					
Species richness (5)	0.11*	0.06*	0.01*	0.12*	1				
Biomass commercial species (6)	0.05*	0.13*	0.25*	0.00	0.12*	1			
Vulnerability (7)	0.02*	0.00	0.00	0.11*	0.01*	0.00	1		
Functional diversity (8)	0.01*	0.01	0.06*	0.17*	0.00	0.00	0.18*	1	
Large specimens (9)	0.01	0.00	0.06*	0.00	0.15*	0.00	0.19*	0.01*	1

CSI_{global} (Fig. 2). The simple addition of standardized variables also allowed for (i) an easy partitioning of the CSI_{global} into its three components of diversity ($CSI_{diversity}$), biomass ($CSI_{biomass}$), and relevant traits ($CSI_{relevant}$) by simply considering their respective variables and (ii) straight ecological interpretation as each variable value contributed directly and proportionally to CSI_{global} (Fig. 2).

2.3. Testing MPA efficiency

We defined MPA efficiency as the difference in CSI between protected and unprotected sites, i.e., the effect size of protection. Thus, larger CSI values in protected sites would show evidence for an efficient MPA with further analyses of the three CSI components (or nine individual variables) pointing to specific benefits over unprotected sites. Equal or larger CSI values in unprotected sites would define inefficient MPAs.

We used general additive mixed models (GAMMs; Wood, 2017) to analyze ecoregion (i.e., Alboran Sea, Canary Is., Atlantic, and Western Mediterranean) and protection (i.e., protected and unprotected) effects on CSI_{global}, $CSI_{biomass}$, $CSI_{diversity}$, and $CSI_{relevant}$ components. Here, GAMM models were fitted using ecoregion and protection as fixed factors and sampling sites nested with protection as random factors to account for hierarchical pseudoreplication. Moreover, we selected GAMM models because we can correct the spatial autocorrelation including latitude and longitude as tensor product interaction covariable (Wood, 2017). All statistical analyses were conducted in R software environment (R Core Team, 2015) using mgcv package for GAMM (Wood, 2017). We tested three null hypotheses: no interaction between ecoregion and protection, no CSI differences between protected and unprotected sites, and no CSI differences among the four ecoregions. Because we defined MPA efficiency as the difference in CSI between protected and unprotected sites, a significant protection factor indicated efficient (or inefficient) MPAs, while a significant interaction term stressed spatial inconsistencies in MPA efficiency (or inefficiency). In other words, the model actually tested for the role of geography (ecoregion) in CSI, MPA efficiency (protection), and reliability of MPA efficiency across ecoregions (interaction).

Afterward, we tested the differences in MPA efficiency matrix between the four marine ecoregions by using permutational multivariate analysis of variance with the function "*Adonis*" of vegan package (Oksanen et al., 2016). Here, we applied Euclidean distance to the matrix comprising $CSI_{biomass}$, $CSI_{diversity}$, and $CSI_{relevant}$ variables with 999 permutations. The pairwise comparisons between ecoregions were calculated using "*adonis.pairwise*" function from the EcolUtils package (Salazar, 2015). We also calculated and plotted MPA efficiency as the CSI effect size of protection (protected minus unprotected sites). By examining the effect size of the three CSI components and corresponding standardized variables, we also quantified whether MPAs were more efficient in some specific benefits and whether such benefits remained consistent across the ecoregions. All the results are reported as mean ± standard error for protected and unprotected areas. The supplementary data and the R codes used to compute the CSI index are in the Git repository: https://github.com/Sanabria-Fernandez/Conservation-Status-Index

3. Results

3.1. Global conservation status index (CSI_{global})

MPA efficiency was unreliable and varied significantly with the ecoregions (Table 3, CSI_{global}, p interaction < 0.001, Fig. 3a). We found larger CSI values in protected areas than in unprotected areas in the Canary Is. (4.51 ± 0.42 and 2.70 ± 0.11; $t = 5.06$, $p < 0.001$) and Western Mediterranean (2.94 ± 0.19 and 1.87 ± 0.07; $t = 3.09$,

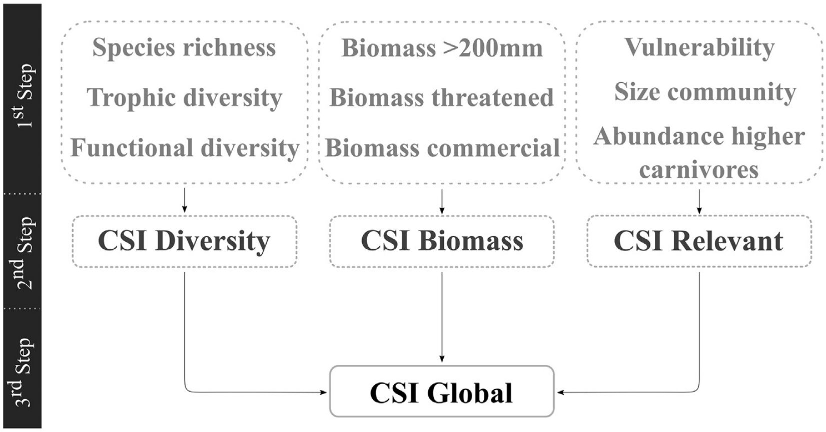

Fig. 2. Summary of the hierarchical structure followed to calculate the CSI_{global}. We used nine individual variables that were standardized to give equal weight to each variable. Second, related variables were pooled to generate the $CSI_{diversity}$, $CSI_{biomass}$, and $CSI_{relevant}$. The CSI_{global} is the sum of the $CSI_{diversity}$, $CSI_{biomass}$, and $CSI_{relevant}$.

Table 3
General additive mixed model (GAMM) on CSI_{global}, $CSI_{diversity}$, $CSI_{biomass}$, and $CSI_{relevant}$ as a function of marine ecoregion (four levels) and protection status (two levels). A significant interaction factor supports for spatial unreliability in MPA efficiency for that variable. A significant protection factor supports for significant MPA efficiency. See text for details of individual indexes.

Variable	Effect	F	*p*-Value
CSI_{global}	Ecoregion	2.786	0.041
	Protection	0.714	0.399
	Ecoregion ∗ Protection	8.895	< 0.001
$CSI_{biomass}$	Ecoregion	1.941	0.125
	Protection	5.281	0.022
	Ecoregion ∗ Protection	7.090	< 0.001
$CSI_{diversity}$	Ecoregion	0.267	0.849
	Protection	0.014	0.904
	Ecoregion ∗ Protection	1.055	0.368
$CSI_{relevant}$	Ecoregion	4.777	0.002
	Protection	0.598	0.439
	Ecoregion ∗ Protection	6.905	< 0.001

$p = 0.002$) ecoregions and no CSI_{global} differences in the Atlantic (2.57 ± 0.54 and 1.83 ± 0.06; $t = 1.39$, $p = 0.163$) and Alboran Sea (2.56 ± 0.12 and 2.27 ± 0.13; $t = 0.84$, $p = 0.4$) ecoregions (Fig. 3a). The Canary Is. had the largest protection effect size (1.818), followed by the Western Mediterranean (1.069), Atlantic (0.737), and Alboran Sea (0.286) ecoregions (Figs. 3a and 6).

3.1.1. Biomass conservation status index ($CSI_{biomass}$)

MPA efficiency was unreliable and varied significantly with the ecoregions (Table 3, $CSI_{biomass}$, p interaction < 0.001, Fig. 3b). We found larger $CSI_{biomass}$ values in protected areas than in unprotected areas only in two out of four ecoregions (Fig. 3b): Alboran Sea (1.01 ± 0.09 and 0.66 ± 0.06; $t = 2.28$, $p = 0.022$) and the Canary Is. (1.9 ± 0.16 and 0.87 ± 0.07; $t = 4.21$, $p < 0.001$). There were no significant differences in the Western Mediterranean (1.12 ± 0.11 and 0.56 ± 0.05; $t = 1.73$, $p = 0.083$) and Atlantic (0.74 ± 0.21 and 0.55 ± 0.02; $t = -0.14$, $p = 0.88$) ecoregions. Specifically, the biomass > 200 mm was significantly greater with protection (0.33 ± 0.01 and 0.24 ± 0.01; $F = 10.31$, $p = 0.001$), and the biomass of commercial species showed significant differences at the ecoregion level, for example, in the Canary Is. (average = 0.28 ± 0.01) and Western Mediterranean (average = 0.25 ± 0.01); ($F = 5.07$, $p = 0.001$) ecoregions. The biomass of threatened species varied significantly between protected and unprotected areas irrespective of the ecoregion ($F = 8.84$, p interaction < 0.001). Alboran Sea (0.45 ± 0.08 and 0.21 ± 0.05) and the Canary Is. (0.40 ± 0.06 and 0.26 ± 0.06) showed the highest values inside the protected areas.

3.1.2. Diversity conservation status index ($CSI_{diversity}$)

We did not find significant differences in the $CSI_{diversity}$ among the studied ecoregions nor between ranges of protection (0.85 ± 0.02 and 0.79 ± 0.01; Table 3, Fig. 3c). An independent analysis of $CSI_{diversity}$ components showed that only species richness ($F = 12.07$, $p < 0.001$) and trophic diversity ($F = 3.73$, $p = 0.01$) exhibited significant differences between the ecoregions. However, there was a significant ecoregion ∗ protection effect over functional diversity ($F = 3.3$, p interaction = 0.02).

3.1.3. Relevant conservation status index ($CSI_{relevant}$)

There was a significant interaction between ecoregion and protection for relevant conservation status index (Table 3, $CSI_{relevant}$, p interaction < 0.001, Fig. 3d). We found larger $CSI_{relevant}$ values in protected areas than in unprotected areas in three out of four ecoregions (Fig. 2d): the Canary Is. (1.51 ± 0.25 and 0.83 ± 0.05; $t = 4.41$, $p < 0.001$), the Atlantic (1.22 ± 0.36 and 0.80 ± 0.05; $t = 2.03$, $p = 0.042$), and the Western Mediterranean (0.88 ± 0.11 and

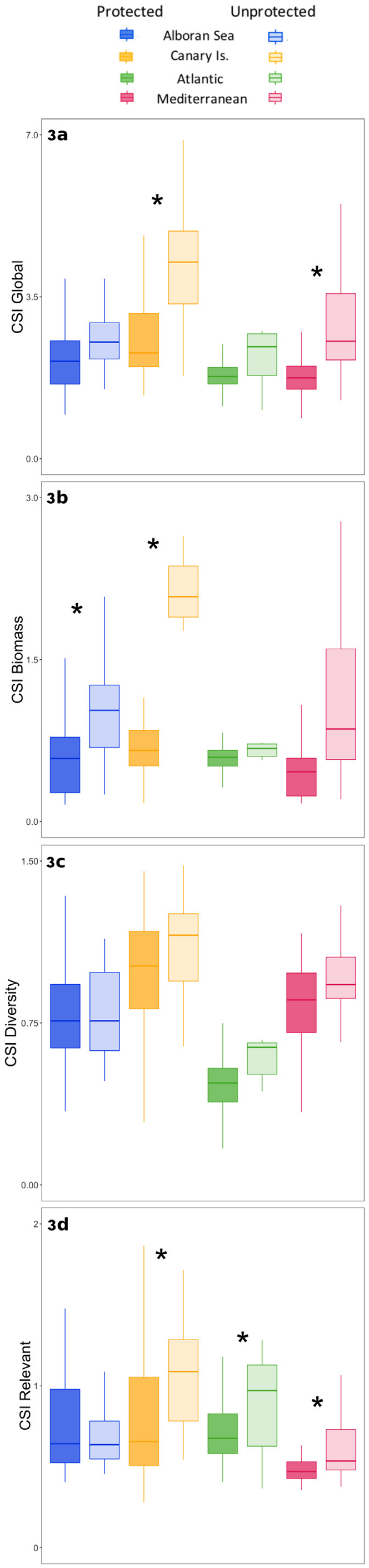

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Fig. 3. Boxplots representation of the conservation status index ($\mathrm{CSI}_{\mathrm{global}}$, 3a; $\mathrm{CSI}_{\mathrm{biomass}}$, 3b; $\mathrm{CSI}_{\mathrm{diversity}}$, 3c; and $\mathrm{CSI}_{\mathrm{relevant}}$, 3d) in protected and unprotected areas of the four ecoregions investigated in our study. * indicates significant differences ($p < 0.05$) between protected and unprotected areas within each ecoregion. See Table 3 for the statistical details.

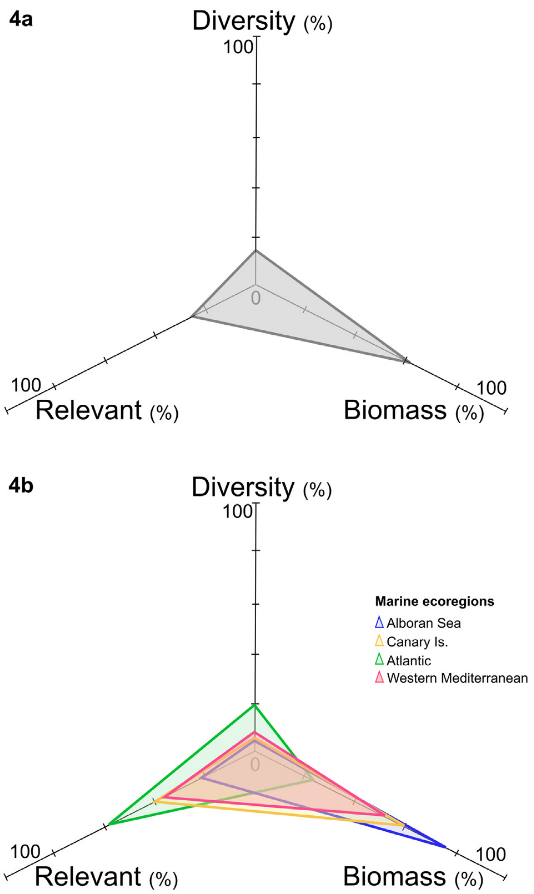

Fig. 4. (A). Percentage contribution of the three components of diversity, biomass, and other relevant traits to the total MPA efficiency. (B). Percentage contributions as in (A) but disclosed for each ecoregion.

0.49 ± 0.01; $t = 3.151$, $p = 0.001$). However, there were no $\mathrm{CSI}_{\mathrm{relevant}}$ differences in the Alboran Sea (0.74 ± 0.06 and 0.84 ± 0.07; $t = -0.77$, $p = 0.441$). In detail, the vulnerability ($F = 3.21$, p interaction = 0.02), size community ($F = 5.58$, p interaction < 0.001) and the abundance of higher carnivores ($F = 6.13$, p interaction < 0.001) varied significantly with the ecoregions. For more information on the $\mathrm{CSI}_{\mathrm{biomass}}$, $\mathrm{CSI}_{\mathrm{diversity}}$, $\mathrm{CSI}_{\mathrm{relevant}}$, and $\mathrm{CSI}_{\mathrm{global}}$ values of each protected and unprotected area, see Table S1.

3.2. *Marine protected areas efficiency*

Overall, the three components of biomass, diversity, and relevant contributed 60.01%, 14.41%, and 25.58%, respectively, to MPA efficiency (Fig. 4a). These contributions varied significantly between ecoregions ($F = 26.59$, $p < 0.001$, Fig. 4b), with $\mathrm{CSI}_{\mathrm{biomass}}$ being the largest contributor in three out of four ecoregions and $\mathrm{CSI}_{\mathrm{diversity}}$ in none of them (Fig. 4b). Biomass of threatened species (48.7%) and abundance of higher carnivores (26.9%) were the largest contributors to MPA efficiency (Fig. 5). Biomass of large fish (9.3%), trophic diversity (8%), and species richness (7.4%) were less important contributors to MPA efficiency, while the contribution of the remaining variables was either marginal or negative, i.e., biomass of commercial fish (2.1%), vulnerability (0.1%), functional diversity (−1.1%), and fish size (−1.4%) (Fig. 5). Biomass of threatened species was consistently a major contributor to MPA efficiency, although the magnitude of the contribution varied largely among ecoregions (from 81.1% in Alboran Sea to 19.3% in the Atlantic, Fig. 6). Vulnerability was consistently a minor contributor, with positive or negative effect sizes close to zero in all ecoregions (Fig. 6). The contribution of the remaining variables to MPA efficiency was highly unreliable among the ecoregions (Fig. 6).

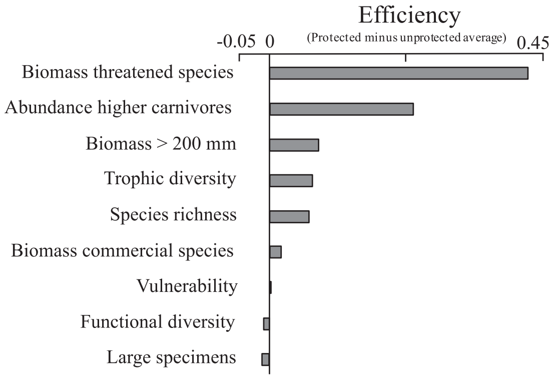

Fig. 5. MPA efficiency, defined as the effect size between protected and unprotected areas, for each of the nine variables investigated in our study.

4. Discussion

MPAs are becoming one of the most prevalent tools to promote biodiversity conservation and sustainable use of marine resources (Gaines et al., 2010; Spalding et al., 2013). Available evidence supports for multiple benefits of protection and points to ineffective MPA management when benefits are missing (Rife et al., 2013). These arguments may lead to believe that MPAs would excel at all their multiple roles under good management practices. Although good management is imperative for effective protection, MPAs differ in many aspects that could contribute to differences in their degree of efficiency at one or multiple roles regardless of their management practices (Villamor and Becerro, 2012). Here, we analyzed nine protection benefits in numerous MPAs of four marine ecoregions of the world and tested whether MPA efficiency was reliable or varied as a function of ecoregion. Our results showed the existence of large differences in MPA efficiency across ecoregions, with varying degree of efficiency at protecting multiple roles. Our results warned against the belief that implementation of an MPA may lead to the achievement of every protection-related benefit as we still lack predictive knowledge on how protection benefits apply into specific protected areas. Our approach may help quantify the degree of achievement of MPA objectives and the circumstances under which MPAs accomplish certain benefits more efficiently.

MPA efficiency varied significantly between ecoregions. We found effective MPAs with larger CSI values in protected areas than in unprotected areas in the Canary Is., Western Mediterranean, and Atlantic ecoregions and ineffective MPAs in the Alboran Sea ecoregion. MPAs in the Canary Is. were the most efficient in our study area, driven by high CSI values in protected areas as compared to those in the remaining geographic regions. Although the causes underlying the good conservation status of MPAs in the Canary Is. are diverse, the high fishing pressure throughout unprotected areas in the archipelago (García-

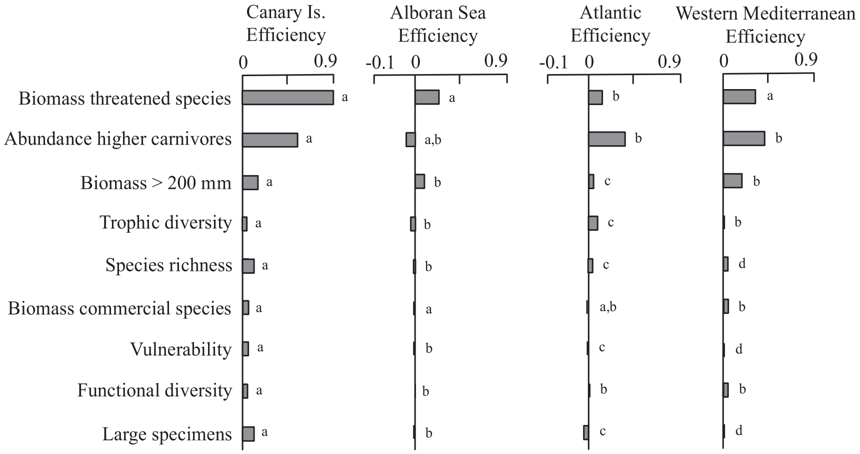

Fig. 6. MPA efficiency, defined as the effect size between protected and unprotected areas for each ecoregion for each of the nine variables investigated in our study. Letters show significant differences between ecoregions for each of the nine variables investigated. Statistical results based on the "*Adonis*" (vegan package in R; Oksanen et al., 2016) and "*Adonis.pairwise*" (EcolUtils package in R; Salazar, 2015). See text for additional details.

Mederos et al., 2015) and the decrease in density of the voracious sea urchin *Diadema africanum* and associated regime shifts in protected areas (Sangil et al., 2012) are likely contributors. Difficulties in surveillance, enforcement, and monitoring may underlie the inefficiency of MPAs in the Alboran Sea ecoregion, as it occurs in other vast offshore MPAs in the ocean (Wilhelm et al., 2014). In addition, the major unprotected sampled points in this ecoregion have been conducted in the Spanish coastal zone; hence, a gap exists in the unprotected Moroccan coastal area. An extensive sampling survey in the northern African coast is needed to shed light on the effects of protection in the Alboran Sea ecoregion.

Biomass-related traits were the largest contributors to MPA efficiency in our study, which was mostly explained by the contribution of the biomass of threatened species within the studied MPAs. The strong positive effect of protection on the biomass of threatened species (49% efficiency) was in contrast with the weak effect of protection on the biomass of commercial species (2% efficiency). Further, the biomass of threatened species was consistently a major contributor to MPA efficiency, while the contribution of the biomass of commercial species to MPA efficiency varied substantially between ecoregions. In the Atlantic ecoregion, the biomass of threatened species was the second major contributor to MPA efficiency. Although the Atlantic is a hotspot of threatened fish species (Nieto et al., 2015), biomass was minor because threatened species were accidental in our sampling stations. These results contrasted with the specific goals of the 22 MPAs investigated in this study. Twelve out of 22 MPAs included commercial fish stock restoration as a specific goal, while only 1 MPA (Cabo de Creus, Western Mediterranean) was designed to protect endangered species. It seems, therefore, that the sought-after goal of fish stock restoration is at risk in the MPAs investigated herein, making these MPAs an unreliable tool to protect coastal fisheries in our study area. Increased biomass of commercial fish species is a common benefit of protection (Barrett et al., 2007; Fenberg et al., 2012; Parravicini et al., 2014; Campbell et al., 2017; Pérez-Ruzafa et al., 2017) and failure to achieve this goal may rely on the small-size of no-take zones, as suggested by other studies (Claudet et al., 2008). The biomass of large fish (> 200 mm) was similar within the studied MPAs from the Canary Is. and Western Mediterranean. However, this biomass was surprisingly lower in the Alboran Sea and Atlantic ecoregions, though these ecoregions are characterized by a high productivity. Hence, the efficiency of MPAs regarding biomass is reliable but showed a high spatial variability among ecoregions, perhaps due to suboptimal MPA surveillance to control illegal fishing.

The effect of protection on fish diversity was reliable but small in the studied MPAs. MPAs were not only a successful conservation tool to preserve biodiversity but, they also seemed to promote an increase in biodiversity within the studied protected areas. Our results suggest that MPAs may function as both biodiversity conservation and restoration areas. European MPAs have demonstrated evidence of preserving biodiversity of local ecosystems (Fenberg et al., 2012) through the re-establishment of biological variables, e.g., trophic interactions that characterized unfished ecosystems. The importance of functional diversity has recently increased in the marine realm because of the advantages of using functional traits as surrogates of the status of coastal environments (Stuart-Smith et al., 2013); further, it has been demonstrated that functional diversity greatly contributes to the stability of marine communities (Bates et al., 2013). In our study, functional diversity showed the highest values in the Canary Is. ecoregion though we found no differences associated with protection in the studied ecoregions.

MPA efficiency on other traits associated with the fish community was highly variable among the ecoregions. We found higher $\mathrm{CSI}_{\mathrm{relevant}}$ values in protected areas than in unprotected areas of the Canary Is., Western Mediterranean, and Atlantic. These differences were mostly driven by the abundance of higher carnivores, which was the second largest contributor to MPA efficiency in our study. Our results showed large abundances of higher carnivores within MPAs, which is likely a consequence of the impact of fishing on the density and structure of fish assemblages (Clemente et al., 2009; Guidetti et al., 2014). Yet, the Alboran Sea showed higher abundances of higher carnivores in unprotected areas. Illegal fishing associated with suboptimal surveillance could lead to these unexpected results in the Alboran Sea. Vulnerability was a minor contributor to MPA efficiency regardless of the ecoregion, probably because of the dominance of species with low vulnerability and high to medium resilience in the studied ecoregions, as it has been shown in other coastal environments (Vasconcelos et al., 2017). Vulnerability showed slightly higher values in protected areas than in unprotected areas of the Canary Is. (1.7%), which is likely to be associated with larger fish size (5.6%). The effect of protection on fish vulnerability was virtually nonexisting in the remaining ecoregions.

The lack of a consistent trend regarding MPA efficiency in the studied ecoregions may be explained by the high spatial unreliability of most of the variables investigated in our study. Except for the biomass of threatened species and vulnerability, the remaining seven variables showed high spatial variability that prevented reliable protection effects. This spatial variability is multifaceted because it is dependent upon fish characteristics, such as fish mobility and spill-over effect (Pérez-Ruzafa et al., 2008; Le Quesne and Codling, 2009) and features regarding protection measures (Edgar et al., 2014) such as size of no-take zones (Claudet et al., 2006), time of creation (Babcock et al., 2010), and enforcement (Brown et al., 2017). The lack of expected benefits in the studied MPAs may be partially explained by the geographic variations of unreliability among ecoregions because these benefits need to be considered at a broad scale. Former studies have demonstrated that MPA characteristics such as number of years of protection, size, isolation, and surveillance are significant factors for the effective operation of MPAs (Stewart et al., 2009; Edgar et al., 2014).

In short, we have found that MPA efficiency greatly varied among the ecoregions because some variables were more reliable than others, but we still lack predictive knowledge to understand how the multiple benefits of protection apply to specific MPAs. Our study showed that traits associated with fish biomass contributed the most to MPA efficiency, but the magnitude of the effect was unreliable. Contrarily, traits associated with fish diversity were minor but reliable contributors to MPA efficiency. Because we used nine distinct variables to calculate CSI values and multiple MPAs in each of the four ecoregions investigated, our MPA efficiency was ecologically and geographically inclusive, allowing for a broader view than more localized studies with fewer numbers of variables or MPAs.

5. Conclusions

The present study showed that MPA efficiency was unreliable and varied with ecoregion, highlighting contrasting differences between effective and ineffective MPAs in multiple geographic areas. Biodiversity conservation, the largest conservation goal present in 17 out of 22 MPAs in our study, is a benefit that MPAs reliably provide in our study area, even though the magnitude of the effect is small. Biomass-related traits were the largest contributors to MPA efficiency, yet the effect of protection on the magnitude of these traits was highly variable. Much work is needed to be done to have a successful fish stock restoration goal in our study area. A 2% MPA efficiency on the biomass of commercial fish species seems to be a low benefit for the second largest protection goal present in 12 out of 22 MPAs in our study. Understanding the environmental and management reasons for this failure is critical to bring this figure more in line with its relevance. On the contrary, MPAs in our study were highly efficient to increase over 60% the biomass of threatened species—a goal only present in one of the 22 MPAs investigated in our study. Different conservation needs between commercial and threatened species might be responsible for such contrasting levels of efficiency. Our approach also represents an opportunity to assess the circumstances under which some variables positively respond or fail to respond to protection. Additionally, because our approach integrates multiple variables grouped in several categories, we could easily incorporate other socio-economic variables to evaluate educational, economic, or cultural benefits associated with MPAs, which along with ecological variables would provide a more comprehensive and accurate vision of the actual roles that MPAs play in our socio-ecological systems.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2019.04.015.

Acknowledgements

This work was supported by the Spanish Ministry of Economy grant MARINERES [grant number CGL2013-49122-C3-1-R], and Josu G. Alday was supported by Ramón y Cajal fellowships (RYC-2016-20528). Besides, we are deeply grateful to the Spanish Ministry of Defense, specifically to “Grupo de Regulares de Melilla n52” and “Regimiento Mixto de Artillería n32” for the strong support to access remote military locations including Peñón Vélez de la Gomera and Archipiélago de Alhucemas. Additional thanks to General Secretary for Fisheries, for their help with sampling permits and logistics in Spanish Marine Protected Areas. We also thank Laura Palacín, Pedro Figueroa, Ángel Orozco, and Club Ánfora de Actividades Subacuaticas (Melilla), and the Reef Life Survey Spain diver community for their help during field surveys. We deeply appreciate the constructive comments of the anonymous reviewer that helped to improve the quality of our study.

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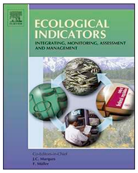
Ecological Indicators 107 (2019) 105565

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Original Articles

Quantifying patterns of resilience: What matters is the intensity, not the relevance, of contributing factors

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ARTICLE INFO

Keywords:
Factor relevance
Alboran Sea
Marine resilience indicators
Temperate rocky reefs
Resilience-based management

ABSTRACT

Ecological resilience, broadly defined as the magnitude of the disturbance a system needs to shift to an alternative stable state, is becoming a critical trait in the Anthropocene era. However, we are far from having baseline resilience data to guide decision makers toward more resilient ecological systems. In the last decade, the resilience assessment framework has taken a sum of products approach to obtain a resilience indicator based on the relevance and the intensity of multiple factors. While factor intensity relies on quantitative data, estimates of factor relevance rely on ordinal data with a lesser understanding of their relative importance to resilience, which may have consequences in the value of the resilience indicator. Here, we computed three resilience indicators to test for the quantitative impact that changes in factor relevance might cause to the resilience indicator. We defined the Inclusive Resilience Indicator of a Site (*IRIS*) as a relevance-free indicator based exclusively on factor intensity. We also computed the *Relative Resilience Potential* (*RRP*) and an *RRP* with random relevance values (RRP_{rrv}) as indicators based on both intensity and relevance. To calculate these three indicators in rocky reefs of the Alboran Sea, we quantified 17 biological, environmental, and human-related factors known to influence resilience. We used correlation analyses, Linear Mixed Models, and Generalized Additive Models to compare the three resilience indicators and to examine their spatial patterns. We found highly significant positive correlations between the *RRP*, RRP_{rrv}, and *IRIS* indicators ($r > 0.9$, $p < 0.001$ for all comparisons). All three indicators had equivalent resilience values ($p = 0.440$), provided non-significant differences in their predictions ($p = 0.097$), and exposed the same resilience gradients in the Alboran Sea ($p < 0.001$ for all indicators). *IRIS* accounted for 94% and 99% of the variance associated with *RRP* and RRP_{rrv}, respectively, suggesting that the intensity-based *IRIS* can estimate resilience without the uncertainties associated with factor relevance. The new *IRIS* indicator proposed in our study may facilitate the acquisition of baseline data needed to further advance in the ecological and management implications of marine resilience.

1. Introduction

Resilience is a broad and complex concept that is increasingly getting the attention of many research disciplines, from mental health (Hu et al., 2015) to economics (Martin, 2012) or politics (Gladfelter, 2018) (Fig. 1). Notably, resilience science has come through in environmental and ecological research (Fig. 1), becoming a very active field that has resulted in many understandings of the same broad concept of resilience. Originally, ecological resilience referred to the ecosystem ability to cope with change without shifting to an alternative stable state (Holling, 1973). Other definitions focus on the ecosystem capacity to resist and to recover from disturbance (engineering resilience, Walker et al., 1969; Holling, 1996). The concept of resilience has evolved over the years integrating numerous levels of comprehension (see Müller et al., 2016 and references therein) and biological organization (Gunderson and Holling, 2002; Micheli et al., 2012; Rice et al., 2013). Along with this conceptual development, we also have a great variety of empirical observations with a high diversity of approaches (Müller et al., 2016). These advancements provide, for example, increased appreciation of the multiple factors that regulate resilience (Bernhardt and Leslie, 2013; Barnett and Baskett, 2015; Ling et al., 2014; Oliver et al., 2015; van de Leemput et al., 2018), which is the first step toward a better understanding of natural patterns of resilience and an opportunity for more resilient ecosystems through proper management actions. Both topics are critical because, despite the progress in this field, quantification of resilience remains somehow elusive in ecological systems. Lack of resilience data prevents further development of this research area and hinders management, as it is hard to manage what is not measured (Spears et al., 2015).

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https://doi.org/10.1016/j.ecolind.2019.105565
Received 16 November 2018; Received in revised form 8 July 2019; Accepted 11 July 2019
1470-160X/

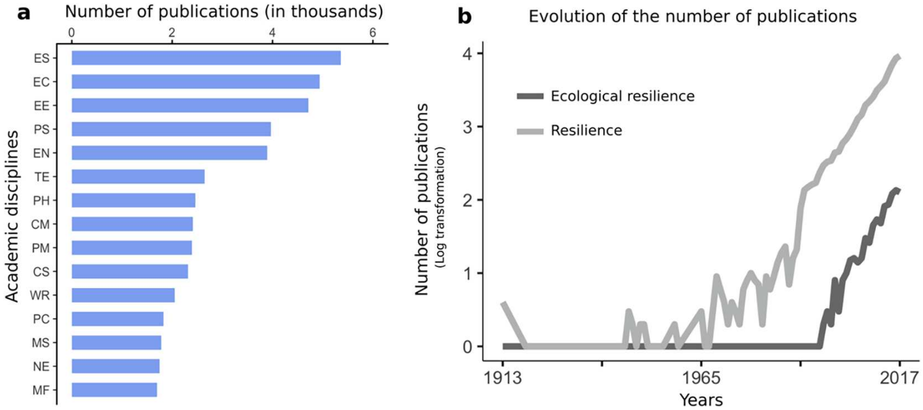

Fig. 1. (a) Top 15 disciplines in the ISI Web of Science core collection based on the number of papers with the term "Resilience" in the title or abstract: (ES) Environmental sciences, (EC) Ecology, (EE) Engineering electrical electronic, (PS) Psychiatry, (EN) Environmental studies, (TE) Telecommunications, (PH) Public environmental occupational health, (CM) Computer science theory methods, (PM) Psychology multidisciplinary, (CS) Computer science information systems, (WR) Water resources, (PC) Psychology clinical, (MS) Multidisciplinary sciences, (NE) Neurosciences, (MF) Marine freshwater biology. (b) Total number of publications in the ISI Web of Science core collection with the terms "Resilience" (light gray) and "Ecological resilience" (dark gray) in the title, abstract, or keywords of the scientific article over the last 104 years.

Resilience also is a sought-after ecosystem trait, from the conservation and management perspective, particularly relevant in an era when human-driven activities have raised biodiversity loss to mass extinction levels (Barnosky et al., 2011; Pimm et al., 2014). Resilience can offer relevant information on the current status of natural communities and on their risk of collapse (Holling, 1973; Obura, 2005) or it can be a useful tool to identify locations with strong recovering capacity. As an example, organizations such as the Convention on Biological Diversity seeks to enhance ecosystem resilience (Aichi Biodiversity Target 15, Leadley et al., 2014) and the United Nations Environment Programme World Conservation Monitoring Centre includes resilience as one of four design principles in marine protected areas (UNEP-WCMC, 2008). The UNEP-WCMC also warns about the current knowledge gap in marine resilience and urges to take steps to resolve it (UNEP-WCMC, 2008). Unfortunately, a decade later, the resilience status of marine ecosystems remains unknown (Díaz et al., 2019).

As a complex concept, quantifying resilience is a challenge that needs integration of numerous factors including biological, environmental, or anthropogenic (Maynard et al., 2010; Maynard et al., 2015). Specifically, factors determine the ecological resilience of a system (Thrush et al., 2009; McClanahan et al., 2012; Timpane-Padgham et al., 2017) including biological (Gunderson, 2000; Rice et al., 2012; Ling et al., 2014), environmental (Wernberg et al., 2009; Maynard et al., 2010; Wernberg, 2010; McClanahan et al., 2012), and anthropogenic elements (Levin and Lubchenco, 2008; Piola and Johnston, 2008; Gladstone et al., 2013). A compelling, meaningful resilience indicator should include multiple factors of the biological, environmental, and anthropogenic dimensions of resilience so that the influence of a single factor does not bias the broader resilience concept. Based on this knowledge and rationale, the resilience assessment framework established an approach to calculate a site-specific resilience indicator with strong management implications (Maynard et al., 2010). The approach has been adapted and used to assess resilience in several tropical locations (Ladd and Collado-Vides, 2013; Maynard et al., 2015). In contrast, studies on the ecological resilience of temperate rocky reefs are scarce (Behrens and Lafferty, 2004; Strain et al., 2015) and mostly focused on the response to climate change (Bates et al., 2013; Bernhardt and Leslie, 2013) or overfishing in kelp forests (Steneck et al., 2002; Ling et al., 2009). The need for site-specific quantitative resilience data in temperate systems is clear, as phase shifts are occurring in many temperate systems worldwide (Ling et al., 2014; Wernberg et al., 2016).

The resilience assessment framework could be instrumental in gaining knowledge about the resilience of temperate systems. Although the resilience assessment method embraces the ecological resilience definition of Holing, (1973), their indicator does not quantify the exact magnitude needed for a specific disturbance to shift the local system to an alternative stable state. Their approach is broader and relies on the relative contribution of multiple individual factors to the overall resilience of a site (Maynard et al., 2010). Thus, the resilience assessment framework approach quantifies the *Relative Resilience Potential* indicator, which can be used to expose resilience patterns (Maynard et al., 2010). The contribution of each factor is the product of two components that estimate a) the relative importance of each factor to resilience (i.e., factor relevance) and b) the impact of each factor to a site (i.e., factor intensity). The overall resilience indicator of a site takes a sum of products approach as the sum of the contributions of every factor (Maynard et al., 2010; Ladd and Collado-Vides, 2013; Maynard et al., 2015). The current definition of the *Relative Resilience Potential* indicator relies on truly quantitative data to estimate factor intensity and ordinal data to estimate factor relevance (Maynard et al., 2015). Although the ordinal data are based on the best available ecological information on resilience (Obura and Grimsditch, 2009; McClanahan et al., 2012; Graham et al., 2015; Maynard et al., 2015), we have a limited understanding of the relative importance of factor relevance to resilience (Maynard et al., 2015). For example, although factor relevance can vary spatially and ordinal data should be re-evaluated accordingly (Maynard et al., 2010), factor relevance has been used as a constant at the local and regional scales investigated in previous studies (Maynard et al., 2010; Ladd and Collado-Vides, 2013; Maynard et al., 2015). As a quantitative indicator, the *Relative Resilience Potential* indicator is somehow restricted by the uncertainties associated with the ordinal nature of factor relevance.

A resilience indicator without the factor relevance limitations would prove more reliable as it would be free of the possible restrictions associated with our current incapacity to accurately quantify factor relevance. In the present study, we proposed a novel resilience indicator based exclusively on factor intensity, the *Inclusive Resilience Indicator of a Site* (*IRIS*), and compared its performance with the latest iteration of the *Relative Resilience Potential* indicator (*RRP*, Maynard et al., 2015). We also computed an *RRP with randomized relevance values* (RRP_{rrv}) to further investigate the effect that the ordinal values of factor relevance have on the resilience indicators. We hypothesized that there were no

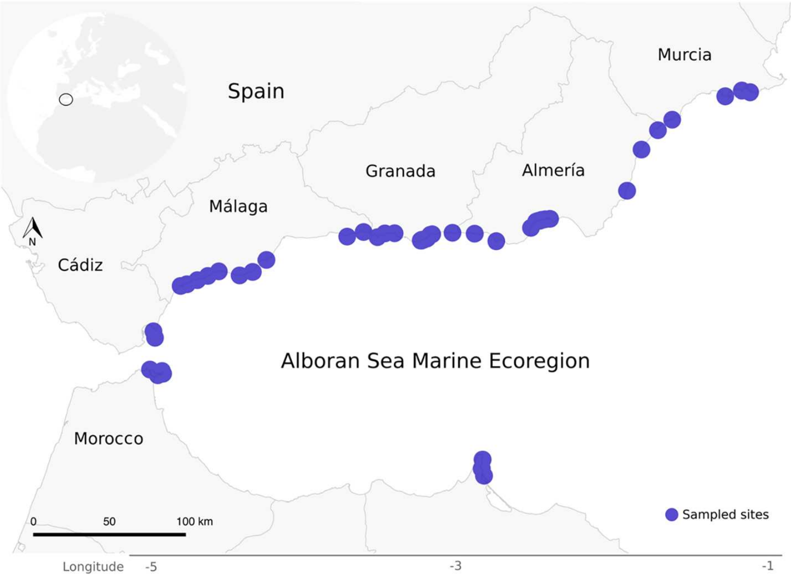

Fig.2. Map of the study area in the Alboran Sea marine ecoregion. The circles represent the sampled sites (N = 54).

differences between the three resilience indicators (first null hypothesis) and, consequently, that the three resilience indicators exposed the same pattern of resilience (second null hypothesis). Failure to reject these hypotheses would make the more straightforward intensity-based *IRIS* indicator better suited to provide baseline resilience data to help track natural patterns of resilience and the consequences that management actions have on the resilience of our oceans.

2. Material and methods

2.1. Study area and field survey

The Alboran Sea marine ecoregion of the world (hereafter the Alboran Sea) is located in the western Mediterranean basin, spreading from the Gibraltar Strait to Cartagena in the Iberian Peninsula and to Arzew Gulf in Algeria (Spalding et al., 2007, Fig. 2). The strong Atlantic influence makes this Mediterranean region unique, with high productivity and diversity differentiated from the western Mediterranean (IUCN, 2009).

We used the Reef Life Survey underwater protocol (Edgar and Stuart-Smith, 2014) to identify and quantify the abundance of fish, invertebrate, and sessile species in 54 unprotected sites spread over 500 km of the Alboran sea, from Gibraltar to Cartagena including some locations in North Africa. Briefly, we used underwater visual surveys to run three quantification methods along the same 50 m-long tape. The first method used a 10 m-wide transect centered along the 50 m-long tape (Edgar and Stuart-Smith, 2014) to identify and estimate the abundance of all conspicuous fish (total length over 2.5 cm). Then, we identified all mobile benthic invertebrates > 2.5 cm in a 2 m-wide transect centered along the same 50 m-long tape (method 2). Finally, we took 20 photographs evenly distributed every 2.5 m along the same 50 m-long tape to calculate the percent cover of sessile organisms and bare rock (method 3). All surveys were above 15 m deep to minimize the variation of coastal communities associated with depth.

2.2. Resilience factors justification

In this paper, we referred to the overall resilience metrics as indicators and used the term (contributing) factor(s) to refer to the quantitative variables used to calculate the indicators (Table 1). We also summarized all the initialisms used in our study in Table 2 to facilitate access to their full description.

The resilience assessment framework uses a sum of products approach that relies on the relevance and intensity of multiple factors to estimate the *Relative Resilience Potential* indicator of a site (*RRP*, Maynard et al., 2010; Ladd and Collado-Vides, 2013). We selected 17 contributing factors that are known to affect the resilience of temperate systems (Table 1). We used the best evidence available in the literature to estimate the direction and strength of the influence between each contributing factor and resilience in temperate systems (Table 1). We classified Factor Relevance (hereafter *FR*) as highly, moderately, or slightly relevant. Factors with a strong influence on resilience classified as highly relevant. Factors with a weaker influence on resilience or with higher uncertainty classified as moderately relevant. Factors with the weakest influence on resilience classified as slightly relevant. Finally, we assigned an FR value of 3, 2, and 1 to highly, moderately, and slightly relevant contributing factors, respectively (Table 1).

The intensity of a factor relied on the actual measurement (truly quantitative data) of each factor in each site. In our study, Factor Intensity (hereafter *FI*) was the normalized value (between 0 and 1) of the quantitative measurement.

2.3. Resilience indicators computation

In our study, we tested whether changes in the criteria to assign ordinal values to factor relevance may lead to differences in resilience, i.e., we tested for the importance of factor relevance in the resilience indicators. To do so, we used 17 contributing factors to calculate three resilience indicators with varying criteria to assign FR values. First, we calculated the *Relative Resilience Potential* (*RRP*), a resilience indicator that takes into account both the relevance (*FR*) and intensity (*FI*) of every factor. The *RRP* assigns *FR* values based on the available ecological literature on resilience (Maynard et al., 2015). Second, we calculated a modified version of the *RRP* that used randomized FR values (RRP_{rrv}) rather than values based on the best ecological evidence. Finally, we calculated the *Inclusive Resilience Indicator of a Site* (*IRIS*), which is an intensity-based resilience indicator that did not consider factor relevance. An irrelevant *FR* role should render no differences

Table 1

Justification, quantification, and link to increased resilience of the 17 factors contributing to resilience. Factors were selected based on the best available resilience literature in temperate systems. All 17 factors were used to compute the three resilience indicators used in our study.

FR - Factor relevance	Contributing factor	Rationale and supporting literature	Factor quantification	Link to increased resilience	Data source
Highly relevant (FR = 3)	Macroalgal cover (MC)	Macroalgae are essential components of littoral rocky reefs in temperate seas. They are primary producers providing oxygen and tridimensional habitat for invertebrate and fish (Mann, 1973; Dayton, 1985; Carr, 1989; Poloczanska et al., 2007; Giakoumi et al., 2012; Strain et al., 2015).	We analyzed the MC in 20 high-quality photographs taken along 50 m-long transects in each site. In each photograph, we used a centered digital square of 400 cm^2 to randomly select 5 points (Cresswell et al., 2017) using CPCe software (Kohler and Gill, 2006). We calculated percent cover as the number of algal points over the total number of points for each transect (1 0 0).	↑ MC	Method 3 of Reef Life Survey
	Fishing pressure (FP)	Overfishing is causing the degradation and fragmentation of marine communities (Micheli and Halpern, 2005; Baskett et al., 2006; Ling et al., 2009; Barnett and Baskett, 2015).	We quantified FP as the total number of metric tons fished yearly in each province divided by the longitude of the coast (km).	↓ FP*	Andalusian Multi-Territorial Information System (https://www.juntadeandalucia.es/institutodeestadisticaycartografia/sima/index2.htm)
	Anthropogenic pollution (AP)	Pesticides, chemical, metal, and liquid pollutants increase the likelihood of disease in macroalgae, invertebrates, and fishes (Folke et al., 2004; Levin and Lubchenco, 2008; Piola and Johnston, 2008; Wernberg et al., 2009).	We quantified the number of sewage emissaries in the vicinity of our sampling sites (≤5km).	↓ AP*	MAPA Ministry Spanish Government (https://www.mapa.gob.es/es/)
	Community richness (CR)	Species richness is intrinsically linked to community stability (Yachi and Loreau, 1999; Bernhardt and Leslie, 2013; Borja et al., 2013).	We quantified the number of fish and invertebrate species present in our sampling sites.	↑ CR	Method 1 & 2 of Reef Life Survey
	Invertebrate herbivory (IH)	Increased abundance of invertebrate herbivores, i.e., sea urchins, is shifting macroalgae dominated communities to barren grounds (Ling et al., 2014; Kraufvelin, 2017).	We used the total abundance of sea urchins in each site (*Arbacia lixula*, *Paracentrotus lividus*, and *Sphaerechinus granularis*) as an estimate of IH intensity.	↓ IH*	Method 2 of Reef Life Survey
	Sea urchin fish predators (SUFP)	The abundance of fish species that feed on juvenile or adult sea urchins, controls sea urchin populations and contributes to enhancing macroalgal cover (McClanahan, 1995; Shears and Babcock, 2002; Guidetti and Dulčić, 2007; Clemente et al., 2010).	We used the total abundance of the 8 fish species in our species list known to feed on sea urchins as an estimate of the intensity of the fish top-down control on sea urchins. See Supplementary Table 1 for the list of species.	↑ SUFP	Method 1 of Reef Life Survey & FishBase information (www.fishbase.com)
	Abundance of top predators (ATP)	The abundance of top predator fishes is a proxy of ocean health. Their presence and abundance point to more resilient, fully functional communities (Jackson, 2001; Crowder and Norse, 2008; Llope et al., 2011).	We used the total abundance of 16 fish species categorized as higher carnivores to estimate ATP in each of our sampling sites. See Supplementary Table 2 for the list of species.	↑ ATP	Method 1 & Method 2 of Reef Life Survey) & FishBase information (www.fishbase.com)
Moderately relevant (FR = 2)	Free anthropogenic physical pressures (FPP)	Impacts from divers, snorkelers, or anchors increase the susceptibility of disease in macroalgae and invertebrates (Claudet et al., 2010; Gladstone et al., 2013; Riera et al., 2016; Siciliano et al., 2016).	We quantified the total number of dive centers within a distance of 10 km from each sampling site.	↓ FPP*	Database of Spanish Underwater Activities (www.bajoelagua.com)
	Fish functional diversity (FFD)	High values of functional diversity provide marine communities a better response to disturbance since the system is likely to have traits that enhance recovery (Folke et al., 2004; Bates et al., 2013; Nash et al., 2017).	We used the {FD} package in R (Laliberté et al., 2014) to calculate FFD using thermal physiology, life history strategy, feeding ecology, behavior, habitat use, and geographic range breadth traits (total of 10).	↑ FFD	Method 1 of Reef Life Survey & FishBase information (www.fishbase.com)
	Trophic redundancy (TR)	Redundancy of fish species in trophic levels confers robustness because trophic groups remain functional despite the loss of a species (Folke et al., 2004; Micheli and Halpern, 2005; Rice et al., 2012).	We categorized every fish species (68 in total) as planktivore, benthic invertivore, browsing herbivore, higher carnivore, and scrapers. See Supplementary Table 3 for the classification of all fish species found in our study.	↑ TR	Method 1 of Reef Life Survey & FishBase information (www.fishbase.com)
	Vulnerability of the fish community (VFC)	Fish are major components of most marine communities. Fish vulnerability depends on	We calculated VFC as the average of the vulnerability (estimates from FishBase) of every fish	↓ VFC*	Method 1 of Reef Life Survey & FishBase information (www.fishbase.com)

(*continued on next page*)

Table 1 (*continued*)

FR - Factor relevance	Contributing factor	Rationale and supporting literature	Factor quantification	Link to increased resilience	Data source
		intrinsic traits (Cheung et al., 2007; Hughes et al., 2005; Berkes et al., 2006).	specimen observed in each site (community-weighted mean).		
	Human population (HP)	Ocean sprawl, recreational fishing activities, or water pollutants are directly related with the size of human population and have strong impacts on biodiversity and resilience (Borja et al., 2013; Ladd and Collado-Vides, 2013; Sanabria-Fernandez et al., 2018).	We used the total number of inhabitants of the municipality of the sampling site.	↓ HP*	Andalusian Multi-Territorial Information System (https://www.juntadeandalucia.es/institutodeestadisticaycartografia/sima/index2.htm)
	Sea urchin invertebrate predators (SUIP)	The abundance of invertebrate species that feed on juvenile or adult sea urchins controls sea urchin populations and contributes to enhancing macroalgal cover (Shears and Babcock, 2002; Clemente et al., 2007). Contrary to SUFP above, we classified SUIP as moderately relevant because of the reduced mobility of invertebrates.	We used the total abundance of the four invertebrate species in our species list that are known to feed on sea urchins (*Charonia lampas, Charonia tritonis, Coscinasterias tenuispina*, and *Marthasterias glacialis*) as an estimate of the intensity of the invertebrate top-down control on sea urchins.	↑ SUIP	Method 2 of Reef Life Survey
Slightly relevant (FR = 1)	Proximity to the nearest city (PNC)	Although the area of influence of human activities reaches the whole planet, some impacts on the environment get diluted with increasing distance to the source (Stuart-Smith et al., 2008; Borja et al., 2013).	We quantified in meters the distance in a straight line between our sampling sites and the nearest city.	↑ PNC	Quantum Geographic Information System software (QGIS, 2018)
	SSTmax deviation (SSTD)	Deviation from the average maximum sea surface temperature (SSTmax) is a major cause of stress in marine organisms, increasing their susceptibility to disease (Wernberg et al., 2009; Wernberg, 2010).	We calculated SSTD as the difference between the SSTmax value of a site and the average of the SSTmax values of all 54 sites in our study.	↓ SSTD*	Bio-ORACLE Database (www.bio-oracle.org)
	Nitrate deviation (ND)	Nitrates play a major role in marine productivity. Anthropogenic activities are increasing the nitrate concentration of marine systems, often leading to eutrophication (Wernberg et al., 2009; Strain et al., 2015).	We calculated ND as the difference between the ND value of a site and the average of the ND values of all 54 sites in our study.	↓ ND*	Bio-ORACLE Database (www.bio-oracle.org)
	Phosphate deviation (PHD)	Phosphates also play a major role in marine productivity. Anthropogenic activities are increasing the phosphate concentration of marine systems, often leading to eutrophication (Wernberg et al., 2009).	We calculated PHD as the difference between the PHD value of a site and the average of the PHD values of all 54 sites in our study.	↓ PHD*	Bio-ORACLE Database (www.bio-oracle.org)

* We used 1 – the normalized value of the factor so that larger factor values were always associated with increased resilience.

Table 2
Initialisms used in our study with their full name.

Initialisms	Full name
RRP	Relative Resilience Potential
RRP_{rrv}	Relative Resilience Potential with random relevance values
IRIS	Inclusive Resilience Indicator of a Site
FR	Factor Relevance
FI	Factor Intensity
FCR	Factor Contribution to Resilience

between the three indices.

2.3.1. Relative resilience Potential (RRP)

The *RRP* is a resilience indicator defined by Maynard et al. (2015) as:

$$RRP = \sum_{k=1}^{N} (FR_k \times FI_k)$$

where k refers to each contributing factor, *FR* is factor relevance, *FI* is factor intensity, and N is the total number of factors.

The *FI* value was the min–max normalized value of each contributing factor. Thus, *FI* values of each of the 17 contributing factors ranged between 0 and 1, regardless of their original units. The product $FI \times FR$ measured the *Factor Contribution to Resilience* (*FCR*), and the sum of all 17 *FCRs* provided the estimate of the resilience of a site. Final *RRP* values ranged between 0 and 1 as they were min–max normalized again.

2.3.2. Relative resilience Potential with random relevance values (RRP_{rrv})

The RRP_{rrv} was the average of 1004 *RRP* values. Most *RRP* values (1000) were calculated assigning random *FR* values of 1 to 3 rather than the corresponding value based on the best available evidence. The remaining 4 *RRP* values were the observed *RRP* value (as explained in the previous section) and the expected *RRP* value obtained if all factors had the same *FR* of 1, 2, or 3.

2.3.3. Inclusive resilience indicator of a site (IRIS)

Conceptually, we defined *IRIS* as the *RRP* value when all *FR* equaled one. Thus, *IRIS* values accounted for just factor intensity, i.e., factor relevance had no influence on *IRIS*. In practice, we defined *IRIS* as

$$IRIS = \frac{\sum_{k=1}^{N} FI_k}{N}$$

where k refers to each contributing factor, *FI* is factor intensity, and N is the total number of factors. As for the *RRP*, *FI* values were the min–max normalized value of each contributing factor. Contrary to *RRP*, we divided the sum of all *FIs* over the total number of contributing factors ($N = 17$ in our study). Thus, possible *IRIS* values ranged between 0 and 1, but these maximum and minimum values were extremely unlikely to occur since a single site should have the maximum (or minimum) values for all contributing factors. The lack of normalization in the final computational step in *IRIS* differed from that in the *RRP* (and RRP_{rrv}) approach and did not force *IRIS* values to spread toward the end values of the range. The R code of the IRIS indicator is available in the next git repository: https://github.com/Sanabria-Fernandez/Inclusive-Resilience-Indicator-of-a-Site-IRIS-.

2.4. Statistical analysis

To test for the first hypothesis of our study, we used Linear Mixed Effects Models (LMEs) using the “nlme” R package (Pinheiro et al., 2018). We tested for differences in resilience values as a function of the resilience indicator (fixed effect factor with three levels: *RRP*, RRP_{rrv}, and *IRIS*) and site (random effect factor with 54 levels). LMEs allowed estimating and accounting for the covariance among sites to address the spatial pseudoreplication associated with this type of sampling design. We also tested for differences in the coefficient of variation between resilience indicators using “cvequality” R package (Marwick and Krishnamoorthy, 2018). To test whether the three resilience indicators behaved similarly, we evaluated their coefficients of determination with *lm()* function of “stats” (R Core Team, 2016).

To test for the second hypothesis of our study (spatial patterns of resilience in the Alboran Sea) we used Generalized Additive Models (GAMs) with the “Gam” R package (Hastie, 2017). To do so, we computed a GAM for each resilience indicator (*RRP*, RRP_{rrv}, and *IRIS*) using a loess smoothing function with longitude as a factor (Zuur et al., 2009). GAMs were selected applying the Akaike Information Criteria (Zuur et al., 2009). To test whether resilience indicators differed in their predictive capacity, we tested whether the GAM fit values and their coefficients of variation differed between resilience indicators using the same methodology explained earlier. We also used the coefficients of determination to test whether the values predicted by the three resilience indicators behaved similarly.

Finally, to analyze the factors that contributed the most to high and low resilient areas, we selected those sites with the highest or lowest 5% of the resilience values. We, then, analyzed the contribution of each factor to the final resilience indicator (i.e., their *FCRs*). For this assessment, we used only the *IRIS* indicator, so the *FCRs* equaled to factor intensity (*FI*). We set up a threshold *FI* value of 0.8 or 0.2 to identify the most relevant factors. Factors with an *FI* higher than or equal to 0.8 had a large influence to increase resilience values, while factors with an *FI* lower than or equal to 0.2 had a large influence to decrease resilient values. We performed the statistical analyses in R software (R Core Team, 2016).

3. Results

The 17 resilience factors used to calculate the three resilience indicators in our study were complementary (average of the correlation coefficients = 0.019). We found no differences in resilience values between the three resilience indicators (*RRP*, RRP_{rrv}, and *IRIS*, $p = 0.44$, Table 3a, Fig. 3a). Resilience indicators differed in their coefficients of variation ($p < 0.001$, Fig. 3a), with *IRIS* showing a lower coefficient of variation than *RRP* and RRP_{rrv} (in percentage, 15.48, 41.98 and 40.85, respectively). The three resilience indicators were highly correlated ($R > 0.9$ and $p < 0.001$ for all comparisons, Fig. 4a, b) and we found significant longitudinal gradients in resilience with all three indicators ($p < 0.01$ for all indicators, Table 4, Fig. 5). The percentage of deviance explained varied between resilience indicators (in percentage, $RRP_{rrv} = 67.0$, $IRIS = 37.0$, and $RRP = 24.5$).

We found no differences in the fitted values predicted by the GAMs for the three resilience indicators ($p = 0.097$, Table 3b, Fig. 3b). Predicted resilience values differed in their coefficients of variation ($p < 0.001$, Fig. 3b), with *IRIS* showing the lowest coefficient of variation (in percentage, 8.04, 41.98, and 40.85 for *IRIS*, *RRP*, and RRP_{rrv}, respectively). Fitted resilience values for the three resilience indicators were strongly correlated ($R > 0.8$ and $p < 0.001$ for all comparisons, Fig. 4c, d) and all three GAMs predicted the same spatial pattern of

Table 3
Linear Mixed Effects Model (LME) on (a) observed and (b) fitted resilience values as a function of the resilience indicator (fixed factor, *RRP*, RRP_{rrv}, and *IRIS*) and site (random factor, 54 sites). Fitted values resulted from significant GAMs.

(a)	LME–observed resilience values	*DF*	*F-value*	*p-value*
	Intercept	159	1279.6	< 0.001
	Resilience indicator	159	0.82	0.440
(b)	LME–fitted resilience values	*DF*	*F-value*	*p-value*
	Intercept	159	3662.7	< 0.001
	Resilience indicator	159	2.36	0.097

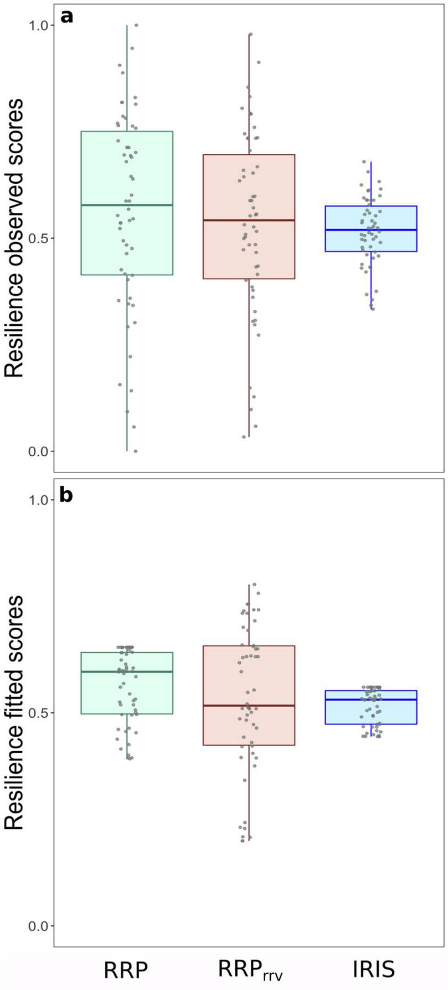

Fig.3. Boxplot representations of the *RRP*, *RRP$_{rrv}$*, and *IRIS* resilience indicators. (a) Observed resilience values. (b) Fitted resilience scores obtained by significant GAMs. Gray dots show the actual observed or fitted resilience values for each site.

resilience with low resilient areas at longitudes between −5° and −4° and high resilient areas at longitudes between −3° and −2° (Fig. 5). IRIS categorized in low, medium, regular, and high resilience showed a longitudinal pattern (Fig. 6). Anthropogenic physical pressures, anthropogenic pollution, human population, invertebrate herbivory, and fishing pressure contributed highly to high resilient areas (Fig. 7a). Sea urchin invertebrate predators, proximity to the nearest city, phosphate deviation, abundance of top predators, fishing pressure, invertebrate herbivory, and nitrate deviation contributed highly to low resilient sites (Fig. 7b).

4. Discussion

Resilience, first defined as the persistence of systems (Holling, 1973), is a critical ecosystem trait with substantial implications in management. Despite the extensive development of the resilience research in ecology, site-specific quantitative estimates of resilience remain elusive, hindering the development of this field. International programs such as the Convention on Biological Diversity or the United Nations Environmental Program actively support the acquisition of resilience data (Aichi Biodiversity Target 15, Leadley et al., 2014). And yet, the recent global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services brought to light the lack of awareness on this particular field (Díaz et al., 2019). Finding pragmatic solutions to build a resilience baseline is, therefore, essential. The resilience assessment framework has successfully quantified the relative resilience potential of some tropical reefs, and its approach could undoubtedly contribute to generating resilience data (Maynard et al., 2010; Ladd and Collado-Vides, 2013; Maynard et al., 2015). In our study, we embraced the resilience assessment approach to quantify resilience, analyzed the relative resilience potential indicator, and simplified its computation to propose a new resilience indicator that it is easier to calculate and could support the acquisition of broadscale resilience data (Fig. 8).

The resilience assessment framework takes a sum-of-products approach to calculate an indicator of the relative resilience potential of a site that adds together the multiplicative effect of the relevance and the intensity of multiple factors known to contribute to resilience (Maynard et al., 2010; Ladd and Collado-Vide, 2013; Maynard et al., 2015). While factor intensity relies on actual quantitative data, factor relevance relies on ordinal data that are categorized based on available literature (McClanahan et al., 2012). Lack of information on the relevance of some factors and the uncertainties associated with wrong assignments could deter otherwise interested scientists and policymakers from generating resilience data. In our study, we tested whether an intensity-based resilience indicator (*IRIS*) could function as the current *Relative Resilience Potential* indicator of reference (*RRP*, Maynard et al., 2015), which would get rid of the least supported and most dubious section of the indicator. We found that the intensity-based *IRIS* had similar resilience values and detected and predicted the same longitudinal resilience pattern than the *RRP*. Further, an *RRP* calculated with random factor relevance values (*RRP$_{rrv}$*) was also equivalent to the original *RRP,* which used ordinal values assigned to each factor after reviewing the literature. We, therefore, accepted our null hypothesis of no difference between the three resilience indicators investigated in our study. We also accepted our second hypothesis as the three indicators exposed the same pattern of resilience in the Alboran Sea. These results are supported by the strong positive correlation between *IRIS* and *RRP*, despite *IRIS* having less variation and no data on factor relevance. Our study also revealed a small number of highly influential factors contributing to the high and low resilient areas in the Alboran Sea. These factors were strongly and negatively associated with human activities prone to management practices (e.g., eutrophication or fishing). Based on our results, we recommend the use of *IRIS* as a suitable indicator to assess resilience in temperate rocky reefs (Fig. 8).

There are a large variety of approaches to estimate the complex concept of resilience. A number of studies approximate to resilience with related ideas such as ecosystem degradation, stability, or phase shifts (Steneck et al., 2002; Thibaut and Connolly, 2013). Other studies focus on the resilience to specific factors such as storms or temperature (Wernberg, 2010; Bates et al., 2013) and others investigate statistical concepts to obtain generic indicators of resilience not often used in the field (Dakos et al., 2015; Scheffer et al., 2015). Although many of these and other studies discuss the implications of their findings to resilience, few studies empirically estimate the broader concept of resilience. With the diversity of approaches available, the need for a resilience assessment framework that allows comparable quantification of resilience is clear (Nyström et al., 2008).

Supported by a number of studies on the factors that affect the capacity of coral reefs to cope with disturbance (Salm et al., 2001; West and Salm, 2003) and the interest to establish a protocol to measure resilience (Obura 2005; Obura and Grimsditch, 2009), Maynard et al. (2010) established a resilience assessment framework that has allowed ranking coral reef sites as a function of resilience (Maynard et al., 2010; Ladd and Collado-Vides 2013; Maynard et al., 2015). The approach

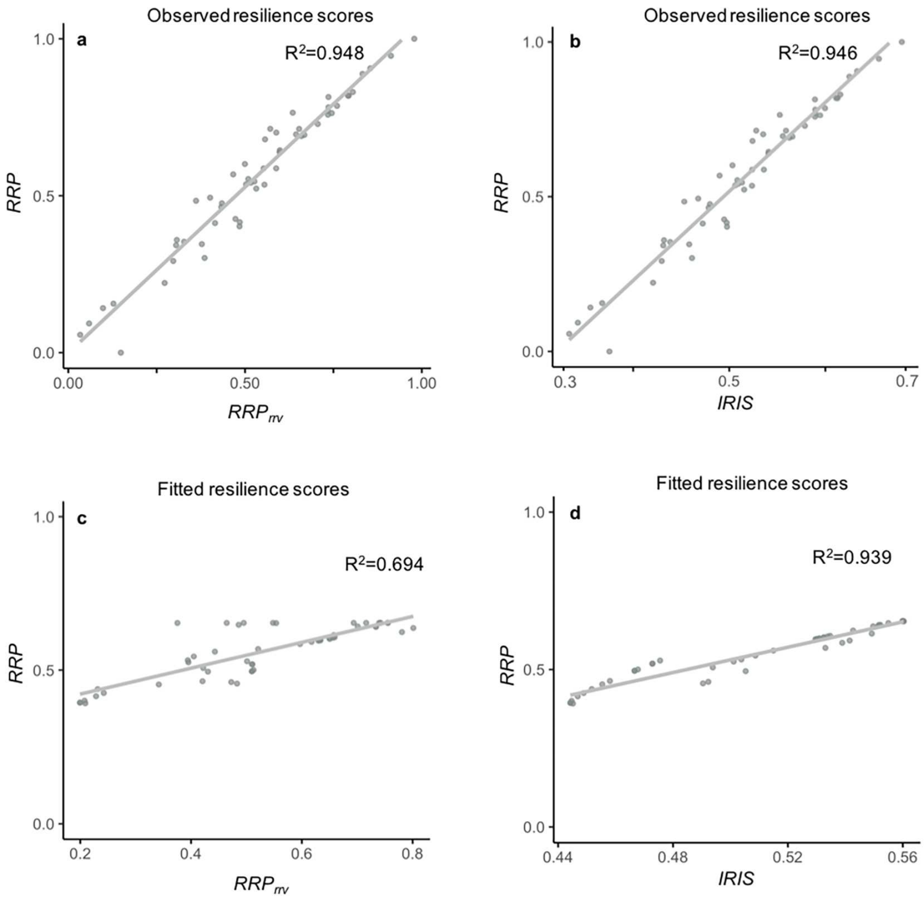

Fig.4. Relationship between the *RRP*, RRP_{rrv}, and *IRIS* resilience indicators. Graphics (a) and (b) based on observed resilience values. Graphics (c) and (d) based on fitted resilience scores obtained by significant GAMs.

Table 4
Generalized Additive Model (GAM) on observed resilience values with geographical longitude as a factor. We ran an independent GAM for each resilience indicator (*RRP*, RRP_{rrv}, and *IRIS*).

(a)	*RRP*	*DF*	Mean Sq	*F-value*	*p-value*
	Longitude	2	0.11	2.6	0.001
	Residuals	49.91	0.040		
(b)	RRP_{rrv}	*DF*	Mean Sq	*F-value*	*p-value*
	Longitude	2	0.26	11.5	< 0.001
	Residuals	36.42	0.020		
(c)	*IRIS*	*DF*	Mean Sq	*F-value*	*p-value*
	Longitude	2	0.03	8.5	< 0.001
	Residuals	49.91	0.004		

taken by the resilience assessment framework to quantify resilience is very encouraging. First, it uses a large number of factors known to contribute to resilience, avoiding a strong influence from a single factor (e.g., temperature). Second, since not all the factors contribute the same to resilience neither they are constant in space nor time (McClanahan et al., 2012), the resilience assessment framework uses an indicator that accounts for both the relevance and the intensity of every contributing factor (Maynard et al., 2015). Third, factor intensity uses min–max normalized values of the factors, so that the factors' original units or scales have no influence on factor intensity nor on the overall resilience metric. Fourth, the approach can be easily extrapolated to other locations, regions, or systems of interest (Maynard et al., 2015). To do so, it is necessary to adjust the list of contributing factors to include those driving resilience in the area of interest (Maynard et al., 2015). It may also be necessary to re-assess the relative importance of the contributing factors and re-evaluate factor relevance based on appropriate ecological literature for the area of interest (Maynard et al., 2010).

Meanwhile, our knowledge of the ecological resilience of rocky reefs is limited (Díaz et al., 2019). Our priority was to adapt the resilience assessment framework approach to temperate rocky reefs. In our study, we used 17 contributing factors to calculate resilience, which is similar to the number of factors used in other studies using the resilience assessment framework (Maynard et al., 2010; Ladd and Collado-Vides, 2013; Maynard et al., 2015). Ecological evidence in temperate systems allowed adjusting the list of contributing factors more easily than estimating *FR*. Contrary to the considerable information on *FR* in the tropics, the relative importance of the factors contributing to resilience is less investigated in temperate systems and created uncertainties in our criteria to assign the ordinal *FR* values. Our results showed that, as currently estimated, *FR* plays a minor role in the *RRP* indicators. Resilience values failed to differ between the *RRP* and the RRP_{rrv}. Since RRP_{rrv} used a random assignment of *FR* values rather than the *RRP* assignments based on the ecological evidence, variation in the criteria to establish the relevance of certain factors seems to have little impact on the resilience indicator. Resilience values also failed to differentiate between the *RRP* and the relevance-free *IRIS*, suggesting a negligible

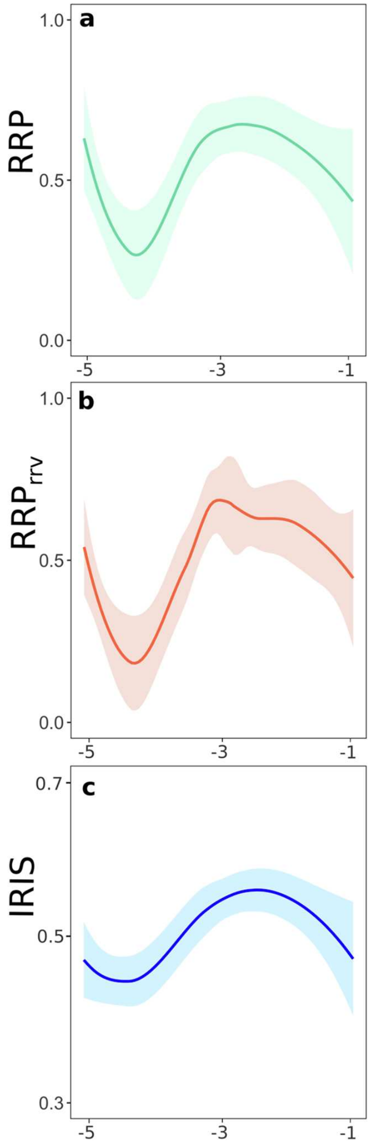

Fig.5. Longitudinal gradient of the (a) *RRP*, (b) *RRP$_{rrv}$*, and (c) *IRIS* resilience indicators along the Alboran Sea. Mean and 95% confidence intervals obtained by significant GAMs.

role of *FR* in the resilience values. Given the constant nature of *FR* and the sum-of-products nature of the *RRP*, *FR* could potentially introduce a three-fold difference in *RRP* values (i.e., when all *FR* values equaled one vs. all *FR* values equaled three). In practice, this is impossible since there are multiple factors with *FR* values of one to three.

An additional consequence of the constant nature of *FR* is that factor intensity (*FI*) is the source of resilience variation between sites. The strong positive correlations found between the three resilience indicators in our study further illustrated this influence. The implications are far from trivial. Since it is *FI* (and not *FR*) what currently drives the patterns of resilience, struggling with the uncertainties (and possible deterrent effects) associated with *FR* to advance in our ecological understanding of resilience is completely unnecessary. It is realistic to argue that *FR* will play the same role than *FI* when we advance in our capacity to obtain site-specific quantitative estimates of *FR*. As for now, our study showed that the three resilience indicators found the same longitudinal pattern of resilience and predicted the same expected resilience values along the longitudinal gradient of the region despite the intensity-based *IRIS* used no *FR* data.

The simplicity of the intensity-based *IRIS* could facilitate the collection of widespread resilience data to understand patterns and trends in resilience and promote resilience-based management. However, the capacity of the *IRIS* to quantify resilience is not a free meal and has a number of limitations. *IRIS* relied on a quantitative database of 17 independent environmental, social, and biological factors, which may be challenging to collect. Of course, factors need to vary, as a constant variable would contribute to the final resilience values but not to the resilience patterns. The need for variation is also associated with site ranking. *IRIS* (and *RRP*) provides a relative value of resilience as it is based on the normalization (i.e., ranking) of sites. The relative nature of *IRIS* can be an important limitation, as resilience values are dependent on i) the exact contributing factors and ii) the actual sites used in the study. Given the large number of factors contributing to resilience that are used in the resilience assessment approach, we believe that the final resilience value of a site is robust enough as to not vary significantly with a small variation in the number (or nature) of the contributing factors. Similarly, given a large enough number of sites, we believe that the resilience pattern exposed would remain the same, despite changes in the actual sites selected in the study. A simple corollary of this limitation seems clear: the more number of contributing factors and the more number of sites, the better. Beyond its limitations, the relative nature of *IRIS* also is a strength, as resilience has to be assessed as relative when producing rankings meant to inform decisions (Maynard et al., 2010). In fact, previous studies using the resilience assessment framework have strong management implications (Walker et al., 2002, Maynard et al., 2010, Ladd and Collado-Vides, 2013, Maynard et al., 2015). The simplicity of the intensity-based *IRIS* could facilitate the collection of widespread resilience data to understand patterns and trends in resilience and promote resilience-based management, for example in the Andalusian coastal marine social-ecological systems (Lazzari et al., 2019). Moreover, *IRIS* could be easily adapted to report species-specific resilience levels, to target threatened, invasive, or commercially interesting species rather than the whole community (Micheli et al., 2012).

Additionally, *IRIS* could point to high resilient sites worth preserving, as for example, sites with high *IRIS* values or sites with low *IRIS* values but prone to improvements through management actions. In our study, the longitudinal patterns of resilience exposed two specific geographic areas with high and low resilience sites, respectively. We found that high resilient sites had low population density, low anthropogenic pollution, low physical and fishing pressures, and a large abundance of invertebrate herbivores. Areas with no fishing pressures are known to have increased resilience (Barnett and Baskett, 2015) and sea urchins are known to function as drivers of resilience in temperate rocky reef systems (Ling et al., 2009). However, the abundance of invertebrate herbivores was also a relevant factor in low resilient sites, so its contribution to the differences between high and low resilient sites was minimal. Low resilient sites were close to cities, had high nitrate and phosphate concentrations, a large fishing pressure, and a low abundance of top predators. A high abundance of top predators is associated with high resilient sites (Llope et al., 2011). Proximity to nearby cities and fisher access points also influence fish communities (Stuart-Smith et al., 2008) and ocean sprawl reduces the number and abundance of many benthic and sessile species, which could play an important role in the resilience of the system (Sanabria-Fernandez et al., 2018). The influential factors found in our study are prone to management practices that could result in increased resilience, providing an example of how our *IRIS*-based approach can help prioritize specific management actions to increase resilience. Biological factors such as (functional) diversity (Bates et al., 2013), trophic redundancy

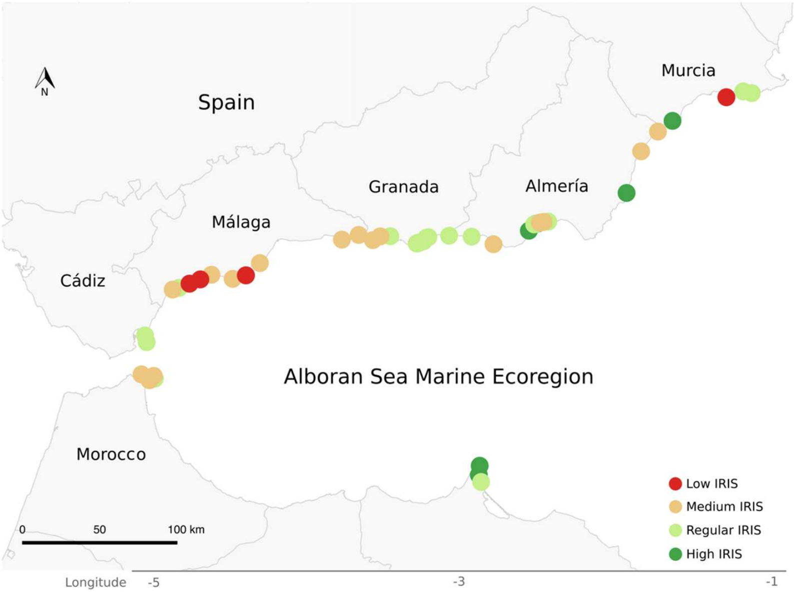

Fig.6. Map of the observed *IRIS* values in the Alboran Sea. We colored sites with low (red), medium (orange), regular (soft green), and high (dark green), *IRIS* values to better convey the information. See text and Table 4 for more information on the significant resilience gradients observed with *RRP*, RRP_{rrv}, and *IRIS*.

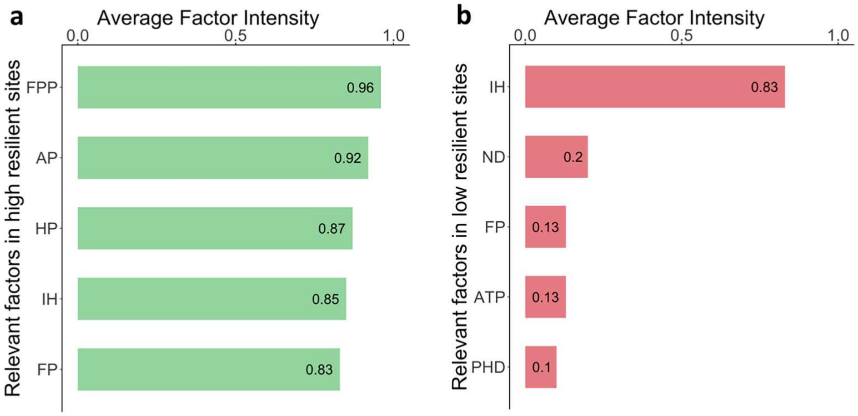

Fig.7. Average factor intensity (*FI*) values of the most relevant factors contributing to high (a) and low (b) resilient sites. We defined the most relevant factors as those with an *FI* ≥ 0.8 or an *FI* ≤ 0.2. Notice we found no factor with an *FI* ≤ 0.2 in high resilient sites. Invertebrate herbivory was the only factor with an *FI* ≥ 0.8 in low resilient sites, but also contributed to high resilient sites. (FPP) Anthropogenic physical pressures, (AP) Anthropogenic pollution, (HP) Human population, (IH) Invertebrate herbivory, (ND) Nitrate deviation, (FP) Fishing pressure, (ATP) Abundance of top predators, and (PHD) Phosphate deviation.

(Micheli and Halpern, 2005; Rice et al., 2012), macroalgal cover (Carr, 1989; Poloczanska et al., 2007) or environmental factors such as temperature (Wernberg et al., 2009; Wernberg, 2010) played a less influential role in the resilience of the Alboran sea marine ecoregion of the world.

5. Conclusion

The intensity-based *Inclusive Resilience Indicator of a Site* (*IRIS*) was as reliable and accurate as the *Relative Resilience Potential* (*RRP*) used by the resilience assessment framework, which is based on both factor intensity and factor relevance. Our study showed evidence that, as currently estimated, factor relevance played a negligible role in resilience, as supported by the non-significant differences between the three indicators and by the same spatial pattern of resilience they exposed along the Alboran Sea. We also showed that the inconsequential capacity of factor relevance to influence resilience was restricted to the final quantitative resilience value and only factor intensity accounted for the variation in resilience between sites. *IRIS* accounted for 94% and 99% of the variance of RRP and RRP_{rrv}, respectively. We, therefore, suggest that the intensity-based *IRIS* can produce proper baseline resilience data to increase our understanding of the spatial and temporal patterns in resilience, which can help boost resilience-based management decisions. Indeed, our *IRIS*-based analysis of the most influential factors contributing to the resilience of the Alboran sea suggests that improved management practices to reduce eutrophication and fishing pressures could boost the resilience of this diverse ecoregion of the world.

Acknowledgments

The Spanish Ministry of Economy grant MARINERES provided funds to support this research [grant number CGL2013-49122-C3-1-R]. We are deeply grateful to Ángel Orozco from the Club Ánfora de Actividades Subacuaticas (Melilla), Francisco Javier Galán Jaramillo from Burbujas PADI Dive center (Ceuta), and Alejandra Pérez from

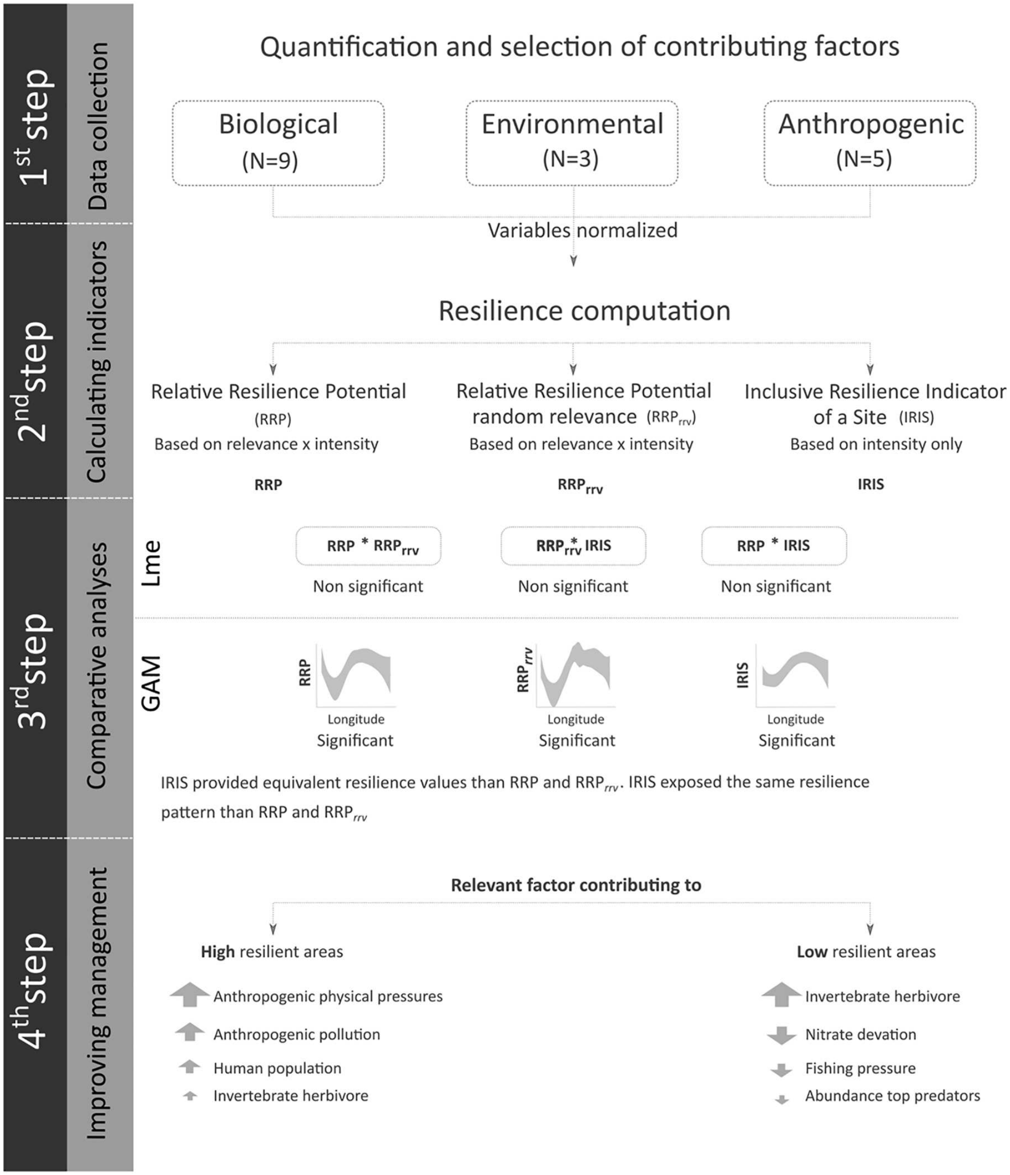

Fig.8. Workflow of our study with the four essential steps, most relevant methods, and main results.

Aquatours Almeria PADI Dive center for their logistic support. We also thank the active diver community of Reef Life Survey Spain for their help during field surveys. We deeply appreciate the constructive comments from the anonymous reviewers that helped improve the quality of our study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105565.

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Resilience = ↑ resistance ↓ resilience
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Resiliencia = 1 - 1 = 0
R = 0 ↑ Resistance
R = 1 ↓ resistance
T1
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+ Resistance = 5 - 1 / 5 = 0'8 (Δ final hay +) Tratado
- Resistance = 1 - 5 / 5 = -0'8 (Δ final hay -) No tratado
Logging
R = 1 - 5 / 5
Cover
density
High density low cover
state1
state2
human density
Regime 1
Regime 2
MA cover
Fixed factor (R1, R2)
NAR = Natural - Artificial / max(Natural, Artificial)