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XXX CICLO DEL DOTTORATO DI RICERCA IN

AMBIENTE E VITA

ASSESSMENT OF ACIDIFICATION IMPACTS IN THE MEDITERRANEAN SEA: FROM META-ANALYSIS TO ECOSYSTEM SERVICES VALUATION

Settore scientifico-disciplinare: **BIO/07**

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Abstract

Since the industrial revolution and the extensive use of fossil fuels, oceans worldwide have absorbed about a quarter of the anthropogenic CO_2 released by human activities. The continued uptake of CO_2 from the atmosphere alters the carbonate chemistry of the oceans and increases the concentration of hydrogen ions, thereby reducing pH, a phenomenon called ocean acidification (OA).

Ocean acidification is expected to cause significant changes in the marine environment over the coming century leading to relevant effects on the biological, biogeochemical and ecological components of the marine environment, as well as potentially relevant – but still not fully quantified – consequences on related socio-economic dimensions.

The aim of the work is to analyse the effects of ocean acidification in the Mediterranean Sea from organisms responses to the ecosystems functioning levels. In particular, this work focuses on two important habitats, the coralligenous formations and *Posidonia oceanica* meadows, and investigates the provisioning and cultural services provided by these habitats. Among the relevant services in the context of OA, we analyse provisioning services using fisheries landing indicators and a food web model and cultural services using values related to the scuba-diving tourism. These assessments are applied to the Italian seas and highlight the potential degradation cost caused by seawater acidification.

Chapter 1 presents a quantitative synthesis (meta-analysis) of the OA studies performed in the Mediterranean Sea within a realistic range of pH alteration in agreement with the expected CO_2 emission trends forecasted by the Intergovernmental Panel on Climate change for the "business as usual" emission scenario for the year 2100. The results of the meta-analysis highlight the existence of direct effects but also suggest the instauration of indirect effects that could trigger habitats modifications. The quantitative results highlight an increase in fleshy algae cover, a reduction of calcification by both algae and corals and a general increase in the photosynthetic activity of macrophytes.

In Chapter 2, the results of the meta-analysis present in Chapter 1 and additional literature information are used to build conceptual models of the responses of two vulnerable habitats of the Mediterranean Sea (coralligenous formations and *P. oceanica* meadows) to OA impacts. The models aim at identifying ecosystem functions, services (ES) and benefits at the current and future acidified conditions in which these habitats are expected to be degraded.

The hypothesis represents by the models is that the OA would change many functions of the coralligenous and *P. oceanica* ecosystems both through the direct effects of OA and the instauration of indirect effects that could trigger habitats modification. The result shows by the models are the loss of coralligenous and *P. oceanica* habitats complexity leading to the shift of high-value ecosystem services to less valuable services. The following part of the work is the analysis of the ecosystem services provided by these habitats and the possible degradation cost due to OA.

Hence, we have develop an index to assess the food provisioning services of these habitats. The index allows the definition of provisioning service at current status and the analysis of the relative change in service provision in future acidified status. According to our analysis, *P. oceanica* and coralligenous ecosystems appear to provide the 24% of the total biomass of the commercial coastal species, and the 30% of the economic benefits in the Italian market. The hypothetical loss of the 2 habitats induces a loss of demersal resource of 15% of the current biomass with a maximum economic loss around 15 million of euros (-20%) per year. Chapter 3 presents an ecological simulation model based on the model developed by Prato et al. (2016)[1]. The simulation model, built on Ecopath with Ecosim, represents the trophic web of the Portofino MPA. The model allows for the analysis of processes on different hierarchical levels of biological organization and is used to represent OA effects at both trophic and non-trophic levels among multiple species. The study uses a combination of scenarios to predict the potential effects of habitat loss due to OA impacts. The results confirm that the values of provisioning services are correlated to *P. oceanica* and coralligenous area, showing in the worst-case scenarios (100% habitats loss and analysis of the effects at both trophic and non-trophic levels) a loss in biomass (33%) and economic revenues (28%) of important economic species.

In Chapter 4 a choice experiment among Italian scuba divers is undertaken to value the impact of OA on the recreational diving activities related to coralligenous and *P. oceanica*. The questionnaire assesses the cultural services of these habitats and the loss in the willingness to pay of the divers due to the habitats degradation related to the possible OA impacts. The results confirm that the degradation of coralligenous and *P. oceanica* habitats related to OA may reduce the attractiveness of the Mediterranean Sea for scuba divers, by reducing the scuba divers' satisfaction, the consumers' surplus and would likely deteriorate the return visit rate.

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Introduction

At the global level, natural capital stocks are subjected to increasing anthropogenic impacts and are exhibiting global environmental change, deteriorating our planet's ability to support human well-being.

The deterioration of natural capital over time leads to a severe decline of the services provided by the ecosystems worldwide and this loss of ecosystem services have broad consequences that cover the ecological, economic, and social spheres (de Groot et al., 2012).

Over the past 50 years, the changes brought by the human enterprise to ecosystems are so substantial that international groups of climatologist and geologist stand that we have entered what Paul Crutzen (2002) has identified as a whole new geologic era—the Anthropocene (Steffen et al., 2011).

The theory is based on the evidence that the human activities have influenced the natural capital more rapidly and extensively than in any comparable period in human history (MA, 2005).

In order to understand these large-scale changes and their consequences for human societies Rockström et al., 2009 identify key biophysical limits at global-scale beyond which humanity should not go introducing the concept of planetary boundaries.

Despite the complexity to define thresholds in which humanities should stay, Rockström et al. (2009) have specified nine areas to delimit the safe operating space for humanity. The guiding idea is that the transgression of any of the nine boundaries would lead to the threat of one or more aspects of human well-being or would undermine the resilience of the Earth system as a whole. These nine areas are climate change, biodiversity loss, excess nitrogen and phosphorus production, stratospheric ozone depletion, chemical pollution, global consumption of freshwater, change in land use for agriculture, air pollution, and ocean acidification.

In this context, the marine environments assume a central role, as shown by the UN Sustainable Development Goals coming up from planetary boundaries framework. Indeed, "Goal 14" focuses specifically on the marine environment, in order to conserve and sustainably use the oceans, seas, and marine resources for sustainable development (www.un.org/sustainabledevelopment/sustainable-development-goals). The Goal 14 further reported that "the increasingly adverse impacts of climate change, including ocean

acidification, overfishing and marine pollution are jeopardising recent gains in protecting portions of the world's oceans" (United Nations, 2017). Ocean acidification is, alongside ocean warming, one of the most concerning consequences of climate change.

Since the industrial revolution, oceans worldwide have absorbed about a quarter of the anthropogenic CO_2 released by human activities due to the seawater natural sink capacity. Seawater alkalinity buffers the effect of the CO_2 reaching the water from the atmosphere. This buffer capacity of the marine ecosystems is helping to mitigate the effects of the anthropogenic increase of CO_2 slowing the climate warming (Sabine et al., 2004). Currently, 95% of the global carbon budget is stored in the world's oceans (~38,000 Gt-gigatonnes) while approximately, the remaining is the stored in the atmosphere (700Gt) and in the terrestrial biosphere (200Gt) (Raven et al., 2005). It has been estimated that annually we produce 6 Gt of CO_2, 2 Gt of which are absorbed by the oceans, therefore, without this reservoir effect, the atmospheric CO_2 would be 55% higher than its current level (Sabine et al., 2004). Nevertheless, CO_2 causes the alteration of the carbonate equilibrium. Indeed, the increased dissolution of atmospheric CO_2 in the water produces carbonic acid (H_2CO_3), which mostly dissociates into bicarbonate (HCO_3^-) and hydrogen ions (Doney, 2009).

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons HCO_3^- + H^+ \rightleftharpoons CO_3^{2-} + 2H^+$$

The increase of hydrogen ions induces a pH reduction, a phenomenon known as ocean acidification (OA). According to IPCC (2013), globally, in the last two centuries, seawater pH has decreased from 8.2 to 8.1 (which corresponds to an increase of 26% in acidity), and it is expected to further decrease in the future, given the projections of anthropogenic CO_2 emissions.
Today, without significant cuts in CO_2 emissions, a 150% increase in the concentration of surface ocean H^+ is predicted by 2100 (Stocker et al., 2013) with a consequent decrease in pH between 0.06 and 0.32.

Since 2005, when the Royal Society working groups highlighted the need for further investigation on the responses of ecosystems to OA, this phenomenon has become a research priority in the frame of climate change, and several research projects have been developed worldwide. Several studies and meta-analyses on OA effects on organisms responses have been performed on a global (Dupont et al., 2010; Hendriks et al., 2010; Kroeker et al., 2013b) and local dataset (Zunino et al., 2017). Results of the EU FPVII MedSea project (2015), concluded

that the effects of the OA are already visible in the Mediterranean Sea, projecting a 30% increase in acidification by the year 2050 if the CO_2 emission trend continues at a business-as-usual rate (MEDSEA Final Report, 2015). Recent studies have suggested that the anthropogenic CO_2 concentration in the Mediterranean Sea is higher than that in the Atlantic and Pacific Oceans at the same latitude, and higher than in other marginal seas in the northern hemisphere (Lacoue-Labarthe et al., 2016 and references therein).

Despite the growing awareness on the direct effects of seawater acidification on the fitness of organisms, the analysis of indirect effects is less obvious and it is difficult to extend this analysis to the effects of the OA and hence to the whole ecosystems functioning. Indeed, the prediction of the impacts of climate change, and in particular OA, is challenging given the species-specific responses at local scales, and the cascading effects of these responses that can be additive, synergistic or antagonistic on the entire ecosystem.

The Mediterranean Sea, despite its small size, (0.82% of total ocean surface) hosts 7% of the world's marine biodiversity (Bianchi and Morri, 2000) and includes a broad range of habitats (UNEP-MAP and RAC/SPA, 2006), ranging from bioconstructors and seagrass meadows to shallow hydrothermal vents and deep-sea beds. It is a semi-enclosed basin between three continents, Africa, Asia, and Europe. Along the 26,000 km of its coastline, the Mediterranean Sea hosts twenty-two countries with an estimated 465.5 million inhabitants (Hilmi et al., 2014) of different economic developmental status. The sea brings security, supporting livelihoods, providing food, cultural and spiritual benefits. Moreover, coastal and marine habitats provide natural shoreline protection against storms and floods, maintain water quality, and support climate regulation. Although health and long-term sustainability of Mediterranean marine ecosystems are important features for the well-being of the population living the area, the marine ecosystems are seriously threatened by anthropogenic pressures and climate change, such as ocean warming and acidification, are further intensifying these threats (Hilmi et al., 2014).

In particular, there has been growing awareness that direct and indirect effects of seawater acidification may affect many goods and services provided by the Mediterranean marine ecosystems services such as aquaculture, fisheries, coastline protection, climate regulation (alteration of the fluxes of carbon), biodiversity and tourism (Turley et al., 2010). The effects of the OA range from the potential negative effects on the foundation species (Gaylord et al., 2015) to the alteration of biogenic habitats (Sunday et al., 2016), passing by the decrease of

communities' variability and the further homogenization and loss of functional diversity at landscape scale (Kroeker et al., 2013a)

Alteration of habitat complexity may represent key alterations to benthic systems, with potentially large effects on the ecosystem functions and consequently on the entire ecosystem services cascade (Sunday et al., 2016).

For this reason, there is a need to improve the quantitative estimates of the potential effects of seawater acidification in the near future. At the same time, it is important to adopt effective and integrated approaches able of combining ecological, economic, and social aspects to achieve adequate answers to mitigate the future impacts of the acidification and the costs at both ecosystems and social levels.

The development of knowledge about the possible consequence of OA is required to adopt mitigation strategies to progress toward a sustainable exploitation of the marine resources, as emphasised by the UN Sustainable Development Goals.

In order to face the impacts of OA in the Italian Sea, we have adopted the Ecosystem Services framework.

In the last two decades, the scientific community has embraced the ecosystem services (ES) framework to understand how ES support human well-being and to improve the environmental decisions making, by providing information on the benefits of nature conservation and the consequence of ecosystems changes for human well-being.

The logic that underlies the ES paradigm can be represented with the services cascade diagram (Haines-Young and Potschin, 2010), which represents the flow from ecological structures and processes, created or generated by living organisms to the benefits that people eventually derive from them.

Despite the high uncertainty of the impacts of climate changes on marine ecosystems in future scenarios (IPCC, 2014), integrating climate change drivers into assessments of ecosystem services provision is essential for designing context appropriate management strategies.

Broad attention to the link between ecological and human well-being was given by Costanza et al. in 1997 when they published "*The value of the world's ecosystem services and natural capital*" in which the authors evaluated -in economic terms- the benefits that the humanity derive from nature (Costanza et al., 1997).

A benchmark for the ES studies is the publication, in 2005, of the Millennium Ecosystem Assessment (MA) by the United Nations. This work was a monumental effort involving over 1300 scientists that recognized four categories of services: supporting (e.g. nutrient cycling, soil formation and primary production); provisioning (e.g. food, fresh water, wood and fiber and fuel); regulating (e.g. climate regulation, flood and disease regulation and water purification); and cultural (aesthetic, spiritual, educational and recreational). The outcomes were designated for policymakers, and one of the key results was the finding that globally 15 of the 24 ecosystem services investigated were in a state of decline (MEA, 2005), and this was likely to have a large and negative impact on future human welfare.

In 2007, another initiative was launched by the UN Environment Programme, called the Economics of Ecosystems and Biodiversity (TEEB) (TEEB Foundations, 2010). The aim of this project was to examine the long-term costs of failing to address the problem of contemporary biodiversity loss firstly given a state-of-the-art account of the economic valuation of ecosystem services. The project intended to inform conventional economic policy about its impacts on ecosystem health and biodiversity; on the other, it would suggest ways to mainstream the economic valuation of ecosystem services into national and local planning and policies as well as business accounting practices (Kumar and Martinez-Alier, 2011). A guiding idea of these projects was to make nature's values visible to human society (Kumar and Martinez-Alier, 2011).

Marine and coastal ecosystems were evaluated among the major contributors to the total economic values generated by the natural capital. Costanza et al. (1997) assessed that their contributions were higher than 60% of the total value assessed by the researchers. Recently, the WWF 2017 report (Randone et al., 2017) assessed that the economic value of ocean-related activities in the Mediterranean Sea is estimated to be US$450 billion annually, making this sea one of the most highly valued globally (Randone et al., 2017).

A turning point for the Italian State was the publication of the National Law 221/2015 *Environmental measures for promoting green economy and limiting the excessive use of natural resources* that sets up the creation of an Italian Natural Capital Committee (INCC), composed by institutional members along with experts appointed by the Italian Minister of Environment, Land & Sea (INCC, 2017).
The mandate of the INCC is to deliver an annual Report on the State of the Natural Capital in Italy to ensure the achievement of the social, economic, and environmental goals. In 2017, the first report of the INCC was delivered providing measures of physical and economic

dimensions of Natural Capital stocks and flows in Italy. The report further highlighted the necessity to consider the Natural Capital within the economic planning in Italy fostering the importance to monitor the implementation, the effectiveness, and the efficiency of policies and actions in order to protect the environment as well as the state of the environment and the Natural Capital (INCC, 2017).

Aims of the work

The aim of the work is to analyse the effects of ocean acidification (OA) in the Mediterranean Sea, and, more in particular at the Italian national level. The work will begin with the analysis of the existent literature related to the Mediterranean Sea and continues with the design of two conceptual model of *Posidonia oceanica* and coralligenous in order to evaluate the potential impacts of future OA scenarios on ecosystem services and benefits that the two important habitats provide. These two habitats are considered the main hot spots of biodiversity of the Mediterranean Sea. Anthropogenic pressures enhanced by the climate change stressors threaten *P. oceanica* meadows and coralligenous concretions that are suffering an alarming decline in the Mediterranean regions. Since their degradation, they are both under protection. *P. oceanica* is included both in the Red List of marine threatened species of the Mediterranean (Boudouresque et al., 1990) and in the priority natural habitats by the Annex I of the EC Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora (EEC, 1992). The coralligenous reefs are incorporated, as habitat that required protection, into the Protocol for Special Protected Areas (SPA/BD, 1995) of the Barcelona Convention for the conservation of Mediterranean biodiversity. An increasing number of works are demonstrating that these habitats proved numerous and highly valuable ecosystem services, despite quantitative measurement of the services still lack.

In this work, we focused on the analysis of some case studies of coralligenous and *P. oceanica* ecosystem services provisioning applied to the Italian area. The aim of this section is the quantification of the degradation costs associated with habitat degradation potentially inducted by ocean acidification.

The work aims at addressing the following objectives:

- Assessment of the current knowledge regarding the impacts of the OA in the Mediterranean Sea through a meta-analysis (i.e. a quantitative synthesis) of the published studies
- Development of conceptual frameworks for analysing the potential effects, both direct and indirect, of OA on two important habitats of the Mediterranean Sea, coralligenous reef and *P. oceanica* meadows
- Valuation of the impacts of OA on the *P. oceanica* and coralligenous' provisioning services in Italy
    - Via the development of an index of habitat use
    - Via the analysis of the potential impact of OA on a food-web model
- Analysis of the impact of OA on cultural services of coralligenous and *P. oceanica* meadows provided to diving tourists.

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Chapter 1 - Effects of Ocean Acidification on benthic organisms in the Mediterranean Sea under realistic climatic scenarios: A Meta-Analysis

This chapter has been published as:

Effects of ocean acidification on benthic organisms in the Mediterranean Sea under realistic climatic scenarios: A meta-analysis

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HIGHLIGHTS

- A meta-analysis on the Mediterranean acidification of benthic organisms is proposed.
- 95 experiments from 41 articles selected with $\Delta pH < 0.5$ were analysed.
- The quantitative results are followed by the review of the literature.

ARTICLE INFO

ABSTRACT

Ocean acidification is expected to cause significant changes in the marine environment over the coming century. The effects of acidification on organisms' physiology have been studied over the past two decades. However, the experimental findings are not always easily comparable because of differences in experimental design, and comparable experiments do not always produce similar results. To rigorously integrate the current knowledge, we performed a meta-analysis of published studies focused on benthic organisms in the Mediterranean Sea, both in controlled manipulative experiments and in situ experiments near vent areas. In each experiment, the effect of acidification was calculated as the log-transformed response ratio (LnRR) of experimental versus control conditions. The quantitative results obtained by the meta-analysis highlight: (a) an increase in fleshy algae cover, which may lead to a competitive advantage over calcifying macroalgae; (b) a reduction of calcification by both algae and corals; (c) an increase in seagrass shoot density under low pH; and (d) a general increase in the photosynthetic activity of macrophytes.

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1.1.   Introduction

The increasing trend in atmospheric CO_2 concentration causes an increase in the dissolution of atmospheric CO_2 into the sea and consequently causes a decline in seawater pH. This phenomenon, known as ocean acidification, may have relevant effects on the biological, biogeochemical and ecological components of the marine environment, a well as potentially relevant – but still not fully quantified – consequences on related socio-economic dimensions. The urgent need to identify and implement multilevel (local, national, and supranational) strategies to mitigate the adverse effects of ocean acidification (OA) has repeatedly been stressed (IOC-UNESCO, IMO, FAO, UNDP, 2011; Turley and Gattuso 2012) and is now clear. Nonetheless, the identification of mitigation strategies requires a full quantitative understanding of the cumulative OA -direct and indirect- effects on the specific system under analysis. In fact, although there is a general consensus on the existence of an effect, there is a large variability in the responses of different taxa, and even of similar organisms collected from different environments. The aim of this work was to determine a synthetic, composite picture of the effects of OA on benthic organisms in the Mediterranean Sea.

The effects of seawater acidification on organism physiology have been studied over the past two decades, and further studies are still underway (Harvey et al., 2013). In 2005, the Royal Society working group on ocean acidification highlighted the need for further investigation on the responses of marine species, communities, ecosystems and their services to changes in ocean CO_2 concentrations (Raven et al., 2005).

Since then, marine acidification has become a research priority in the frame of climate change, and several research projects have been developed worldwide. In the European Region, research has specifically focused on acidification, such as the EPOCA (FP7) and MedSea (FP7) projects, or the analysis of acidification among other stressors, such as the VECTORS (FP7) and OPEC (FP7) projects. The final report of the MedSea project (2015) highlights how acidification in the Mediterranean Sea has already been observed from field data and has projected a 30% increase in acidification by the year 2050 if the CO_2 emission trend does not change (MedSea final report, 2015).

The number of studies analysing the response of organisms to a decrease in seawater pH is large and increasing, although some of the results are contradictory (Gattuso, 2013). Indeed, as Doney et al. (2009) have highlighted in their review, numerous studies have revealed potential dramatic responses of calcifying organisms to altered seawater carbonate chemistry, whereas

others do not support similar conclusions, possibly because of the complicated nature of the calcification response. For example, the calcification response can differ depending on shell and skeleton composition, the Mg/Ca ratio, or nutrient availability (Doney et al., 2009 and citations therein). Furthermore, although the degree of sensitivity to acidification, manifested as different physiological responses, varies among species, response studies exist for only a limited number of species in many marine groups (Doney et al., 2009).

Meta-analyses are useful tools to evaluate the current state of knowledge and integrate the available information on a research topic. A meta-analysis is a set of formal methodologies designed to draw rigorous inferences from multiple studies (Gurevitch, 2001). This approach offers major advantages over more traditional qualitative reviews of the literature. The underlying approach and objectives are to quantify the emergent patterns by applying specific statistical procedures (Hughes et al. 2002). In detail, a meta-analysis allows for the computation of both the magnitude and significance of an overall effect shared among studies, as obtained by calculating the size effects for each contributing study. The meta-analysis technique also acknowledges that studies on large sample sizes are more reliable and offers the possibility to weight studies on the basis of such measures of reliability (Borenstein et al., 2009).

Meta-analyses on ocean acidification effects that have been performed on a global data set (Dupont et al., 2010; Hendriks et al., 2010; Kroeker et al., 2010) have shown that the effects are significant, but not uniform, owing to variations in responses and adaptations of marine organisms. Nevertheless, those researchers have analysed a wide variety of species inhabiting environments with very different biogeochemical characteristics. In contrast, we decided to focus on a narrower area, the Mediterranean Sea, to reduce the source of variability due to the high degree of species-specific responses. We argue that comparison among species belonging to the same physical and chemical environment (i.e., similar salinity, light irradiance or alkalinity) is more accurate than comparison among species adapted to extremely different conditions, ranging from polar to tropical regions. Thus, we limited our analysis to the species living in the Mediterranean Sea, while taking advantage of the recent studies conducted in the MedSea project (MedSea).

The Mediterranean Sea, despite its small size, contains 7% of the world's marine biodiversity (Bianchi and Morri, 2000) and includes a broad range of habitats (RAC/SPA, 2006), ranging from bioconstructors and seagrass meadows to shallow hydrothermal vents and deep-sea beds. It is a semi-enclosed basin, and along the 26,000 km of its coastline, the Mediterranean Sea hosts twenty-two countries of varying economic developmental status on three continents,

Africa, Asia, and Europe, with an estimated 465.5 million inhabitants (Hilmi et al., 2014). Several pressures together threaten the health of the Mediterranean Sea ecosystem. It is now clear that the Mediterranean area will be a hotspot for climate change effects (IPCC 4th, 2007), thus resulting in an intensification of extreme events (Lejeusne et al., 2010).

There has been growing awareness that direct and indirect effects of seawater acidification may affect many goods and services provided by the Mediterranean marine ecosystems services (Turley et al., 2010). For this reason, there is a need to improve the quantitative estimates of the potential effects of seawater acidification in the near future. Services such as aquaculture, fisheries, coastline protection (reduction of rocky substrata, which constitute a natural defence), climate regulation (alteration of the fluxes of carbon), loss of biodiversity and tourism may all be affected by human-induced seawater acidification with potentially severe consequences that are not yet fully understood.

OA studies analyse a spectrum of pH levels that range from the actual ambient levels to projected future pH levels. Different studies have addressed different ranges of pH variation; some have assessed the physiological responses induced by a reduction of 0.5 pH units, in agreement with the projected 2100 level (IPCC 4th, 2007), but several studies have examined higher ranges of pH variation in both the mesocosm and *in situ* at vent sites. Moreover, studies have been carried out at different times, spanning periods of several days up to several months, and only a few studies have analysed organisms' responses on a yearly basis.
Systematically combining quantitative results of acidification effects at the regional organism level would aid in drawing conclusions about this body of research and guiding adaptive management actions for the potentially affected economic sectors (Cicin-Sain et al., 2011).

1.2. Methods
Data selection
We conducted a literature search of scientific articles published in ISI journals through 1 July 2015 by selecting studies reporting the effects of altered seawater chemistry on physiological responses. The literature search was conducted in the SCOPUS database using the keywords: organism AND acidification AND Mediterranean AND *response.

The results were cross-checked against the database of ocean acidification experiments compiled by EPOCA, OA-ICC (Ocean Acidification International Coordination Centre), and

MedSea, and with the results reported by previous meta-analysis studies on this topic (Dupont et al., 2010; Harvey et al., 2013; Hendriks et al., 2010; Kroeker et al., 2010, 2013).

In the analysis, we considered both controlled manipulative experiments and *in situ* experiments close to vent areas and both single species responses and responses of species assemblages.

From each article, we collected the data regarding the response of different taxa to decreasing pH. We identified five main types of effects (abundance, calcification, growth, survival and photosynthesis), as responses of organisms to acidification. These responses were used as the response variables in our analysis.

The selection of the response variables was based on the number of articles available for analysis. Furthermore, it is consistent with the classification used in the MedSea final report (2014). We considered other response variables (Shannon Index, metabolism, respiration, and development rate), but it was not possible to include them in our quantitative analysis because there were too few studies that considered those variables (see supplementary information Tab S2).

The analyses were limited to studies that explored the response to a variation in pH_T of less than 0.5 units. This value is consistent with the ocean acidification prediction provided by the Intergovernmental Panel on Climate change (IPCC 4th, 2007) for the IS92a "business as usual" emission scenario for the year 2100. This choice led to the exclusion of studies that explored wider pH variations, considering that under extreme environmental pressures an organism might exceed resilience thresholds and therefore might exhibit a response that could not be rescaled under the hypothesis of the linear regressions. Many studies have used different parameters (total alkalinity, $p\text{CO}_2$, DIC, pH) to characterise the changes in the carbonate system, but the pH value is the most frequently reported, and it was chosen in this study to produce a more homogeneous setup among experiments.

Most of the data used in our analysis were obtained from the PANGAEA data repository (www.pangaea.de). The use of raw data allowed for the selection of the specific data that were the most relevant for our study. When the raw data were not available, we extracted the data from the articles or graphs by using ENGAUGE software (Mitchell, 2002). To confirm that the range of pH values was suitable for our purpose and to allow for full comparability across all data sets, we recalculated the pH values in Total scale by using CO2SYS software (Lewis & Wallace, 1998) using the constants of Mehrbach et al., (1973) refit by Dickson and Millero and

Dickson (1990) for KSO_4 (Tab S1). The effect of acidification was analysed at the ambient seawater temperature as reported in the original study.

When a single study reported multiple response variables (e.g., abundance, calcification and growth), they were included in separate meta-analyses. If a study reported different measures of the effects on a single response type (such as growth rates based on changes in biomass and growth rates based on changes in length) for that response variable, we selected the most frequently used metric. Survival effects were taken from the percent survival or mortality data. Survival rates were reported in our analysis as the measure obtained either at the end of the study or at the latest point at which the experimental conditions were suitable for comparison between control and treatment experiments.

Calcification response measures were taken primarily from estimates of net calcification. Growth responses were obtained using change in biomass, shell length and growth rate measures. Photosynthesis responses were derived from the measures of changes in the photosynthetic rate or efficiency. Abundance responses were derived from the number of individuals, including the number of newly settled individuals, as well as percent cover estimates. If a study provided information on more than one species, all data were used, even if multiple species were examined in the same experimental tank, according to Wittmann and Pörtner, (2013).

In experiments lasting several months, we considered the response observed after the longest exposure time.

Data Analysis

Effect size

For each experiment reported in the literature considered in our analysis, we registered the mean response, the estimates of the error (transformed to standard deviation *sd*) and the sample sizes (n) in the control group and the treatment with low pH.

For each experiment, the effect of acidification was calculated as the log-transformed response ratio (LnRR, Eq. 1), which was defined as the ratio of the mean effect in the acidification treatment $\bar{X}_E$ on the mean effect in a control group $\bar{X}_C$ (Hedges et al., 1999).

$$LnRR_i = \ln\left(\frac{\bar{X}_E}{\bar{X}_C}\right) = \ln(\bar{X}_E) - \ln(\bar{X}_c) \qquad \text{(Eq.1)}$$

When LnRR< 0, the effect of acidification on the response variable in the treatment group is negative, and when LnRR> 0, the effect on the response variable is positive. A response ratio

of zero indicates that there is no effect, and the responses in the control and treatment groups are the same.

The variance of the *LnRR* (Eq. 2) for each study was calculated as (Hedges et al., 1999):

$$V_i = \frac{sd_E^2}{n_E + \bar{X}_E^2} + \frac{sd_C^2}{n_C + \bar{X}_C^2}$$
(Eq. 2)

The overall effect on a given response variable of a given group of organisms was calculated using a weighted mean among the LnRR of the primary studies, mean*LnRR* (Eq. 4), in agreement with a random-effects model. Under a random-effects analysis, the effect size is not assumed to be fixed, but its size differs between experiments, and the estimated summary effect is the mean of the effects observed across the studies (Borenstein et al, 2009). This assumption was made because the analyses take into account different species studied with different techniques and in different environments (i.e., mesocosm or vent sites).

Under a random-effects model, the total observed variability (Eq. 3) in the effect size estimate contains within-study variance V_i and between-study variance τ^2, which together were used to weight the studies (W*).

$$W^* = \frac{1}{V_i + \tau^2}$$
(Eq. 3)

Therefore, the studies with higher replication and lower variance were considered more precise and were weighted accordingly (Stewart, 2010). The between-study variance was estimated using the DerSimonian Laird method (DerSimonian and Laird, 1986). Statistical significance was attributed to each summary effect size by calculating the 95% confidence interval (CI) (see Hedges and Olkin, 1985) and comparing it to zero. If the summary effect size did not overlap zero, then it was considered to be significantly different.

$$\text{mean}LnRR = \frac{\sum_{i=1}^{k} W^* LnRR_i}{\sum_{i=1}^{k} W^*}$$
(Eq. 4)

Heterogeneity

Owing to the variability among studies, a statistical test of heterogeneity was performed to investigate the hypothesis that the size of the effect would be equal in all included studies.

In fact, if a group of studies shares an effect of similar magnitude, the result of the meta-analysis is unambiguous. In contrast, if the studies included in a meta-analysis show different results, the result of the meta-analysis is more ambiguous (Sutton and Higgins, 2008).

The statistical test was calculated by summing the standard deviation of each effect size study estimate from the overall meta-analytic estimate mean effect size estimate, and then

weighting each one according to the inverse of its sampling variance (Cochran, 1954; (Higgins et al., 2003). P values were obtained by comparing the statistic with a χ^2 distribution with n-1 degrees of freedom.

Heterogeneity in mean effect sizes was determined on the basis of a significant ($\alpha = 0.05$) QT statistic.

$$Q_T = \sum_{i=1}^{k} W_i(meanLnRR - LnRR_i)^2 \qquad \text{(Eq. 5)}$$

Heterogeneity in sub-groups of organisms was investigated by limiting Eq. 5 to the sub-group (Gurevitch et al., 1992). The differences between sub-groups (when found; e.g., calcification of deep azooxanthellate corals versus zooxanthellate corals) were investigated with a test for heterogeneity (Q_M), thus identifying the total heterogeneity explained by that particular categorical moderator (Gurevitch et al., 1992), by using the same formula that we introduced earlier. A significant Q_M indicated a difference between the sub-groups.

Analyses were carried out using the R (R Development Core Team, 2012) package "Metafor" (Viechtbauer, 2010).

1.3.   Results

The meta-analysis included 67 published articles reporting the effect of acidification on Mediterranean organisms; three articles were excluded because they did not report error estimates, and 11 were excluded because they evaluated a pH value lower than those expected in the IPCC projection for the end of the century. A total of 15 additional articles were excluded because they focused on response variables (e.g., Shannon Index) that were measured in too few (less than three) experiments. From the remaining 41 articles, we extracted the final set of 95 unique experiments (Tab 1). A posteriori, we noted that all of the 95 selected experiments referred to benthic organisms, and all experiments that focused on other groups were filtered out, a result that by itself indicates a knowledge gap.

Abundance

The effect of acidification on organism abundance (Fig 1) varied among groups (Q_M (df = 5) = 50.29, P < .0001).

The responses of calcifying algae and sea urchins were significantly negative (meanLnRR < 0; P<0.01), whereas the responses of fleshy macroalgae (P<0.01) and microalgae (P = 0.08) were

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positive. All responses showed significant heterogeneity within the mean effect (P < 0.05) (Tab 1).

The effect size for seagrass was positive but not significant (mean LnRR = 0.35, P = 0.1330).

Organisms	N.of studies	Mean LnRR (log scale)	Mean LnRR [95% CI]
Abundance			
Fleshy Macroal	(8)		0.89 [0.65 , 1.14]
Microalgae	(5)		0.78 [0.20 , 1.36]
Calcifying algae	(9)		−1.56 [−2.36 , −0.76]
Seagrass	(3)		0.35 [−0.11 , 0.82]
Sea urchin	(7)		−1.57 [−2.81 , −0.34]
Mollusc	(7)		−0.01 [−0.73 , 0.71]
Cnidaria zoox	(6)		0.12 [−0.24 , 0.47]
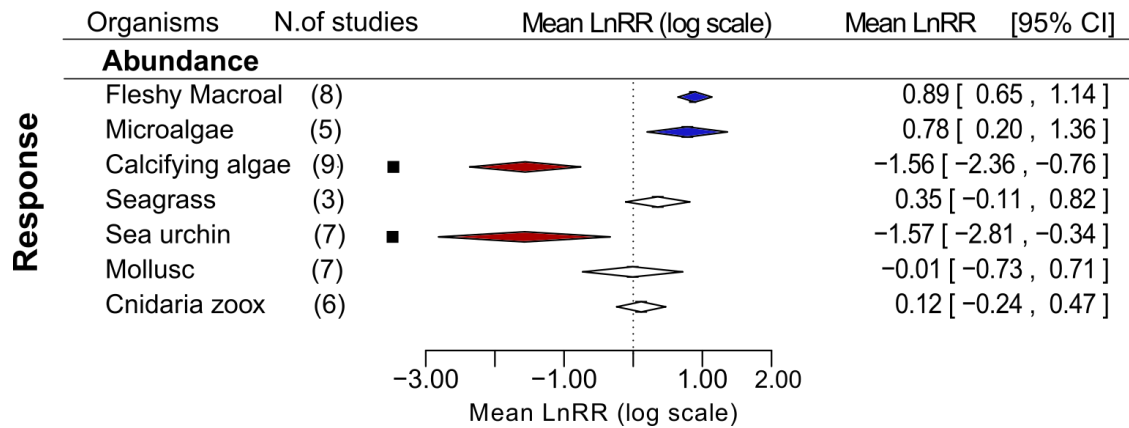
Fig 1 The effect (mean LnRR) of the expected Mediterranean acidification on the abundance of marine organisms from weighted, random effects meta-analyses. The mean effects and 95% confidence intervals are shown for separate groups of organisms. The number of experiments in each analysis is shown in parentheses. The zero line indicates no effect, and the significance of mean effects is determined when the 95% confidence interval does not overlap zero.

Blue shapes represent significant positive responses in the mean effect size; red shapes represent significant negative response; and white shapes are the responses that are not statistically significant (95% CI that overlaps zero, P>0.05)

Calcification

The effect of acidification on calcification resulted in a significant negative response for corals (mean LnRR = - 0.23, P= 0.026). A more detailed sub-group analysis was performed to detect different possible results between zooxanthellate and deep-water corals. Although the sub-group of shallow zooxanthellate corals (from 3 to 40 m depth) had a more negative mean effect than the sub-group of deep water corals, the difference was not significant (Q_M (df = 1) = 0.06 , P = 0.79).

Bryozoans and molluscs were both unaffected (mean LnRR =0), whereas algae were negatively affected, but not significantly (meanLnRR= -0.85, P= 0.25; Fig 2).
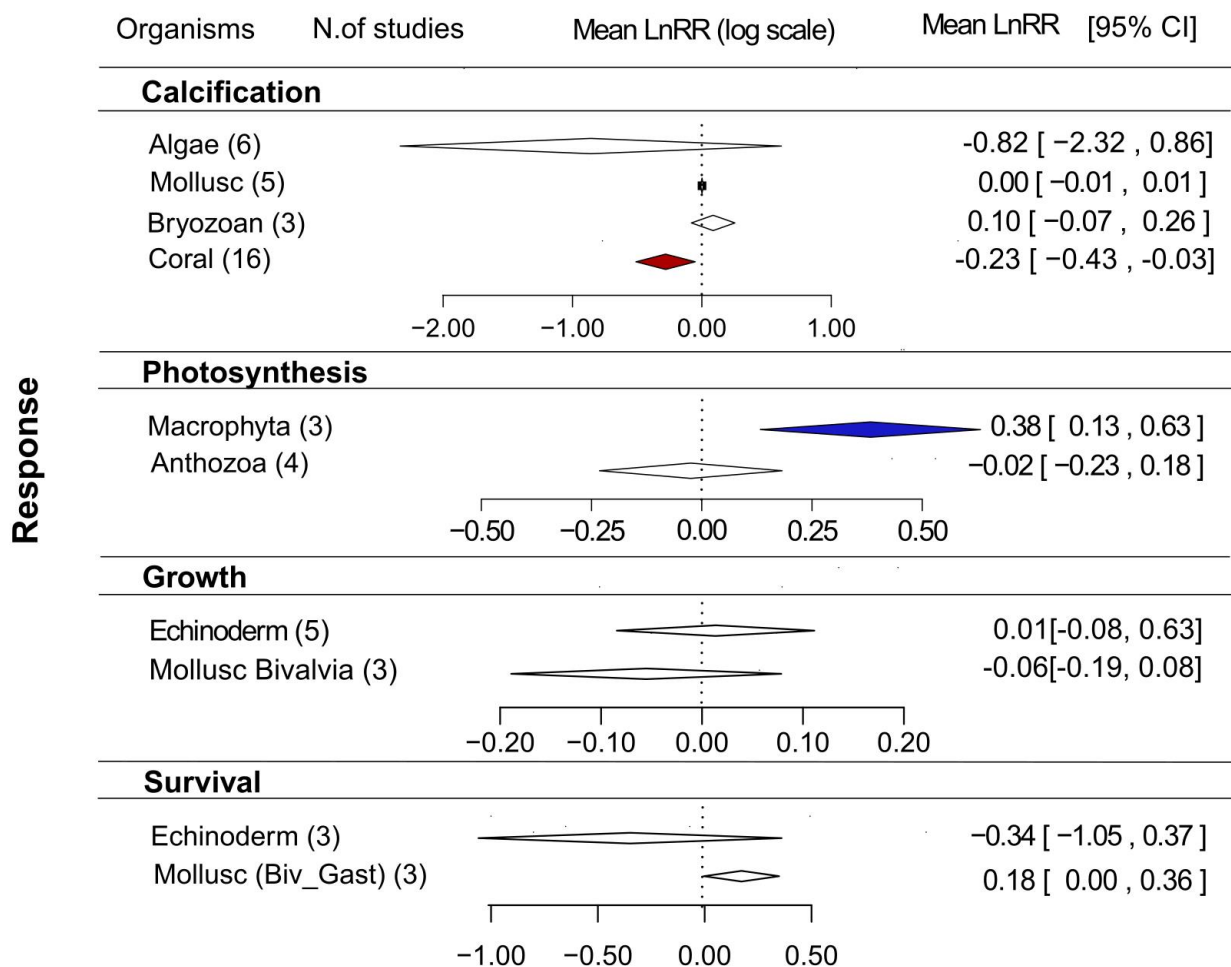
Fig 2 *The mean log response ratio and 95% confidence intervals of Mediterranean acidification on physiological responses. The number of experiments in each analysis is shown in parentheses. The zero line indicates no effect, and significance of the mean effects is determined when the 95% confidence interval does not overlap zero. Blue shapes represent the significant positive responses in the mean effect size; red shapes represent significant negative responses; and white shapes are the responses that were not statistically significant (95% CI that overlaps zero)*

Photosynthesis

A significantly positive (meanLnRR= 0.38, P = 0.026) and coherent effect was detected in response to a pH decrease on photosynthesis of the macrophyta group ($Q_T = 17.59$, d.f. = 2, P = 0.77; Fig 2).

In contrast, seawater acidification did not have an effect on zooxanthellae symbionts, thus suggesting that these organisms are not limited by carbon dioxide availability.

Growth and Survival

Seawater acidification did not have a significant overall mean effect on the growth of echinod erms and bivalve molluscs (Fig 2), whereas it had a negative effect on echinoderm survival (meanLnRR = -0.34) although the mean effect was not significant (P= 0.35) and there was hete rogeneity among studies (Q_T = 52.16, d.f. = 8, P < 0.001; Fig 2).

Tab 1 *Summary of effects of acidification on different biological responses among key groups. Effects are represented as either mean percentage increase (+) or percentage decrease (-) in a given response. Percentage change estimates were back-transformed from the mean LnRR and represent geometric means that are more conservative than the arithmetic means. Dark colours represent consistency in the mean effect size, and light colours highlight the positive or negative trend in the case of inconsistency with the results (95% CI that overlaps zero). The number of experiments in each analysis is shown in the N column.*

RESPONSE	GROUP	EFFECT	N	Q_T	P-VAL
ABUNDANCE	ZOOXANTHELLAE CNIDARIA	+12%	5	49.75	< .0001
	SEAGRASS	+ 42%	3	20.44	< .0001
	FLESHY MACROAL.	+143%	8	2.72	0.909
	MICROALGAE	+118%	5	22.55	0.0002
	CALCIFYING AL.	- 79%	9	43.41	<.0001
	MOLLUSCS	=	7	39.90	<.0001
	SEA URCHINS	-79%	7	110.21	<.0001
CALCIFICATION	ALGAE	-56%	6	737.1	< .0001
	MOLLUSCS	=	5	0.413	0.98
	BRYOZOANS	=	3	0.15	0.93
	CORALS	-20%	16	338.65	<.0001
GROWTH	BIVALVIA	=	3	81.70	0.92
	ECHINODERMS	-28%	5	12.55	0.0855
SURVIVAL	MOLLUSCS	=	3	26.36	<.0001
	ECHINODERMS	-28%	3	18.46	<.0001
PHOTOSYNTHESIS	ANTHOZOA	=	4	17.59	0.0005
	MACROPHYTA	+46%	3	0.52	0.77

1.4. Discussion and Conclusion

The results of our meta-analysis showed different responses to ocean acidification in different groups of organisms. Even though the study was limited to the Mediterranean basin, the outcomes supported some of the findings from previous meta-analyses on acidification on a worldwide scale (Kroeker et al., 2013; Hendriks et al., 2010 and Harvey et al., 2013) (Tab 2).

Tab 2 Comparison of the summary of the effects of acidification among groups obtained from this study, Kroeker et al., 2013 and Hendriks et al., 2010. Effects are represented as either mean percentage increase (+) or percentage decrease (-) in a given response. Percentage change estimates were back-transformed from the mean LnRR.

	Reduced
	Enhanced
	95% CI overlaps 0
	Not tested

Group	Response	Mean Effect			Harvey et al., 2013
		This work	Kroeker et al. 2013	Hendriks et al. 2010	
Calcifying algae	Abundance	-79%	-80%		
	Calcification	-56%	-61%	-16%	3%
Corals	Calcification	-20%	-32%	-29%	-14%
	Photosynthesis				-50%
Molluscs	Abundance				
	Calcification		-40%	-39%	-22%
	Growth		-17%		-24%
	Survival		-34%	25%	-22%
Echinoderms	Abundance	-79%			
	Growth		-10%	-62%	-5%
	Survival	-28%		-12%	-2%
Fleshy macroalgae	Abundance	143%			
	Growth		22%	48%	18%
	Photosynthesis	49%			7%

Algae

On average, the cover of turf and canopy-forming algae is expected to increase (more than double), and these organisms may experience a stronger competitive success against calcifying macroalgae (Asnaghi et al., 2013). In particular, our analysis shows a loss of calcified algae (-79%), mainly corallinales (Tab 1), which might have been caused by a reduced ability to build or maintain the calcified component of their tissues at the lower pH value. This possibility was

confirmed by the reduction of calcification functional response, which decreased by 58%, thus hindering the algae fitness, in accordance with Kuffner et al., (2006).

There is widespread evidence that coralline algae are sensitive to ocean acidification, and even tolerant species can be outcompeted by non-calcifying algae at elevated CO_2 levels (Brodie et al., 2014); Kroeker et al., 2013). Several studies have shown that the projected acidification conditions negatively affect various functional traits of coralline algae, such as community growth, recruitment, calcification, size and abundance (Hall-Spencer et al., 2008; Porzio et al., 2011; Kroeker et al., 2013; Donnarumma et al., 2014), and epithelial integrity (Baggini et al., 2014 and reference therein). However, some studies have shown how increased atmospheric pCO$_2$ may have a positive effect on calcifying algae (Kamenos et al., 2013; Martin et al., 2013) on the basis of evidence of increased calcification under OA. Nevertheless, even if some coralline algae sustain calcification over long periods of exposure to elevated pCO$_2$, a loss of structural integrity is inherent (Kamenos et al., 2013; Martin et al. 2013) and presumably comes with an energetic cost to growth (Bradassi et al., 2013). In contrast, recent studies have found that crustose coralline algae are more sensitive to the rates of pH fluctuations than to the magnitudes, thereby reducing growth in an articulated coralline algae: high variability in pCO$_2$ at vent sites may therefore lead to an over-estimation of its negative effects on coralline algae (Kamenos et al., 2013).

Calcifying algae are an important component of the temperate marine ecosystem, in which they support different functions through carbon cycling, provision of habitats and associated biodiversity hotspots and are associated with recruitment processes. Additionally, they are major structural components of coralligenous habitats and vermetid reefs. Thus, any change in the three-dimensional structure and structural integrity of coralline algae may have significant effects on the ecosystem functions with which they are involved.

Linares et al., (2015) have found that at lower pH, dominant habitats at mesophotic depths, such as coralligenous outcrops and rhodolith beds, are replaced by deep-water kelp (*Laminaria rodriguezii)* forests, which become dominant at shallower depths than under normal seawater conditions. The results of these studies suggest that high CO_2 concentration enhances the competitiveness of *L. rodriguezii* at depths shallower than its common bathymetric range, thereby offsetting other existing environmental limitations (e.g., light or temperature). These results appeared to be confirmed by our meta-analysis, which suggested a strong increase in fleshy macroalgae cover (Tab 1).

Martin et al. (2013) have found that calcification in *Lithophyllum cabiochae* is stimulated by increased temperature under current CO_2 conditions, but the combination of high temperature and CO_2 negatively affects net calcification rates.

Sea urchins

Changes in seawater pH may lead to direct effects on a specific group of organisms, owing to their physiological vulnerability to elevated CO_2 conditions, but it is important also to consider the indirect effects determined by changes in species composition that might trigger antagonistic or synergic responses of the organisms to acidification.

This analysis highlighted a possible reduction in some grazer species that specialise on fleshy algae for feeding. For example, sea urchins, which had a projected decrease in abundance by 79%, were among the most negatively affected organisms in our analysis. Urchins are key organisms that play an important role in controlling the equilibrium among different algal communities. Sea urchins appear to be particularly susceptible to OA, and a reduction of 0.4 pH appears to be the critical level below which Mediterranean Sea urchins do not survive (Hall-Spencer et al., 2008).

Studies performed at the vent sites have found a reduced density in the high CO_2 areas in *P. lividus* (Calosi et al., 2013; Hall-Spencer et al., 2008; Johnson and Carpenter, 2012; Kroeker et al., 2013b; Suggett et al., 2012), which appears to be less resilient to elevated CO_2 than the more tolerant *Arbacia lixula* (Asnaghi et al., 2014; Bray et al., 2014). The decrease in *P. lividus* density in high CO_2 areas could be interpreted as a long-term consequence of its relatively poor ability to regulate its extracellular acid–base balance (Calosi et al., 2013). In contrast, Hendriks et al. (2010) have found a reduction of growth up to 62% for sea urchins, whereas Asnaghi et al. (2013,2014) have highlighted the importance of the threatened calcifying algae (i.e., *Corallina*) in sea urchins' diet, as a source of essential elements (e.g., calcium, magnesium) that increase the skeleton robustness. The decreased robustness of sea urchin skeletons makes juveniles less resistant to predator attack, e.g., the *Diplodus spp.* (Asnaghi et al., 2014, 2013) even if neutral or undetectable effects are found in the skeleton growth (Asnaghi et al., 2013; Kroeker et al., 2013a; Martin et al., 2011; Wangensteen et al., 2013) as well as in the survival response of early settlers of *A. lixula* and *P. lividus*.

The loss of sea urchins combined with the advantages that fleshy algae may have as a result of acidification may trigger a phase shift towards fleshy algae dominated environments (Asnaghi et al., 2013). This effect may be important, from an ecological perspective, in barren ground habitats where the reduced abundance of sea urchins would favour the recolonisation of non-

calcifying macroalgae and the recovery of foundation species (e.g., *Cystoseira*) (Asnaghi et al., 2013) but may be deleterious in undisturbed vegetated areas where sea urchins have important structural roles (Asnaghi et al., 2013). Indeed, grazing events are important to create new patches for the settlement of invertebrate planulae. This change in biodiversity is enhanced by the loss of coralline species, which favours recovery and complexity in rocky reef communities promoting species succession and increasing turf species colonisation (due to the increasing availability of dissolved inorganic carbon). Turf species are characterised by fast and rampant growth strategies able to inhibit the settlement of propagules of slower-growing species (e.g. corals species) (Vermeij et al., 2009).

The coralligenous habitat is the second most important hotspot of biodiversity in the Mediterranean Sea, after the *Posidonia oceanica* meadows (Boudouresque, 2004). In this unique environment, there is intense competition among sessile benthic organisms that tends to completely saturate the available space. The competition for light and space is especially strong between algae and corals, because these are resources of primary importance for the survival of both organisms. It is known that the competition of macroalgae with corals for fundamental resources exhibits a range of detrimental effects on corals, including inhibition of coral recruitment, growth and fecundity (Kuffner et al., 2006). Many macroalgae produce secondary metabolites (i.e., allelochemicals) that exert some of these negative effects on corals in different life stages. Filamentous algae, especially the species belonging to the eco-physiological turf algae group, can cause hypoxia, lower coral fecundity, and inhibition of coral recruitment (Linares et al., 2012).

In seagrass meadows, sea urchin reduction may not be relevant to the physiology of the leaves or the epibiont community associated with the seagrass. This hypothesis is supported by the evidence that urchin grazing events are compensated for and enhanced by the intense activity of herbivorous fish (i.e., *Sarpa salpa*) (Garrard et al., 2014) attracted by the loss of encrusting and less palatable calcareous epibionts (Apostolaki et al., 2014).

Seagrass

The seagrass studies were mainly performed *in situ* along the vent sites. The density of *P. oceanica* increased at the vent sites (Hall-Spencer et al., 2008, MedSea final report, 2014) whereas the abundance of *C. nodosa* was higher at the control site. This result implied, as suggested by our meta-analysis (Fig 1), a species-specific response towards increased CO_2 (Apostolaki et al., 2014).

It is likely that the responses to CO_2 also depend on other factors, such as the interactions with temperature and nutrients (e.g., nitrogen (Alexandre et al., 2012)) and light (Palacios and Zimmerman, 2007). Investigations of single drivers (i.e., the change in seawater carbonate chemistry) with no control over other concurring factors can produce misleading inferences about organismal responses and -as a consequence- may provide highly uncertain projections. Indeed, in a multivariate natural environment, interactive (additive, synergistic, or antagonistic) effects are often not predictable from single-driver studies (Gattuso et al., 2015).

Longer term experiments (months) with seagrass species *in situ* have found no significant differences in leaf growth rates of plants exposed to current and elevated CO_2 concentrations (Palacios and Zimmerman 2007; Alexandre et al., 2012). However, CO_2 enrichment does have an effect on belowground growth rates, increase of non-structural carbohydrate content and shoot proliferation of seagrass species (i.e., *Z. marina* Palacios and Zimmerman 2007; Apostolaki et al., 2014 and reference therein). Finally, the increase in seagrass biomass may have been limited, owing to the high grazing pressure of large herbivorous fish (*Sarpa salpa*) as aforementioned (Apostolaki et al., 2014).

OA may lead to a consistent loss of crustose coralline algal epiphytes on seagrass leaves along the vents, and greater seagrass density close to the seeps with lower pH. A load of lower epiphytes may have positive consequences for seagrasses, because it reduces shading and nutrient uptake by the epiphytes (Apostolaki et al., 2014). However, a shift from dominant corallines to fleshy macroalgae in seagrass meadows may reduce light availability on the benthos, thus accelerating the regression of seagrasses, without taking into account benefits due to their enhanced photosynthesis (Harley et al., 2012; Koch et al., 2013).

Calcified organisms (including calcified algae and corals), echinoderms and fleshy algae presented similar trends in each analysis: the former two groups were negatively affected by seawater acidification, whereas the latter appeared to benefit from acidification. These results are consistent with the meta-analysis performed by Hendriks et al., (2010). In contrast, although our analysis did not detect a negative effect on molluscs, Kroeker et al. (2013), Harvey et al. (2013) and Hendriks et al. (2010) have detected significant reductions in calcification, growth and survival of this group, probably because of their poor ion regulation and inability to buffer their internal compartments (Harvey et al., 2013 and citations therein). Similar conclusions have also been drawn by Wittman and Pörtner (2013) from a meta-analysis indicating that most echinoderms and molluscs exhibit relatively low metabolic rates and do not compensate well for acid–base disturbances. Their analysis suggests that most echinoderm (63%) and mollusc

(51.6%) species analysed are negatively affected even by the lowest levels of experimental $p\mathrm{CO}_2$ (500–650 µatm).

Results obtained from the MedSea project (MedSea, Final Report, 2014) also suggest dramatic changes in seagrass meadows. Seagrass meadows are expected to suffer from elevated seawater temperature and invasion by non-indigenous algae species, which benefit from increased CO_2 and elevated temperature.

Photosynthesis

The effect of OA on photosynthetic organisms is not straightforward. Our analysis detected a positive trend in the photosynthetic response of macrophytes to acidification, which was not found in the analyses of Kroeker et al. (2010, 2013). In contrast, Hendriks et al. (2010) have found higher growth rates in photosynthetic organisms, up to five-fold or higher for seagrasses, possibly as a result of the increased photosynthetic activity. The lack of effect found in Kroeker et al. (2010, 2013) may be explained by the highly species-specific response of photosynthesis.

Koch et al. (2013) have indicated that the majority (95%) of the marine macro-autotrophs examined in their review are able to utilise HCO_3^-, which at ambient seawater pH represents 92% of the dissolved inorganic carbon (DIC) (Stepien, 2015 and references therein). This process is possible because marine algae have carbon-concentrating mechanisms (CCMs), which transport HCO_3^- across cell membranes to Rubisco (the enzyme that fixes CO_2) by using ion transporters, or they catalyse the dehydration of HCO_3^- to CO_2 via the membrane-associated external carbonic anhydrase. There are energetic costs to operating CCMs; hence, the increased percentage of dissolved CO_2 (which at the current level represents approximately the 1% of the DIC (Stepien, 2015 and references therein)) may increase the competitiveness of macrophytes with CCMs (Stepien, 2015), owing to the lower cost associated with the use of CO_2. For example, seagrass photosynthesis is frequently limited by DIC availability under natural conditions (Beer and Koch, 1996). Furthermore, there is evidence that CCMs are down-regulated under elevated CO_2 conditions. This reaction may allow for a reduction in the energy demands necessary to produce ion transporter proteins and enzymes (Raven, 2011). In addition, the higher photosynthetic activity of seagrasses may lead to an additional accumulation of carbohydrates in belowground organs, thus conferring an advantage on macroalgae that do not have a site for carbohydrate storage (Koch et al., 2013).

Molluscs

Bivalve molluscs and shellfish aquaculture represent an important sector of the Mediterranean economy. Our meta-analysis highlighted that relatively few experiments related to projected acidification have been performed in Mediterranean waters, as already stressed by Lacoue-Labarthe et al. (2016) despite the potential for molluscs to be influenced by the acidification projections (Hendriks et al., 2010; Kroeker et al., 2013).

The effects of ocean acidification on bivalves vary among species and even within the same species, thus precluding the possibility of deducing a general picture (Hilmi et al., 2015). The available literature suggests that although detrimental effects on adults remain uncertain, the most sensitive life stage appears to be the larval stage, and a large majority of studies on this critical stage of development have revealed negative effects (Gazeau et al. 2013). Among bivalves, mussels appear to be fairly resilient and can even thrive in low pH waters. Indeed, it has been found that *Mytilus galloprovincialis* starts to show a significant decrease in shell and soft body growth after exposure to pH 7.3 (Michaelidis et al., 2005), a level expected to occur within the next 300 years (Caldeira and Wickett, 2003).

Results obtained by the MedSea project (MedSea Final Report, 2014), show that after a year-long experiment on the Mediterranean mussel *M. galloprovincialis,* no lethal effects of hypercapnia (i.e., condition of elevated CO_2 in the seawater) were found, whereas there were significant effects due to a temperature increase (Gazeau et al., 2014). However, Lacoue-Labarthe et al. (2016) suggest that in the coming decades, Mediterranean mussels will be exposed to sub-optimal conditions for increasingly long periods, thus probably leading to decreased survival and growth (Lacoue-Labarthe et al., 2016 and citations therein).

Milazzo et al. (2014) have shown that vermetid might be affected by OA. Vermetids play an important role in the Mediterranean ecosystem. They are constructor organisms that build reefs, which provide coastal protection from erosion, regulate sediment transport and accumulation, serve as carbon sinks and provide habitats for fish and invertebrates of commercial and recreational interest (Milazzo et al., 2014). Vermetid reefs are built by the gastropod *Dendropoma petraeum* (Monterosato, 1884) and the coralline alga *Neogoniolithon brassica-florida* (Harvey) (Setchell & Mason 1943) which cements the reef and triggers vermetid settlement. The OA level expected to occur this century and beyond is expected to impair recruitment success, cause shell dissolution and alter the shell mineralogy of the reef-building gastropod *D. petraeum* (Milazzo et al., 2014) even if the post-settlement survival of new recruits appears to be resistant to very low pH conditions (7.31).

In line with some of the results mentioned above, our meta-analysis did not show the clear effect of acidification on mollusc responses that has been obtained in previous meta-analyses. This difference may be due to variances in the range of the experimental acidification considered and/or the species-specific differences between the responses given by the Mediterranean-temperate bivalves-gastropods considered in our study and the worldwide distributed bivalves-gastropods-

cephalopods used in the analysis performed by Kroeker et al. (2013) and Hendriks et al. (2010) (Tab 2). Indeed, our analysis was constrained by our selecting only those studies that reported the effects expected for the end of the century (IPCC 4th, 2007), whereas others (i.e., Hendriks et al. (2010)) have used ΔpH >0.5, a value that is expected by the end of 2300 (IPCC 4th, 2007). Moreover, differences in the response may also have been because the majority of the Mediterranean studies on molluscs have focused on the most exploited commercial species, *Mytilus galloprovincialis*, in which the outermost $CaCO_3$ shell layer consists of calcite (less soluble than aragonite) covered by an organic periostracum. This organic layer is important in protecting the $CaCO_3$ layers from dissolution (Gazeau et al., 2013). Nevertheless, the result of this analysis reflects only the studies currently available, and therefore we cannot completely exclude other possible effects on the mollusc population. In fact, there are some alterations in physiological traits that were not considered in this analysis, owing to the limited number of studies available, such as the retraction of the periostracum layer when mussels are exposed to lowered pH conditions (Gazeau et al., 2014).

Corals

Our analysis indicates that OA inhibits corals calcification in the Mediterranean temperate and deep water corals. Our results indicate a lower reduction compared with the results from Kroeker et al. (2013) for tropical corals (Tab 2). Even if the effect is relatively small, a 22% decrease (Tab 1) in coral calcification may lead to strong disadvantages during future acidification and, given the potential occurrence of other synergic drivers such as the already mentioned increase in the competitive advantages of algae; this effect may be further enhanced.

Studies on temperate corals have shown controversial responses. The cold water coral (CWC) *Lophelia pertusa* is the most common reef framework-forming and ecosystem engineering species with a cosmopolitan distribution. However, in the Mediterranean basin, *M. oculata* is more widespread (Maier et al.,2012). Studies have found that cold water corals (CWC) are not

sensitive to seawater acidification (Maier et al., 2013; Movilla et al., 2014) even though Maier et al. (2012) have found that acidification has had a detrimental effect on the calcification rates of *M. oculata*. A calcification reduction of 50% has been found since pre-industrial times. Other analyses have shown an increase in energetic cost for calcification in *L. pertusa* with decreasing pH (Maier et al., 2009).

Laboratory experiments on *C. rubrum,* one of the most valuable precious corals, have indicated a significant decrease in average calcification rates (Bramanti et al., 2013; Cerrano et al., 2013), possibly because the skeleton is built of high Mg-calcite, which is more soluble than aragonite.

Similarly, Movilla et al. (2012) have found a high sensitivity of the zooxanthellate corals *O. patagonica* and *C. caespitosa* to future (2100) acidification in the Mediterranean Sea, with a reduction in the calcification rate up to 35% and the fastest growing colonies displaying greater sensitivity to low pH values. In contrast, Rodolfo-Metalpa et al. (2011) have found no significant effects of altered seawater chemistry on *C. caespitosa* and *B. europea* gross calcification rates. Nevertheless, they have found that the net calcification rate is reduced, owing to the increase in the skeleton dissolution process. These results suggest that the different responses among species may be explained by the presence of a protective external organic layer that has been documented to modulate the effects of seawater acidification on corals and in other organisms (Ries et al., 2009). The majority of the Mediterranean temperate coral are slow-growing species that grow up to 5 times slower than their tropical counterparts (Rodolfo-Metalpa et al., 2006). It is conceivable that the requirement for carbonate ions of slow growing corals is low and the concentration of carbonate ions would not be limiting, even under high pCO$_2$ concentrations (ca. 700 µatm) (Rodolfo-Metalpa et al., 2010).

Our analysis was not able to identify whether the response could be interpreted as a reduction in the ability of individual species to calcify or as an increase in the rate of dissolution over the rate of gross calcification. Nevertheless, to address the aim of our analysis, it is important to understand which organisms might be the losers and the winners in the projected acidified environment. Indeed, even if some organisms can up-regulate their calcification at lowered pH values, they rely on protective organic layers to avoid dissolution (Rodolfo-Metalpa et al., 2010). Projected levels of ocean acidification are likely to increase the erosion of unprotected biogenic carbonate structures.

Wittmann and Pörtner, (2013) have reported similarly controversial results in their meta-analysis. Indeed, they have highlighted that some extant coral species appear to be surprisingly resistant to pCO$_2$ levels projected by RCP scenarios 6 and 8.5. However, they have found that

sensitivity is highly variable in these ranges of pCO_2, in which 38.5 and 44.4% of the species were negatively affected. The authors suggest that resilience may depend on a significant capacity for the upregulation of pH at calcification sites, thus increasing internal aragonite and calcium carbonate saturation states (Ω) and facilitating carbonate precipitation.

At the global scale, according to Kroeker's meta-analysis (2013), acidification affects coral abundance, and its effects, with an average reduction of 47%, were greater than any other response variables, which were reduced by less than 34% (Tab 2). These findings once again highlight the high species-specific response of corals. It is important to bear in mind that the studies examined by Kroeker et al. (2013) have found that the response is dependent on the exposure of the settlement substrate to reduced seawater pH, a detail that—until now—has never been addressed by studies conducted in the Mediterranean basin, owing to the absence of temperate coral species (i.e., *C. caespitosa, O. patagonica*) in acidified vent habitats. These results suggest that ocean acidification affects the settlement of coral larvae both directly by altering their fitness, and indirectly by affecting the community composition via substrata alteration, as aforementioned.

Although we found different consistent effects related to acidification (both positive and negative effects), the high heterogeneity associated with almost all of the considered groups (Tab 1) suggested that the presence of different factors can either enhance or reduce the response to acidification. First, the species-specific responses of the organisms represent an important source of heterogeneity (Q statistic, P<0.05). Thus, the analysis of different species pooled in the same group may have masked different responses. Another source of heterogeneity is the potential pressure of other factors in the experimental design (i.e., light, nutrients, temperature and duration of the experiments), which may have led to non-additive, antagonistic or synergistic effects that might have compensated or enhanced the effects of acidification on the organisms' responses.

The Mediterranean basin is highly exposed to substantial human impacts (e.g., aquaculture, water degradation, destructive fishery activities, species invasion, urbanisation, and sedimentation increase) that are threatening the conservation of species and ecosystems. In addition, global warming has a strong influence on the Mediterranean basin. These other stressors were not considered in this analysis, but it must be kept in mind that the response to

the acidification that we found might be enhanced or completely masked by other stressors acting on the species and the ecosystems. For instance, seagrass meadows are degrading globally at a rate of 7% because of coastal development, dredging activities and declining water quality (Waycott et al., 2009), thus nullifying all the possible benefits derived from OA. Harvey et al. (2013) have found in a global meta-analysis that the combined stressors of acidification and warming cause significant negative effects on calcification, reproduction, and survival, and a significant positive effect on photosynthesis but no effect on growth. Importantly, they have also found that calcification, photosynthesis, reproduction, and survival show a synergistic interaction between the two stressors, thus increasing the unpredictability of the responses. Similarly, Wittmann and Pörtner (2013) have found that in several corals, fishes, crustaceans, echinoderms and molluscs, tolerance to warming is reduced under elevated CO_2 levels, thus indicating a narrowing of species-specific thermal windows. Moreover, even a weak response of a group of organisms may lead to indirect and cascading effects on other groups, thus triggering a shift in species composition. The estimation of the consequences represents a challenge because of the difficulties in projecting the results over a long period obtained in short-term experiments. Only a few studies to date have attempted this difficult task (i.e., Asnaghi et al., 2013). For this reason, we believe, in agreement with Harley et al. (2006), that a further step should be a stronger effort to scale up the studies from individuals and populations to the community and ecosystem levels within a larger temporal frame that allows for the analysis of adaptive responses.

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1.6. Supplementary

Tab S3: List of the studies chosen for the meta-analysis

Year	First Author	Species	Group	Response	Treatment
2014	Donnarumma, L	chlorophyceae-phaeophyceae	fleshy algae-biofilm	abundance	in situ transplant
2013	Johnson, V	cyanobacteria	fleshy algae-biofilm	abundance	in situ
2013	Johnson, V	diatoms communities	fleshy algae-biofilm	abundance	in situ
2013	Kroeker, K	biofilm	fleshy algae-biofilm	abundance	in situ
2011	Porzio, L	chlorophyta	fleshy algae-biofilm	abundance	in situ
2011	Porzio, L	phaeophyceae	fleshy algae-biofilm	abundance	in situ
2014	Baggini, C	calcifying algae	calcifying algae	abundance	in situ
2014	Donnarumma, L	Hydronapneo spp.	calcifying algae	abundance	in situ transplant
2008	Hall-Spencer, J	calcifying algae	calcifying algae	abundance	in situ
2013	Kroeker, K	encrusting calcareous alg.	calcifying algae	abundance	in situ transplant
2008	Martin, S	corallines epiphites	calcifying algae	abundance	in situ transplant
2014	Baggini, C	canopy forming algae	fleshy algae-canopy	abundance	in situ
2013	Porzio, L	phaeophyceae	fleshy algae-canopy	abundance	in situ transplant
2012	Suggett, D	macroalgae	fleshy algae-canopy	abundance	in situ
2014	Borell, E	*Anemonia Viridis -* Symbiont	cnidaria	abundance	in situ
2013	Meron, D	*Anemonia Viridis-* Symbiont	cnidaria	abundance	in situ
2012	Suggett, D	*Anemonia Viridis-* Symbiont	cnidaria	abundance	in situ
2014	Goffredo, S	*Balanophyllia Europaea*	coral	abundance	in situ
2012	Movilla, J	*C. Caespitosa*-Symb	coral	abundance	mesocosm
2012	Movilla, J	*Oculina Patagonica-* Symbiont	coral	abundance	mesocosm
2010	Rodolfo-Metalpa, R	*C. Caespitosa-* Symbiont	coral	abundance	mesocosm
2013	Calosi, P	*A Lixula*	echinoderm	abundance	in situ
2013	Calosi, P	*P.Lividus*	echinoderm	abundance	in situ
2008	Hall-Spencer, J	*P. Lividus; A.Lixula*	echinoderm	abundance	in situ
2012	Johnson, V	*P. Lividus*	echinoderm	abundance	in situ
2013	Kroeker, K	*Arbacia Lixula*	echinoderm	abundance	in situ

2013	Kroeker, K	*Paracentrotus Lividus*	echinoderm	abundance	in situ
2012	Suggett, D	sea urchin	echinoderm	abundance	in situ
2014	Goffredo, S	*Acetabularia Acetabulum*	fleshy algae	abundance	in situ
2014	Goffredo, S	*Padina Pavonica*	fleshy algae	abundance	in situ
2012	Johnson, V	*Padina Pavonica*	fleshy algae	abundance	in situ
2013	Kroeker, K	encrusting turf algae	fleshy algae	abundance	in situ transplant
2013	Porzio, L	Chlorophyte	fleshy algae	abundance	in situ transplant
2010	Cigliano, M	Invertebrates	mollusc	abundance	in situ
2014	Goffredo, S	*Vermetus Triqueter*	mollusc	abundance	in situ
2008	Hall-Spencer, J	Limpets	mollusc	abundance	in situ
2008	Hall-Spencer, J	*Osilinus Turbinata*	mollusc	abundance	in situ
2011	Kroeker, K	bivalvia	mollusc	abundance	in situ
2011	Kroeker, K	Gastropoda	mollusc	abundance	in situ
2014	Milazzo, M	dendropoma petraeum	mollusc	abundance	in situ transplant
2014	Apostolaki, E	*Cymodocea Nodosa*	seagrass	abundance	in situ
2014	Donnarumma, L	*Posidonia oceanica*	seagrass	abundance	in situ transplant
2008	Hall-Spencer, J	*Posidonia oceanica*	seagrass	abundance	in situ
2013	Porzio, L	Rhodophyta	calcifying algae	abundance	in situ transplant
2012	Suggett, D	coralline algae	calcifying algae	abundance	in situ
2011	Porzio, L	rhodophyta crust	calcifying algae	abundance	in situ
2011	Porzio, L	rhodophyta erect	calcifying algae	abundance	in situ
2011	Lombardi, C	*Myriapora Truncata*	bryozoan	calcification	in situ transplant
2011	Lombardi, C	*Schizoporella Errata*	bryozoan	calcification	in situ transplant
2010	Rodolfo-Metalpa, R	*Myriapora Truncata*	bryozoan	calcification	in situ transplant
2014	Goffredo, S	*Balanophyllia Europaea*	coral	calcification	in situ
2012	Movilla, J	*Cladocora Caespitosa*	coral	calcification	mesocosm
2012	Movilla, J	*Oculina Patagonica*	coral	calcification	mesocosm
2011	Rodolfo-Metalpa, R	*Balanophyllia Europaea*	coral	calcification	in situ transplant
2011	Rodolfo-Metalpa, R	*Cladocora Caespitosa*	coral	calcification	in situ transplant
2010	Rodolfo-Metalpa, R	*Cladocora Caespitosa*	coral	calcification	mesocosm
2013	Bramanti, L	*Corallium Rubrum*	coral-azooxanthellatae	calcification	mesocosm
2013	Cerrano, C	*Corallium Rubrum*	coral-azoox	calcification	mesocosm
2013	Maier, C	*Lophelia Pertusa*	coral-azoox	calcification	mesocosm
2013	Maier, C	*Madrepora Oculata*	coral-azoox	calcification	mesocosm
2014	Movilla, J	*Dendrophyllia Cornigera*	coral-azoox	calcification	mesocosm

2014	Movilla, J	*Desmophyllum Dianthus*	coral-azoox	calcification	mesocosm
2014	Movilla, J	*Lophelia Pertusa*	coral-azoox	calcification	mesocosm
2014	Movilla, J	*Madrepora Oculata*	coral-azoox	calcification	mesocosm
2014	Goffredo, S	*Acetabularia Acetabulum*	macroalgae	calcification	in situ
2014	Goffredo, S	*Padina Pavonica*	macroalgae	calcification	in situ
2008	Hall-Spencer, J	calcifying algae	calcifying algae	calcification	in situ
2012	Johnson, V	*Padina Pavonica*	macroalgae	calcification	in situ
2009	Martin, S	*Lithophyllum cabiochae*	calcifying algae	calcification	mesocosm
2013	Martin, S	*Lithophyllum cabiochae*	calcifying algae	calcification	mesocosm
2014	Gazeau, F	*Mytilus Galloprovincialis*	mollusc	calcification	mesocosm
2014	Goffredo, S	*Vermetus Triqueter*	mollusc	calcification	in situ
2011	Rodolfo-Metalpa, R	*Mytilus Galloprovincialis*	mollusc	calcification	in situ transplant
2011	Rodolfo-Metalpa, R	*Patella Caerlulea*	mollusc	calcification	in situ transplant
2013	Vihtakari, M	*Mytilus Galloprovincialis*	mollusc	calcification	mesocosm
2014	Asnaghi, V	*Paracentrotus Lividus*	echinoderm	growth	mesocosm
2013	Asnaghi, V	*Paracentrotus Lividus*	echinoderm	growth	mesocosm
2013	Kroeker, K	*Arbacia Lixula*	echinoderm	growth	in situ
2013	Kroeker, K	*Paracentrotus Lividus*	echinoderm	growth	in situ
2011	Martin, S	*Paracentrotus Lividus*	echinoderm	growth	mesocosm
2013	Vihtakari, M	*Mytilus Galloprovincialis*	mollusc	growth	mesocosm
2013	Wangensteen, O	*Arbacia Lixula*	echinoderm	growth	mesocosm
2014	Gazeau, F	*Mytilus Galloprovincialis*	mollusc	growth	mesocosm
2011	Rodolfo-Metalpa, R	*Mytilus Galloprovincialis*	mollusc	growth	in situ transplant
2012	Suggett, D	*Anemonia Viridis*	cnidaria	photosynthesis	in situ
2012	Meron, D	*Balanophyllia Europaea*	coral	photosynthesis	in situ transplant
2012	Meron, D	*Cladocora Caespitosa*	coral	photosynthesis	in situ transplant
2010	Rodolfo-Metalpa, R	*Cladocora Caespitosa*	coral	photosynthesis	mesocosm
2012	Johnson, V	*Padina Pavonica*	macroalgae	photosynthesis	in situ
2014	Apostolaki, E	*Cymodocea Nodosa*	seagrass	photosynthesis	in situ
2012	Suggett, D	*Anemonia Viridis*	cnidarian	photosynthesis	in situ
2014	Gianguzza, P	*Arbacia Lixula*	echinoderm	survival%	mesocosm
2011	Martin, S	*Paracentrotus Lividus*	echinoderm	survival%	mesocosm
2013	Wangensteen, O	*Arbacia Lixula*	echinoderm	survival%	mesocosm
2014	Gazeau, F	*Mytilus Galloprovincialis*	mollusc	survival%	mesocosm

Year	First Author	Species	Group	Response	Treatment
2014	Milazzo, M	*Dendropoma Petraeum*	mollusc	survival%	in situ transplant
2013	Vihtakari, M	*Mytilus Galloprovincialis*	mollusc	survival%	mesocosm

Tab S2: List of studies which were not considered in meta-analysis since they reported unusual physiological responses.

Year	First Author	Species	Group	Response	Treatment
2014	Kerfahi, D	communities	bacteria	Shannon Diversity	in situ
2012	Lidbury, I	microfilm	bacteria	Shannon Diversity	in situ
2011	Lombardi, C	*Myriapora truncata*	bryozoan	metabolism	in situ transplant
2011	Lombardi, C	*Schizoporella errata*	bryozoan	metabolism	in situ transplant
2013	Meron, D	*Anemonia viridis*	cnidaria	metabolism	in situ
2013	Meron, D	*Anemonia viridis*	cnidaria	Shannon Diversity	in situ
2013	Maier, C	*Lophelia pertusa*	coral-azoox	respiration	mesocosm
2013	Maier, C	*Madrepora oculata*	coral-azoox	respiration	mesocosm
2014	Zervoudaki, S	*Acartia clausi*-Copepod	crustacean	development	mesocosm
2013	Calosi, P	*Arbacia lixula*	echinoderm	metabolism	mesocosm
2013	Calosi, P	*Paracentrotus lividus*	echinoderm	metabolism	mesocosm
2014	Gazeau, F	*Mytilus galloprovincialis*	mollusc	metabolism	mesocosm
2013	Matozzo, V	*Mytilus galloprovincialis*	mollusc	metabolism	mesocosm
2013	Matozzo, V	*Chamelea gallina*	mollusc	metabolism	mesocosm
2014	Gazeau, F	*Mytilus galloprovincialis*	mollusc	respiration	mesocosm
2013	Vihtakari, M	*Mytilus galloprovincialis*	mollusc	respiration	mesocosm
2012	Arnold, T	*Cymodocea nodosa*	seagrass	metabolism	in situ
1997	Invers, O	*Posidonia oceanica*	seagrass	no carbonatic refere	

Tab S3: Treatment and control pH (reported in total scale, last column) from the 41 studies considered in this meta-analysis. Original pH values and pH scale along with the auxiliary variables (S, T, AT, pCO2 and DIC) used for computing the missing value of the total scale pH of the aforementioned studies (columns 4-10). The conversion of pH values from NBS to TotalScale requires S and T, while the calculation of missing pH values are based on the available carbonate system variables and the K1K2 constants of Mehrbach et al., (1973) refit by Dickson and Millero and KSO4 constant of Dickson (1990). All calculations are made using CO2SYS software (Lewis & Wallace, 1998).

N.	Reference		pH measured	Scale	S	T	AT μmol/kg	pCO$_2$ [μatm]	DIC	Recalculated using CO2SYS pH$_T$
1	Apostolaki et al. Mar. Environ. Res. 99, 9–15 (2014).	CONTROL	8.01	NBS	38.2	19.74				7.889
		TREATMENT	7.65	NBS	38.2	19.68				7.529
2	Asnaghi, V. *et al. Mar. Environ. Res.* 93, 78–84 (2014).	CONTROL	8.09	Total scale						8.09
		TREATMENT	7.84	Total scale						7.84
3	Asnaghi et al. PLoS ONE (2013)	CONTROL	8.09	Total scale						8.09
		TREATMENT	7.84	Total scale						7.84
4	Baggini et al. PLoS One 9, e106520 (2014).	CONTROL	8.11	NBS	39	24.95				7.977
		TREATMENT	7.67	NBS	38.94	23.73				7.54
5	Borell et al. Ecol. Evol. 4, 441–449 (2014).	CONTROL	8.14	NBS	38	19				8.02
		TREATMENT	7.9	NBS	38	19				7.78
6	Bramanti, L. et al. Glob. Chang. Biol. 19, 1897–1908 (2013).	CONTROL	8.097	Total scale						8.097
		TREATMENT	7.808	Total scale						7.808
7	Calosi et al. Mar. Pollut. Bull. 73, 470–484 (2013).	CONTROL	8.06	NBS	38	23.01				7.931
		TREATMENT	7.69	NBS	38	23.01				7.561
8		CONTROL	8.09	NBS	38	13.5				7.983

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#	Reference							
	Cerrano et al. Sci. Rep. 3, 1457 (2013).	TREATMENT	7.77	NBS	38	13.5		7.663
9	Cigliano et al. Mar. Biol. 157, 2489–2502 (2010).	CONTROL	8.15	Total scale				8.15
		TREATMENT	7.77	Total scale				7.77
10	Donnarumma et al. Mediterr. Mar. Sci. (2014).	CONTROL	8.1	Total scale				8.1
		TREATMENT	7.7	Total scale				7.7
11	Fantazzini, P et al. *Nature Communications*, 6, 7785. (2015).	CONTROL	8.07	Total scale				8.07
		TREATMENT	7.78	Total scale				7.78
12	Gazeau et al. Frontiers in Marine Science, 1, 62. (2014)	CONTROL	8.09	Total scale				8.089
		TREATMENT	7.73	Total scale				7.73
13	Gianguzza et al. Mar. Environ. Res. 93, 70–77 (2014).	CONTROL	8.2	NBS	38	20		8.078
		TREATMENT	7.9	NBS	38	20		7.778
14	Goffredo et al. Nat. Clim. Chang. 4, 593–597 (2014).	CONTROL	8.1	Total scale				8.1
		TREATMENT	7.81	Total scale				7.81
15	Hall-Spencer, J. M. et al. Nature 454, 96–99 (2008).	CONTROL	8.14	Total scale				8.14
		TREATMENT	7.83	Total scale				7.83
16	Johnson, V. R., et al. Glob. Chang. Biol. 18, 2792–2803 (2012).	CONTROL	8.08	Total scale				8.08
		TREATMENT	7.71	Total scale				7.71
17	Johnson, V. R. et al. Mar. Biol. 160, 1813–1824 (2013).	CONTROL	8.06	NBS	38	18.6		7.941
		TREATMENT	7.93	NBS	38	18.6		7.811
18	Kroeker, K. J.et al. Proc. Natl. Acad. Sci. USA 108 (2011).	CONTROL	8.18	Total scale				8.18
		TREATMENT	8.05	Total scale				8.05
19	Kroeker, K. J et al. Proc. Natl. Acad. Sci. USA 110 (2013).	CONTROL	8.18	Total scale				8.18

#	Reference	Group	pH	Scale					Final
		TREATMENT	8.05	Total scale					8.05
20	Lombardi, C. et al. Zoomorphology 130, 135–145 (2011)	CONTROL	8.07	Total scale					8.07
		TREATMENT	7.83	Total scale					7.83
21	Lombardi, C., et al. Mar. Ecol. 32, 211–221 (2011).	CONTROL	8.07	Total scale					8.07
		TREATMENT	7.66	Total scale					7.66
22	Maier, C., et al. Proc. R. Soc. B 279, 1716–1723 (2012).	CONTROL			38	12.5	2643	2349	8.141
		TREATMENT			38	12.5	2534	2426	7.769
23	Maier, C. *et al. PLoS ONE* 8(4), e62655 (2013).	CONTROL			38	13	2575	2331	8.055
		TREATMENT			38	13	2512	2417	7.729
24	Martin, S., et al., .Biology Letters, 4(6), 689–692 (2008).	CONTROL	8.1	Total scale					8.1
		TREATMENT	7.87	Total scale					7.87
25	Martin, S. & Gattuso, J.-P. Glob. Chang. Biol. 15, 2089–2100 (2009).	CONTROL	8.1	Total scale					8.1
		TREATMENT	7.87	Total scale					7.87
26	Martin, S. et al. J. Exp. Biol. 214, 1357–1368 (2011).	CONTROL	8.08	Total scale					8.08
		TREATMENT	7.87	Total scale					7.87
27	Martin, S., et al. Ecol. Evol. 3, 676–693 (2013).	CONTROL	8.06	Total scale					8.06
		TREATMENT	7.87	Total scale					7.87
28	Meron, D. et al. Int. Soc. Microb. Ecol. J. 6, 1775–1785 (2012).	CONTROL	8.06	Total scale					8.053
		TREATMENT	7.77	Total scale					7.763
29	Meron, D.,et al.Microb. Ecol. 65, 269–276 (2013).	CONTROL	8.06	Total scale					8.06
		TREATMENT	7.77	Total scale					7.77
30	Milazzo, M. et al. Scientific Reports 4, 4189 (2014).	CONTROL	8.03	NBS	38	25.6			7.895
		TREATMENT	7.76	NBS	37.2	25.3			7.625

31	Movilla, J. et al. J. Exp. Mar. Biol. Ecol. 438, 144–153 (2012).	CONTROL	8.09	Total scale			8.09
		TREATMENT	7.83	Total scale			7.83
32	Movilla, J. et al. Coral Reefs (2014).	CONTROL	8.097	Total scale			8.097
		TREATMENT	7.808	Total scale			7.808
33	Movilla, J. et al. Water 6, 59–67 (2014).	CONTROL	8.09	Total scale			8.09
		TREATMENT	7.808	Total scale			7.808
34	Porzio, L., et al. J. M. J. Exp. Mar. Bio. Ecol. 400, 278–287 (2011).	CONTROL	8.1	Total scale			8.1
		TREATMENT	7.8	Total scale			7.8
35	Porzio, L., et al. Mar. Biol. 160, 2247–2259 (2013).	CONTROL	8.06	Total scale			8.06
		TREATMENT	7.75	Total scale			7.75
36	Rodolfo-Metalpa et al. Biogeosciences 7, 289–300 (2010).	CONTROL	8.08	Total scale			8.08
		TREATMENT	7.85	Total scale			7.85
37	Rodolfo-Metalpa et al. Mar. Ecol. 31, 447–456 (2010).	CONTROL	8.07	Total scale			8.07
		TREATMENT	7.66	Total scale			7.66
38	Rodolfo-Metalpa, R. et al. Nat. Clim. Chang. 1, 308–312 (2011).	CONTROL	8.06	Total scale			8.06
		TREATMENT	7.77	Total scale			7.77
39	Suggett, D. J. et al. Glob. Chang. Biol. 18, 3015–3025 (2012).	CONTROL			35	26	8.105
		TREATMENT			35	26	7.885
40	Vihtakari, M. et al. Water 5, 1890–1915 (2013).	CONTROL	8.06	Total scale			8.06
		TREATMENT	7.88	Total scale			7.88
41	Wangensteen et al. J. Exp. Mar. Bio. Ecol. 449, 304–311 (2013).	CONTROL	8.09	Total scale			8.09
		TREATMENT	7.69	Total scale			7.69

Fig S1: LnRR estimates for abundance (the literature reference for each study is given in brackets): a) fleshy-macroalgae, b) microalgae, c) calcifying algae, d) echinoderms, e) seagrass, f) molluscs and g) symbionts. The forest plots consider each study individually; the LnRR is plotted with its 95% confidence interval and their values are reported on the right side as LnRR [95% CI]. The summary estimate (mean LnRR) and its confidence interval plotted below.
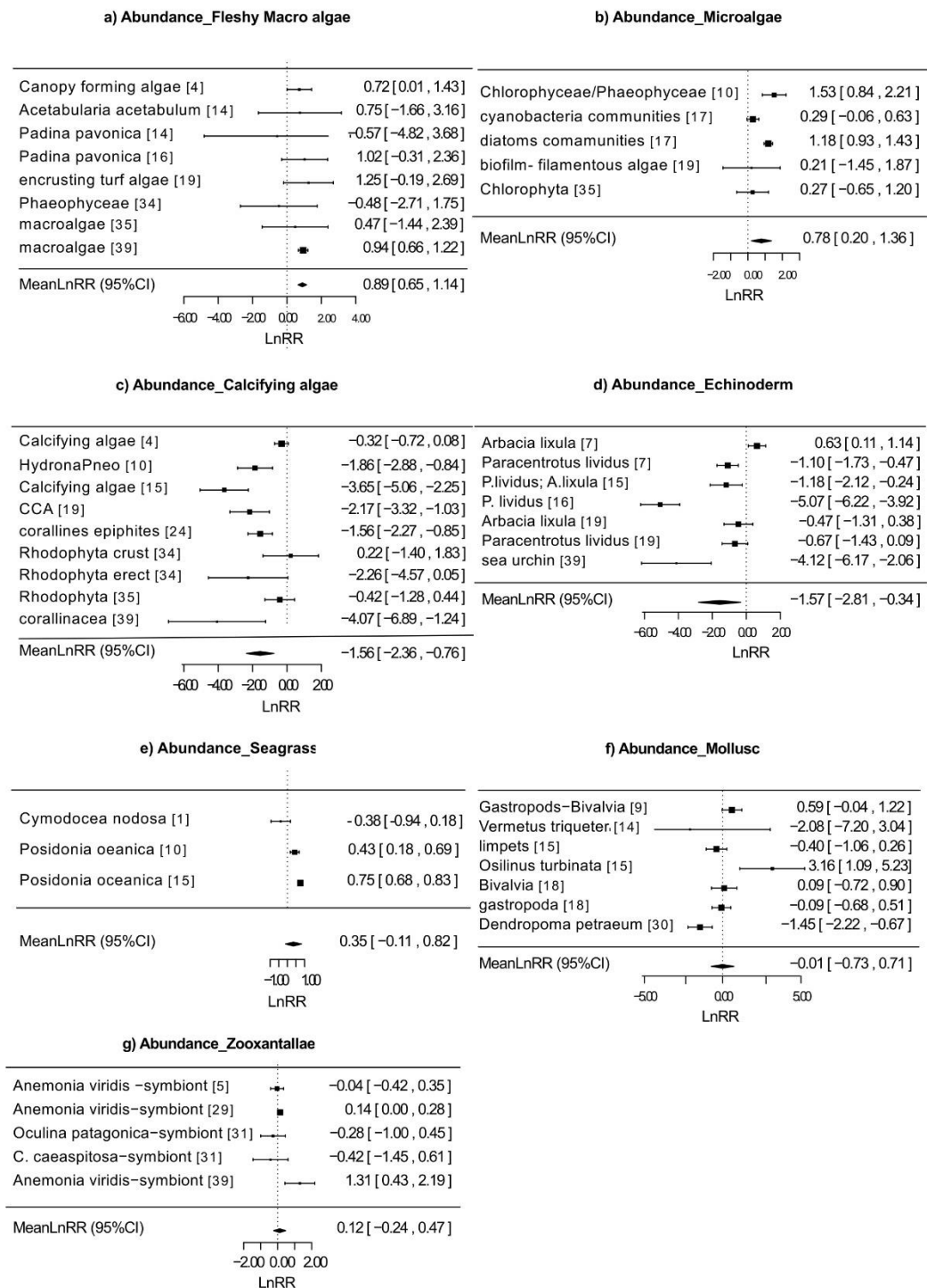
Fig S2: LnRR estimates for calcification (the literature reference for each study is given in brackets): a) algae, b) molluscs, c) bryozoans and d) corals. The forest plots consider each study individually; the LnRR is plotted with its 95% confidence interval and their values are reported on the right side as LnRR [95% CI]. The summary estimate (mean LnRR) and its confidence interval plotted below.

a) Calcification_Algae

	LnRR [95% CI]
Acetabularia acetabulum [14]	−0.57 [−1.16 , 0.01]
Padina pavonica [14]	−0.22 [−0.49 , 0.06]
Padina pavonica [16]	−1.46 [−1.98 , −0.94]
epiphytes algae [15]	−3.13 [−3.22 , −3.04]
Lithophyllum cabiochae [25]	−0.02 [−0.38 , 0.34]
Litophyllum cabiochae [27]	0.50 [0.25 , 0.76]
MeanLnRR (95%CI)	−0.82 [−2.50 , 0.86]

b) Calcification_Mollusc

	LnRR [95% CI]
Mytilus galloprovincialis [12]	0.11 [−0.52 , 0.73]
Mytilus galloprovincialis [38]	−0.09 [−1.71 , 1.53]
Mytilus galloprovincialis [40]	0.11 [−1.39 , 1.60]
Vermetus triqueter [14]	0.00 [−0.01 , 0.01]
Patella caerlulea [38]	0.45 [−1.24 , 2.14]
MeanLnRR (95%CI)	0.00 [−0.01 , 0.01]

c) Calcification_Bryozoan

	LnRR [95% CI]
Schizoporella errata [20]	0.11 [−0.07 , 0.28]
Myriapora truncata [21]	−0.03 [−0.67 , 0.61]
Myriapora truncata [37]	0.08 [−0.95 , 1.11]
MeanLnRR (95%CI)	0.10 [−0.07 , 0.26]

d) Calcification_Coral

	LnRR [95% CI]
Balanophyllia europaea [11]	−0.15 [−0.28 , −0.01]
Balanophyllia europaea [14]	0.00 [0.00 , 0.01]
Cladocora caespitosa [31]	−0.43 [−1.17 , 0.31]
Oculina patagonica [31]	−0.39 [−1.00 , 0.21]
Cladocora caespitosa [36]	−0.41 [−0.91 , 0.08]
Balanophyllia europaea [38]	−0.33 [−1.02 , 0.35]
Cladocora caespitosa [38]	−1.89 [−3.02 , −0.76]
Corallium rubrum [6]	−0.85 [−2.90 , 1.20]
Corallium rubrum [8]	−0.36 [−0.40 , −0.32]
Madrepora oculata [22]	−0.10 [−1.09 , 0.90]
Lophelia pertusa [23]	0.00 [−2.19 , 2.19]
Madrepora oculata [23]	0.41 [−1.56 , 2.37]
Dendrophyllia cornigera [32]	0.20 [−0.68 , 1.08]
Desmophyllum dianthus [32]	0.12 [−1.84 , 2.08]
Madrepora oculata [33]	0.03 [−0.80 , 0.86]
Lophelia pertusa [33]	0.06 [−0.54 , 0.66]
MeanLnRR (95%CI)	−0.23 [−0.43 , −0.03]

Fig S3: LnRR estimates for growth a) echinoderms, b) molluscs; survival c) echinoderms d) molluscs; photosynthesis e) macrophytes and f) anthozoa (the literature reference for each study is given in brackets). The forest plots consider each study individually the LnRR is plotted with its 95% confidence interval and their values are reported on the right side as LnRR [95% CI]. The summary estimate (mean LnRR) and its confidence interval plotted below
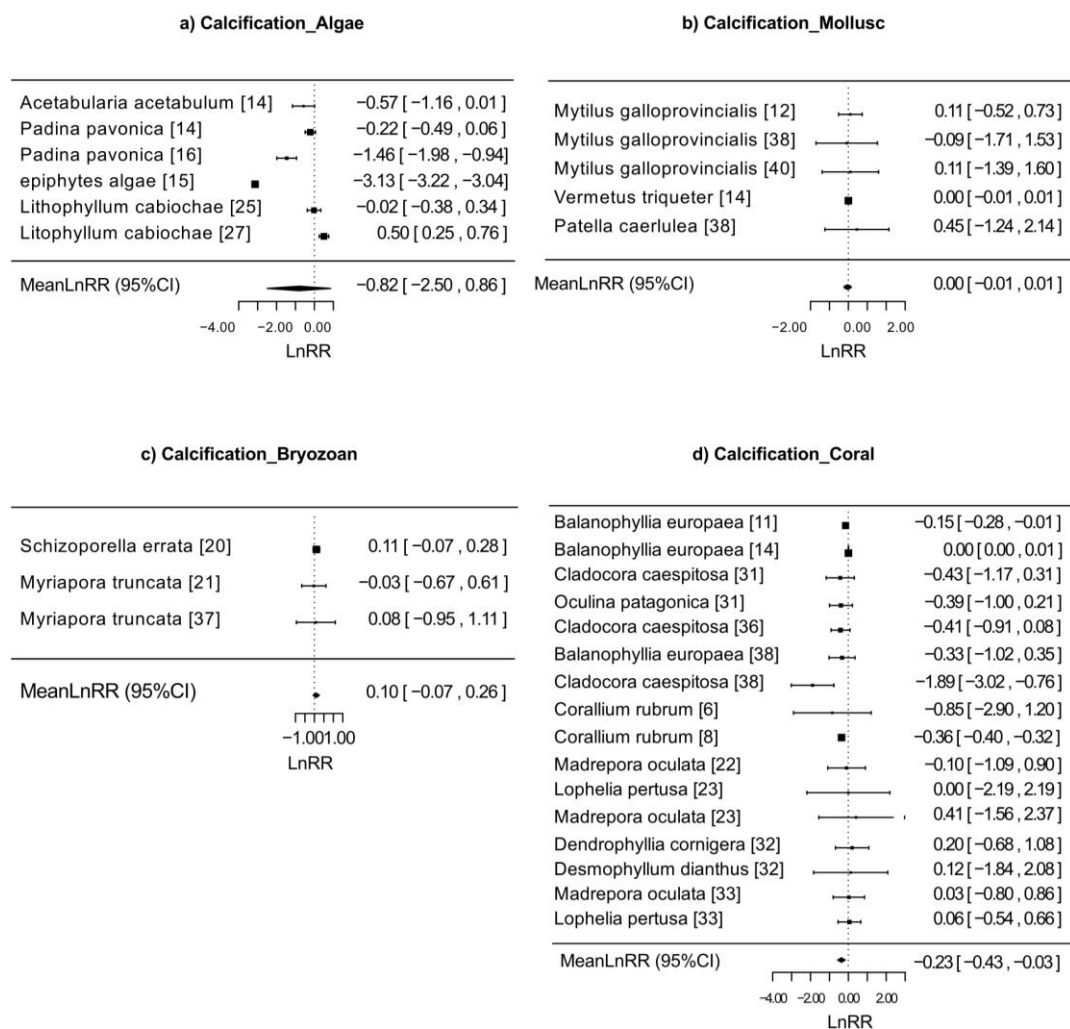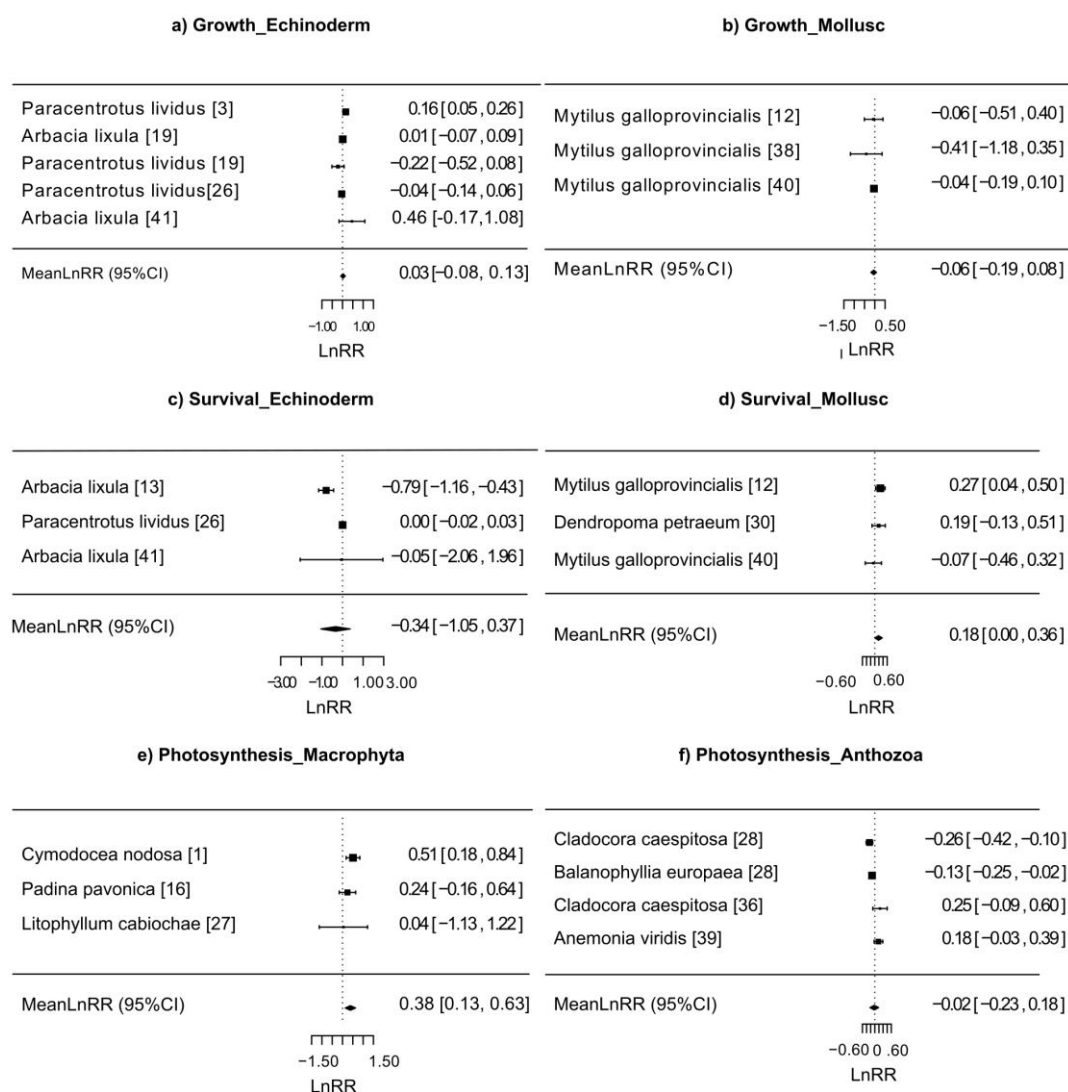
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Chapter 2 - Impacts of marine acidification on the Mediterranean benthic ecosystem services cascade

2 Introduction

The Mediterranean Sea is a largely overexploited basin and threatened by the anthropic pressures (Claudet and Fraschetti, 2010) and has been identified as an hotspot of climate change (Giorgi et al., 2006) by climatic models that predict an increase in warming trend and in the occurrence of extreme events. Along with warming, the Mediterranean Sea is experiencing also the acidification impacts (Lejeusne et al., 2010), for brevity called Ocean Acidification (OA), due to the increased dissolution of CO_2 that alter the carbonate chemistry and lower the pH of the seawater. OA is a phenomenon that could lead to large consequence on marine species, ecosystems, and their functions with potentially large economic and societal consequences. Literature studies have focused on the physiological response of the organisms to the OA, but there is still a lack of knowledge regarding the effects at the ecosystem scale, despite the growing awareness of the need for an ecosystem-based approach in environmental policy and management.

There is a growing body of work demonstrating that seawater acidification has the potential to affect foundation species (Gaylord et al., 2015) and biogenic habitats (Sunday et al., 2016). Recent studies performed on natural acidified sites (vents) demonstrated that acidification decreases the variability of communities, resulting in homogenized and reduced functional diversity at a landscape scale (Kroeker et al., 2013). It is known that changes of habitat complexity may represent key alterations to benthic systems, with potentially large effects on the ecosystem functions and consequently on the entire ecosystem services cascade. Airoldi et al., (2008) reported that habitat loss is one of the major threats to marine biodiversity (Gray, 1997) leading to lower abundances (biomasses) and often to declines in species richness (Airoldi et al., 2008).

Mediterranean marine ecosystems provide a range of goods and services, many of which are of fundamental importance to human well-being, for health and lively- hoods (Costanza et al., 1997; Millennium Ecosystem Assessment (MA), 2005; TEEB Foundations, 2010).

The logic that underlies the ecosystem services paradigm can be represented with the services cascade diagram (Figure 1) originally proposed by Haines-Young and Potschin (2010). The diagram represents the distinction between ecological structures and processes created or generated by living organisms and the benefits that people eventually derive from them. Once the relationship between ecosystem functions and services is known (Figure 1), the consequences of an impact (in our case the acidification) could be assessed in order to project future scenario and create tools to orient the adaptation strategies.
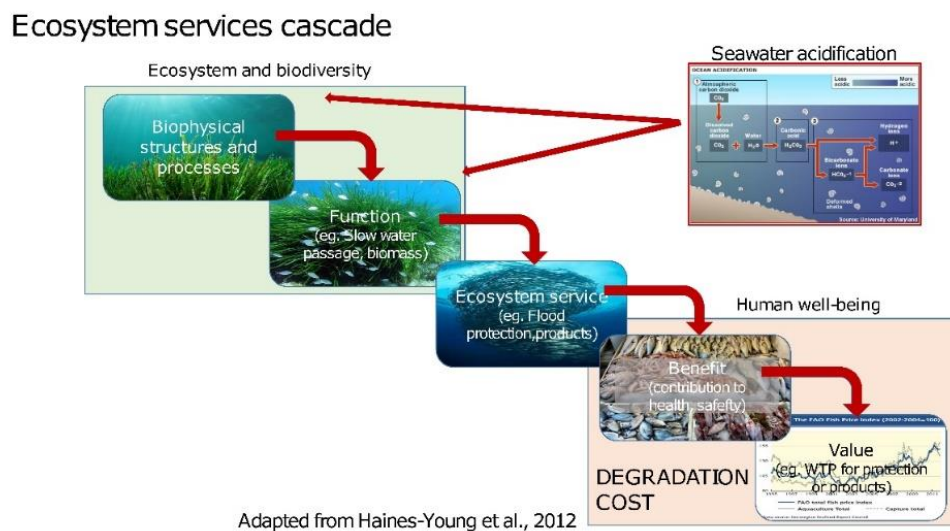

Figure 1: Framework for linking ecosystems to human well-being (adapted from de Groot et al., 2010 and Haines-Young and Potschin, 2010) and the impact of the acidification on the ecosystem service cascade (red arrows). The adverse impacts of the alteration of the seawater chemistry on human well-being could be quantified as 'cost degradation'.

In our work, we focus on *Posidonia oceanica* and coralligenous ecosystems because they are known to provide important and valuable ecosystem services. Due to the vast amount of benefits, that the human society pull out from these ecosystems, it is necessary to value the coupled social-ecological system in order to highlight the impact of the modification on the resource availability on the wellbeing of people (Cullen-Unsworth et al., 2014).

The ecosystem services (ES) are mainly categorised into four types of services: supporting, regulating, provisioning, and cultural. From all these services humans will derive goods and benefits (GB) (Haines-Young and Potschin, 2010 – Figure 2). One of the grand challenges to

be faced by marine ecology in the 21st is the quantification of ecosystem functioning (Borja, 2014), that is the first step to be addressed in order to quantitatively derive the ecosystem services (de Groot et al., 2010). Moreover, being ES anthropocentric, by definition, they need to be addressed considering the specificity of the coupled social-ecological systems in order to take into account the feedbacks between the two systems. This will allow highlighting the effect of changes in resource availability on people wellbeing (Cullen-Unsworth et al., 2014), and the changes of people values on the state of ecosystems and to project future scenarios in order to inform adaptation strategies plans.
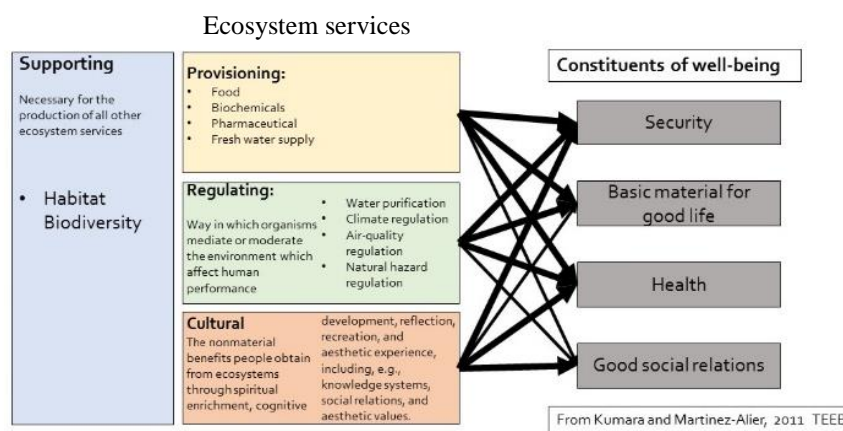

Figure 2: Ecosystem services are the benefits people obtain from ecosystems. These include provisioning, regulating, and cultural services, which directly affect people, and supporting services needed to maintain the other services. Changes in these services affect human well-being through impacts on security, the basic material for a good life, health, and social and cultural relations. These constituents of well-being are, in turn, influenced by and have an influence on the freedoms and choices available to people. Source: Millennium ecosystem assessment, 2005

This work is articulated in 3 sections aiming to, respectively: 1) review the ecosystem services offered by the seagrass and coralligenous ecosystems through literature review; 2) analyse the overall response of the ecosystems to both direct and indirect effects of the acidification using conceptual models; 3) quantify the negative impacts of marine acidification on ecological services related to the provisioning services.

2.1 Services review of seagrass and coralligenous
Seagrass services

Seagrass meadows play important ecological functions in the marine environment as habitat formers providing important ecosystem services (Orth et al., 2006) (i.e. supporting, providing, cultural and regulating) and supporting the well-being of societies by providing many benefits (Cullen-Unsworth et al., 2014).

Seagrass meadows with high structural complexity, such as *P.oceanica,* host a broad range of motile fish and invertebrate fauna and are more valuable habitats compared to other meadows (Mccloskey and Unsworth, 2015). Indeed, higher habitat complexity guarantees species survival, offering protection from predators to juveniles and to adults' specimen (Figure 4-white circles), and allowing the aggregation of individuals thus improving their reproductive success (Tscharntke et al. 2012, Cormont et al. 2016).

Seagrass beds have a fundamental role in maintaining populations of commercially exploited fisheries species (of both fish and invertebrate species) (Jackson et al., 2015) by providing permanent habitat and allowing completion of the full life cycle. Moreover, they serve as a temporary nursery area for the successful development of the juvenile stages; a feeding area for various life-history stages; a refuge from predation; indirectly supporting coastal food webs (Vizzini et al. 2002) and water oxygenation (Chen et al., 2012).

For example, the *P. oceanica* meadows host more than 400 species of algae and thousands of animals (Personnic et al., 2014) at different life phases. Heck et al., (2003) performed a review of the extensive literature in order to test the importance of the seagrass meadows as nursery areas for juvenile fish and invertebrates. The authors found that juvenile abundance, growth and survival were generally higher in stable seagrass meadows compared to unstructured habitats (Heck, 2003).

Shoot density and leaves length increase the bottom roughness and are among the major contributor to the reduction of the near-bed water velocity (Infantes et al., 2012) enhancing the deposition of sedimentary particles and the sediment stabilisation and therefore improving water clarity.

Furthermore, in autumn, a massive shedding of leaves that build up on the beaches in dense deposits occurs. When conditions are suitable, the accumulated material can consolidate and then produce compact and resistant structures that can stay in place for several years, providing very effective protection against coastal erosion (Boudouresque et al., 2012).

Seagrass meadows are highly productive ecosystems with a net primary production (NPP) equivalent to 14.8 tons CO_2 ha yr^{-1} (Duarte et al., 2013) that accumulates below-ground almost

the 30% of the fixed organic matter (Pergent et al., 2014). The organic compound is buried into the so-called "matte", which is the soil fraction composed by rhizomes, roots and sheaths. These structures, that could reach 6 meters height in case of *P. oceanica* meadows, constituting a long-term carbon sink (sequestration) (Pergent et al., 2014, Figure 3A). Moreover, *P. oceanica* meadows produce a considerable quantity of oxygen and this function is relevant to enhance the quality of the water column and the wellbeing of the ecosystem. For example, it has been estimated that *P. oceanica* meadows at 10m depth produced more than 14 litres of oxygen per day per m^2 (Bay, 1978).

Another important service that the seagrass provides to humans is the bioremediation of waste by trapping and storing the nutrients, thus filtering the land inputs to the coastal water (Hemminga and Duarte, 2000). Recently, Lamb et al., (2017) have discovered that the presence of seagrass meadows reduce the relative abundance of potential bacterial pathogens to humans and marine organisms, by 50%.

The Mediterranean seagrass meadows can provide different levels of structural complexity that depend on the different plant morphology and bed architecture and is determinant of the habitat value of seagrass beds. Pergent (al., 2014) distinguished 3 levels of meadow's complexity. The lowest is found in *Halophyla stipulacea* meadows. *Cymodocea nodosa* and *Zostera* spp. meadows show comparatively high structural complexity and constitute the pioneer species in the succession, while *P. oceanica* meadows constitute the ultimate stage, "climax", (Pergent et al., 2014).

Coralligenous services

The underwater seascape of the Mediterranean Sea is enriched by hotspots of bioconstructions such as coralligenous outcrops and mäerl beds, comprising coralline algal frameworks that grow in dim light conditions. Because of their extent, biodiversity and production, coralligenous and mäerl habitats rank among the most important ecosystems in the Mediterranean Sea, and they are considered of great significance both for fisheries and carbon regulation (Martin et al., 2014). According to some recent estimates, the coralligenous is known to host over 1600 species (Ballesteros, 2006). Many commercially important species are known to live, feed or reproduce in this biotope among which the precious red coral *Corallium rubrum* (Ballesteros, 2003). Coralligenous assemblages are considered the most important hotspots of species diversity in the Mediterranean, together with *P. oceanica* meadows (UNEP, 2007).

The Protocol for Special Protected Areas (SPA/BD) of the Barcelona Convention for the conservation of Mediterranean biodiversity (SPA/BD, 1995) incorporated coralligenous reefs among the habitats that need a rigorous protection, and in 2008 was developed the "Action plan for the conservation of coralligenous and other calcareous concretions in the Mediterranean Sea" (Unep-Map-Rac/Spa, 2008).

Coralline algae bioconstructions represent a shelter, nursery, and/or refuge for many invertebrates (Spotorno-Oliveira et al., 2015) and fishes both at juvenile and adult stages. Nevertheless, the role of coralligenous reefs is still under study since the great complexity of this habitat makes finding juveniles in cavities difficult (Guidetti and Boero, 2002).

Rocky banks dominated by coralligenous algae are well known by fishermen as they aggregate fish, especially during spawning of species like e.g. *Epinephelus marginatus* and *Spondyliosoma cantharus* (Sahyoun et al., 2013). They are also known as places where fish aggregate for feeding, which is the case of many large predators like *Dentex dentex, Seriola dumerili* and *Sphyraena viridensis* (Vacchi et al., 1999).

Corals and coralline algae, due to their calcareous skeleton, are some of the major contributors to CO_2 fluxes acting as a carbon dioxide sink in geological times and a carbon source on a human time scale. They take carbon from seawater where it is available as dissolved ions and fixed into their skeletal structures. When these skeletal structures disaggregate, they become important sources of inorganic carbon (Paoli et al., 2016).

Coralligenous creates spectacular seascapes built by gorgonians that are among the preferred diving sites in the Mediterranean Sea (Paoli et al., 2015).
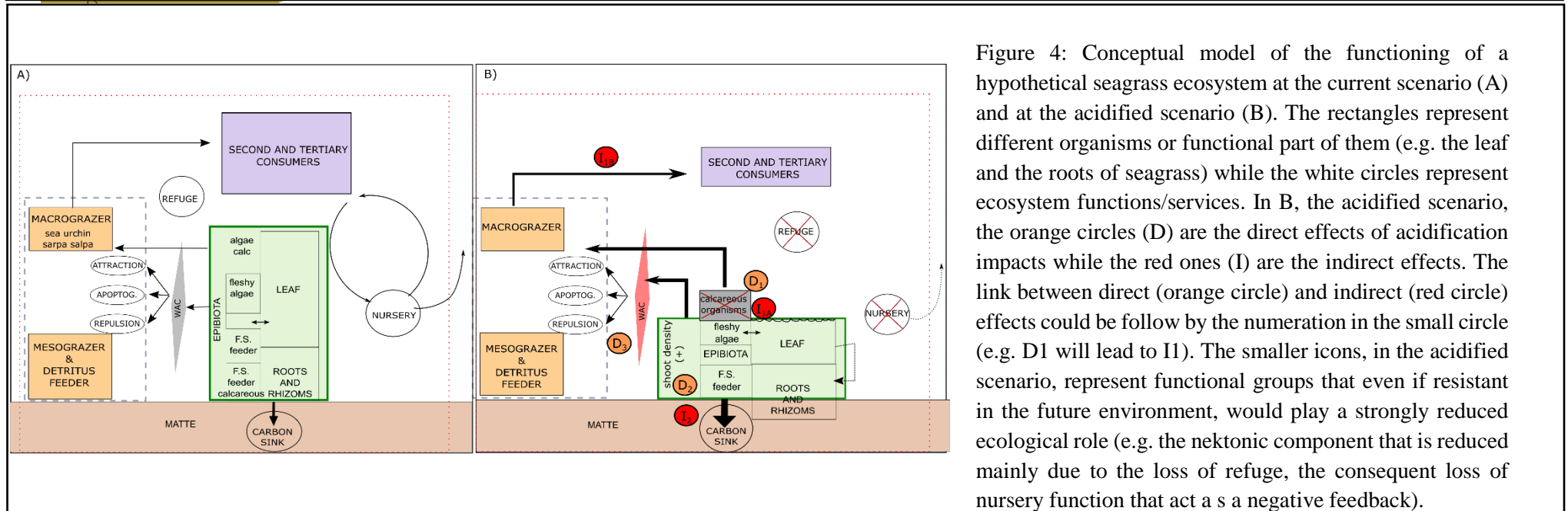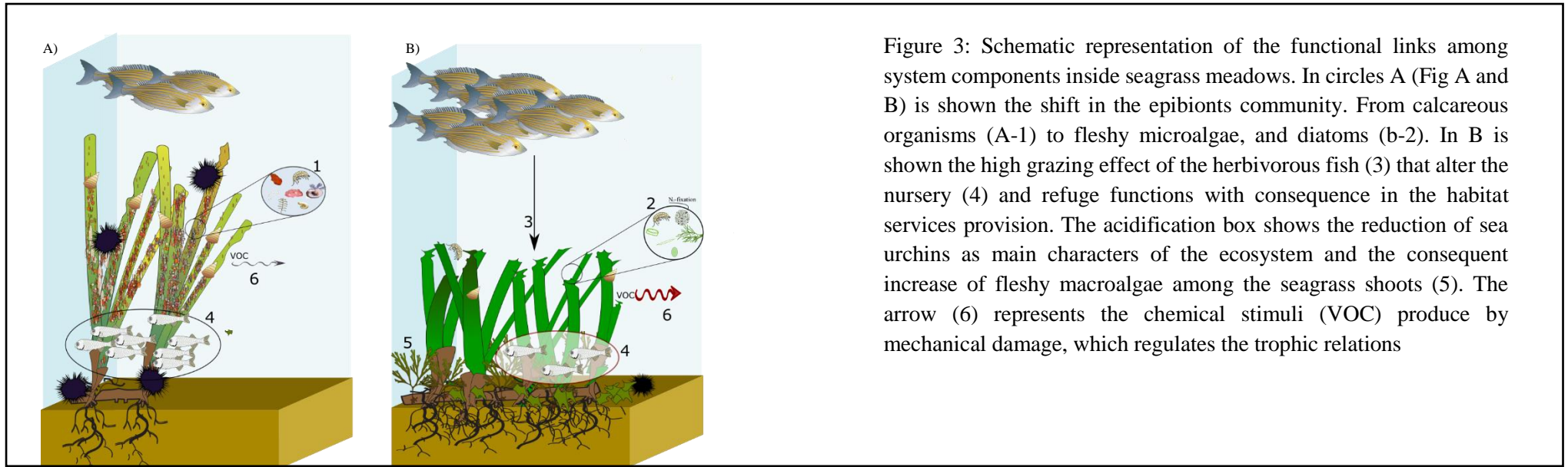
Assessment of the ecosystems responses to direct and indirect acidification effects through conceptual models

In this section, two conceptual models are presented, based on the best available knowledge on these ecosystems and on the effects induced by the acidification. The first model represents the seagrass meadows, in particular the foundation species - *P. oceanica* - and the second represents the coralligenous reefs. The models analyse the complex interactions between the structuring elements of these ecosystems direct and indirect effects of OA on these ecosystems (from Figure 3 to Figure 7). In particular, the models identify i) the major systems components (SC) and their interactions, synergies and feedbacks; ii) the functions that the SC create, iii) the impacts of the OA on each of the above-mentioned SC's and functions. The scenarios created from the combination of the direct and indirect effects of the acidification can provide indications about the direction of OA impacts. Even though qualitative, the analysis based on conceptual models is a useful tool to identify the status of the ecosystem services at current conditions and hypothesised the status at future acidified conditions. The conceptual models are propaedeutic to the quantitative assessment of ecosystem services values before and after OA impacts. Different preference-based approaches to assess the values of coralligenous and P. oceanica ecosystems have been further applied in the next sections of this thesis.

Posidonia oceanica model

The seagrass conceptual model has been represented in Figure 3 and Figure 4. In these figures, the pristine and the acidified states, are compared in panels [A] and [B].

Seagrass leaves and roots host a large variety of epibiont organisms (Figure 3A-1), micro and macroalgae, both fleshy-filamentous and calcareous (i.e. coralline algae). On turn, the epibionts support a diverse community of mesograzers (small invertebrate grazers: decapod crustaceans, gastropod molluscs, and polychaetes (Gambi et al., 1992; Scipione, 2013) including fishes that are targeted by artisanal fishers. Seagrass leaves and shoots host a community of the filter feeders, suspensive feeder (i.e. molluscs, foraminifera, spirorbids, hydrozoans, bryozoans, sponges and protected bivalves such as *Pinna nobilis*) and the detritus feeders (Figure 3A).

Figure 3: Schematic representation of the functional links among system components inside seagrass meadows. In circles A (Fig A and B) is shown the shift in the epibionts community. From calcareous organisms (A-1) to fleshy microalgae, and diatoms (b-2). In B is shown the high grazing effect of the herbivorous fish (3) that alter the nursery (4) and refuge functions with consequence in the habitat services provision. The acidification box shows the reduction of sea urchins as main characters of the ecosystem and the consequent increase of fleshy macroalgae among the seagrass shoots (5). The arrow (6) represents the chemical stimuli (VOC) produce by mechanical damage, which regulates the trophic relations

Figure 4: Conceptual model of the functioning of a hypothetical seagrass ecosystem at the current scenario (A) and at the acidified scenario (B). The rectangles represent different organisms or functional part of them (e.g. the leaf and the roots of seagrass) while the white circles represent ecosystem functions/services. In B, the acidified scenario, the orange circles (D) are the direct effects of acidification impacts while the red ones (I) are the indirect effects. The link between direct (orange circle) and indirect (red circle) effects could be follow by the numeration in the small circle (e.g. D1 will lead to I1). The smaller icons, in the acidified scenario, represent functional groups that even if resistant in the future environment, would play a strongly reduced ecological role (e.g. the nektonic component that is reduced mainly due to the loss of refuge, the consequent loss of nursery function that act a s a negative feedback).
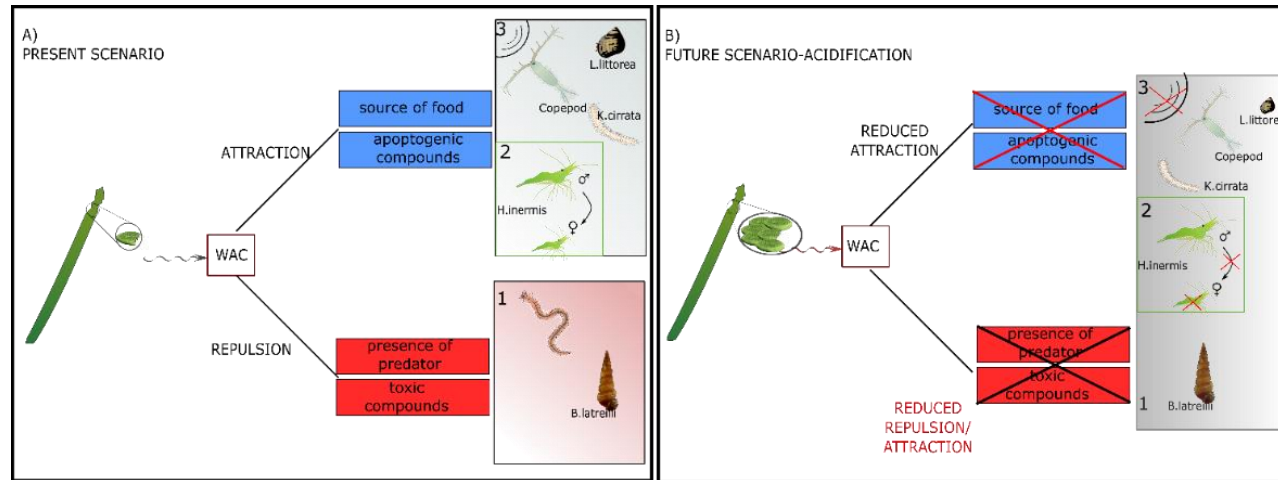
Figure 5: Schematic representation of the consequence of the acidification on invertebrates' reaction to the chemical compounds. After a mechanic damage, seagrass and algae produce WAC (wound-activated compound) compounds that trigger specific reactions in some invertebrates (Maibam et al. 2014). Individual species of invertebrates (in the green box in A) could be attracted by the localization of a food source (e.g. the microalgae) or, conversely, be deterred by the WAC compounds (A red boxes-1) because the odour of damage leaves may indicate the presence of predators.

Some diatoms found in association with the seagrass leave (genus *Cocconeis*) produce particular volatile compounds that act as apoptogenic compounds for some species of shrimps (*Hippolyte inermis* –A green box 2) (Zupo and Messina, 2007). Conversely, in an acidification scenario is observed a weaker repulsion even converted in slight attraction (e.g *Bittium latreilli*; B -1→ from red to green boxes), a loss in the signal reception (B-3) and alteration in the proterandric sex reversal action of *H. inermis* (B-2) leading to the loss of *H. inermis* population stability (Zupo et al., 2014).

Acidification studies performed both in mesocosm and at natural vents sites have suggested that the seagrass will benefit directly from OA, increasing the photosynthetic rate (Apostolaki et al., 2014). However, for *P. oceanica* the evidences are limited and not uniform (Guilini et al., 2017) suggesting that the extent of benefit for *P. oceanica* productivity over the next century may be minimal. Indeed, the available data of significant changes in photosynthetic rate refer to studies in which the change in pH was larger than the expected from the end of the century at business at usual scenario (IPCC 4th, 2007) (Invers et al. (1997): 9.2 to 7.9 pH; Invers et al. (2001): 8.2 to 6.0 pH; Cox et al. (2015) 8.1 to 7.3 pH_T; Guilini et al. (2017) 7.6 to 5.5 pH_T). On the contrary, no difference in *P. oceanica* photosynthesis (Cox et al., 2016, 2015; Guilini et al., 2017; Hendriks et al., 2017) and in electron transport rate or shoots density (Hall-Spencer et al., 2008) were found at the expected condition for the end of the century (pH_T 7.7). The exceptions are Donnarumma et al. (2014) and Garrard et al. (2014) that reported an increase in the shoot density at Ischia Island that may depend on the shorter leaves (due to mechanical damages) found in the acidified site that enhance the quantity of light reaching the leaves enhancing the shoot density. On the contrary, Guilini et al. (2017) at Panarea Island and Cox et al. (2015, 2016) in mesocosm studies at Villefrance did not found any significant difference in the shoots density between control and acidified sites highlighting how the increase in shoot density may be related to other factors. Considering all these results we opted to adopt the degradation hypothesis related to the *P. oceanica* meadows that are more consistent with the continuing decline of *P. oceanica* meadows happening since 1990 (Pergent et al., 2010).

Considering the indirect effects, studies suggest that seawater acidification leads to a consistent loss of crustose coralline algal epiphytes living on the seagrass leaves (Apostolaki et al., 2014; Figure 3B [2]) promoting the increase of fleshy algae (Figure 3B [5]) and diatom communities. The increasing abundance of fleshy algae and diatoms will likely inhibit the light availability for the plant -thus promoting the regression of seagrass (Pergent et al., 2014). Moreover, the change in epiphytic composition, from crustacean coralline algae to fleshy ones, may favour the grazing pressure due to the increased palatability of the leaves (Apostolaki et al., 2014, Figure 3B [3]). The palatability of the plant further increases with the reductions of the phenolic content of seagrass leaves (Arnold et al., 2012). The phenolic are volatile organic compounds, VOCs that act as a natural deterrent of the grazing activities. The volatile organic compounds -VOCs among which there are the WAC -wound activated compounds – (Figure 3 [6]) reach the meadows community mediating the species responses (Zupo and Nelson 1999; see Figure 3A). The WAC compounds are dispersed in the water after mechanical damages of the leaves or of

the epiphyte community. The odour represents an attractant for some invertebrates that need to maximise the search for food, and a repellent for other invertebrates, for which mimicry and defence from predators represent the most important behavioural constraints (Jüttner et al., 2010; Figure 3 [6] and Figure 5).

The VOCs control grazer preference and grazing rates altering the palatability and feeding rate in a range of consumers, including fishes and sea urchins (Arnold et al., 2012 and references therein). The acidification yields a chemical alteration of these compounds and a consequent change in the behavioural responses of the associated species (Zupo et al., 2015) up to community levels due to the change in the prey-predator interactions (Figure 5).

Epiphytic diatoms cover of seagrass highly increases at acidified conditions -up to 6-fold (Johnson et al., 2013)- and the consequence higher production of VOCs altered by the acidification could lead to deep change in the seagrass meadows associated communities. The biomass of epibionts are regulated by grazing gastropods, populations of which have been found to decrease at low pH (Hall-Spencer et al., 2008; Johnson et al., 2013) (Figure 5 [see *Littorina littorea*]). These invertebrate grazers play a pivotal organizing role facilitating seagrass dominance by consuming their competitively superior epiphytic (Duffy et al., 2003).

The macrograzer community of the Mediterranean meadows (especially *P. oceanica*) feeds directly on the leaves (Figure 3 and Figure 4 orange box). Sea urchins (i.e. *Paracentrotus lividus*) and teleost fishes, in particular *Sarpa salpa*, mostly represent it. Sea urchins are both the main grazers of the seagrass leaves but also key organisms that play an important role in controlling the equilibrium among different algal communities (Asnaghi et al., 2013).

Seagrass meadows host many secondary consumers such as meso-carnivores that rely on the sessile epibiota, carnivores as decapod crustaceans, cephalopods and gastropod molluscs, echinoderms and fishes; Figure 4 purple box, they also host tertiary consumers and higher level consumers (i.e Scorpaena spp. or *Conger conger*), whose diet is exclusively piscivorous (Boudouresque et al., 2012; Giakoumi et al., 2015).

The above-mentioned reduction and alteration of the epibionts community (mostly composed of calcareous algae that are threatened by acidified conditions Figure 4B:D1) and the reduction in phenolic contents will increase the palatability of the herbivorous fishes for the leaves (Figure 4B: I-1A (Arnold et al., 2012)). *P. oceanica* has a shoot lifespan estimated up to 50 years and a slow growth strategy, thus it is not able to cope with high levels of grazing. Under optimal conditions, the grazing of leaves is estimated at 5% (mean) of net primary production (Cebrian

and Duarte, 2001) but it has been assessed to reach the 57% of the leaf production (19% and 33% by urchins and *S. salpa* respectively) in some areas (Boudouresque et al., 2015; Prado et al., 2007). The grazing activity of the herbivorous fish *S. salpa* is responsible for the reduction of the canopy height (Garrard, 2013) that may strongly affect the spatial distribution of marine fishes and invertebrates (Farina et al., 2009; Pagès et al., 2012). It is known that extremely high grazing pressure can in some cases exceed the leaf production (Prado et al., 2008). In addition, it has been estimated a higher abundance, more than double, of the *S. salpa* under acidified in situ conditions (Mirasole, 2017). In order to counterbalanced the grazing pressures, it has been hypothesised an increase in translocation of photosynthate into belowground compartments, which leads to an increase in the growth of roots and rhizomes (Hall-Spencer et al., 2008; Zimmerman et al., 1997; Russell et al., 2013) at least until the leaves can afford the physical damage and the sedimentation rates.

Our assumption about the loss of habitat complexity is even reinforced by the increase presence of the alien species, in particular herbivorous fish (e.g. Siganidae) which may compete with Mediterranean species (i.e. *S. salpa* and *Sparisoma cretense*) increasing the herbivorous pressure. The invasion of alien species (i.e. *Siganus* spp.) is already responsible for the loss of seagrass meadows in the southern Mediterranean (Bianchi et al., 2014; Ozvarol et al., 2011) and for the formation of barren grounds in this area (Pergent et al., 2014).

As a result of a meta-analysis made on Mediterranean marine organisms, Zunino et al. (2017) found that sea urchins are among the losers in a future acidified sea. In turn, their decreasing abundance will favour the algal communities that are generally advantaged by the acidification (Asnaghi et al., 2013). Based on literature review (Apostolaki et al., 2014; Caronni et al., 2015; Garrard and Beaumont, 2014) the conceptual model shows that urchins grazing events are compensated for and enhanced by the intense activity of herbivorous fish that prefer the seagrass leaves to macroalgae (i.e. *S. salpa* see above) (Figure 4B: I1a).

The acidification impacts and the consequent change in the habitat complexity could lead to the shift of high-value ecosystem services, provide by complex seagrass meadows (i.e. *P.oceanica*) (Mccloskey and Unsworth, 2015) to less valuable services.

Ocean acidification is closely coupled with other anthropogenic stressors, notably ocean warming. Warming has been predicted to result in a complete extinction of *P. oceanica* meadows by the year 2049 (Jordà et al., 2012), therefore the hypothesis that increased CO_2 availability would enhance seagrass production and help to alleviate thermal stress was not fully supported (Cox et al., 2016; Guilini et al., 2017). In addition, as many authors highlighted, the

continuing decline of *P. oceanica* meadows from 1990 despite the increase in CO_2 is a further demonstration of the limited capacity of ocean acidification to buffer seagrass vulnerability to disturbances (Cox et al., 2016). *P. oceanica* has been on the IUCN Red List since November 2010 (Pergent et al., 2010) and studies have shown the decline of its meadows since the second half of the 20th century: lost between 10% and 38% in areal extent in 100 years, especially near urban areas (Thomas et al., 2005; Deter et al., 2013; Marbà et al., 2014). The origin of this regression is mainly coastline artificialization (Campagne et al., 2015).

Coralligenous model

The crustose calcareous algae (CCA) have an important role in structuring the habitat both as builders and also as inducers of larval settlement of hard corals (Tebben et al., 2015, Figure 6-A[11]). The corals, both zooxanthellatee and azooxanthellatee, as living structures protruding from the seafloor, increase the habitats complexity providing structural habitat for other species ("habitat engineer" *sensu* (Jones et al., 1994), Figure 6 [8-9]). The corals' shapes allow the intercept of settling propagules and their relations with substrata create favourable habitats for both larval and adult settlement, increasing food sources, and contributing to the species richness (Paoli et al., 2016). The conceptual model that we proposed is a synthesis of the different typology of coralligenous. It is observable the concretion made by coralline algae (Figure 6A [6]), the corals aggregation (Figure 6A [1,4]), and the mäerl substrate (Figure 6A [5]).
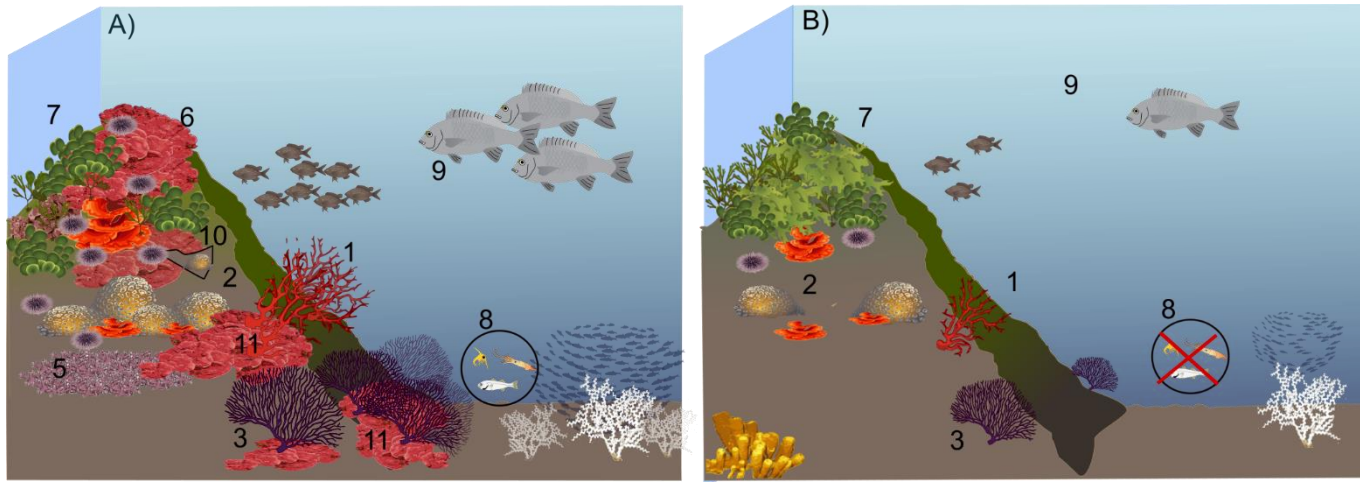
Figure 6: Schematic representation of the coralligenous ecosystem. In box A are shown the azoxanthellatee corals (1-3, I.e the precious *Corallium rubrum* and the gorgonians) the zooxanthellatee corals- 2- (i.e. *Cladocora caespitosa*) and the mäerl bed (5).

These components of the ecosystem are important as organisms aggregating points (9) and nursery (8). The sea urchins and the coralligenous algae (6) play an important role allowing the creation of recruitment spaces (10) and keeping under control the growth of the fleshy algae (7). The abundance reduction of both corals, coralligenous algae and sea urchins (box B) could lead the fleshy algae to dominate the environment. Ephemeral fleshy algae do not create high levels of habitat complexity. The consequences could be the loss of the aggregation points (9) and the nursery functions (8)
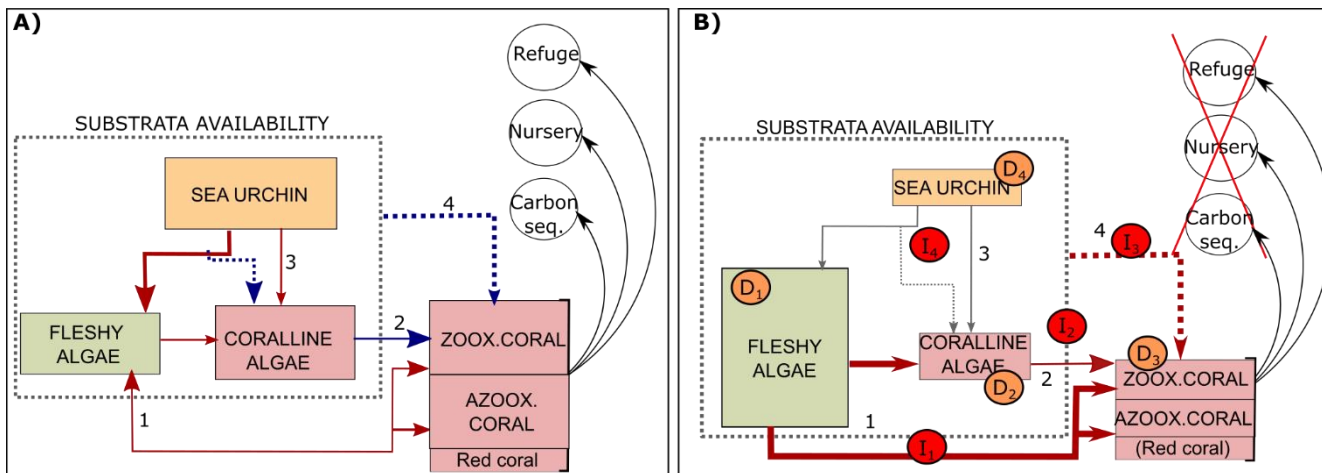

Figure 7: Conceptual model of the functioning of coralligenous ecosystems at the current scenario and at the acidified scenario. The rectangles represent different organisms while the white circles represent the ecosystem functions. The orange circles are the direct effects (D) of acidification impacts while the red ones are the indirect effects (I). Smaller icons represent functional groups that may still be present in future scenario but play a strongly reduced ecological role. Blue and red arrows represent, respectively, positive and negative effects of one species on another that may be reversed in the acidification scenario. Dotted lines indicated indirect effect (e.g., the interaction among sea urchins, coralline algae, and fleshy algae Figure 7, [box A – 4]) makes substrata available for coral settlement. Grey lines (Figure 7, [box B – 3]) indicate a loss of relationship.

In coralligenous environment, there is an intense competition between sessile benthic organisms that can completely saturate the available space (Ballesteros, 2006). The competition is especially strong between algae and corals since access to light and space is fundamental to the survival of both (Figure 7A [1]). The macroalgae, competing with corals for the fundamental resources, have a range of detrimental effects on them (Figure 7, [box A]). Relative to present-day conditions (A panel), future acidification (B panel) will favour fleshy/filamentous algae (D1) (Zunino et al., 2017) and have direct and indirect negative impacts on coralline algae (Figure 7D2- I1), corals (Figure 7 D3-I1) and sea urchins (Figure 7 D4).

Filamentous algae, especially the ones belonging to the eco-physiological group of the turf algae, can lead to hypoxia, lower corals fecundity, and can inhibit corals recruitment (Linares et al. 2012). The coralline algae have important role (Figure 7A [3]) to ensure a recruitment place for the coral larvae (Figure 6A [10-11]; Figure 7A [dotted box]). Sea urchins, which have a projected decrease in abundance by 79% (Zunino et al., 2017) due to the ocean acidification (Figure 7B [D4]), are key organisms that play an important role in controlling the equilibrium among different algal communities. The loss of sea urchins (Figure 7 box B-D4) and calcareous algae (Figure 7 box B-D2) combined with the advantages that fleshy algae may have (Figure 7 box B-D1 and I1), due to the acidification, may trigger a phase shift towards fleshy algae dominated environments (Asnaghi et al., 2013).

Moreover, the negative effects of OA on coral calcification (Figure 7, [box B-I3]) and indirectly on coral recruitment (by reduction of available substrata for recruitment) would lead to a reduction in habitat complexity. Indeed, the estimated reduction in calcification rate of the calcareous organisms (Zunino et al., 2017) could become substantial if extrapolated through the lifespan of the long-lived species such as corals. Recent field studies in the Mediterranean Sea vents have demonstrated a strong impact of low pH up to inhibit the presence of calcareous corals (Hall-Spencer et al. 2008; Cigliano et al. 2010; Dias et al. 2010; Rodolfo-Metalpa et al. 2010). The studies indicate that seawater acidification at levels predicted for different 2100 IPCC scenarios will decrease the already very low growth rates of these species (Cerrano et al., 2013). Fabricius et al. (2014) highlighted that the OA and the climate-change-related disturbance (i.e. warming, severe storms, coral bleaching) would affect the growth and survival of tropical scleractinian corals likely shifting the corals' habitat toward structurally simplified coral communities (Fabricius et al., 2014). Similarly, the reduction in complexity associated

with the temperate coral reef may cause a shift in the associated community of consumers and thus the modification of the ecosystem services that coralligenous assemblages can provide.

2.2 Assessment of the acidification impacts on functioning and services provision

P. oceanica and coralligenous provide a number of important provisioning, regulating, habitat, and cultural services. Below we assessed some of these services grouped according to MEA (2005). We evaluated them by applying indexes, indicators, and using literature data in order to evaluate how OA will affect the provisioning of those services in the future. This study refers to the country-scale level of Italy and the valuation is directed in the Italian socio-economic context.

Among the relevant services in the context of OA, we analysed provisioning services using fisheries landing indicators (following section 2.2.1) and cultural services using values related to the scuba-diving tourism (Chapter 4). For each of these services, we have estimated an economic value and/or a cost of degradation due to the impacts of the OA. The measurement of monetary value is straightforward when there is an institution (market), where demand and supply meet. In these cases, we have used the trade price as an indicator of the market value (provisioning service case). When an institution where trade occurs is lacking, and no price exists, valuation methodologies that mimic market behaviour can be adopted, such as revealed and stated preference techniques (cultural service case).

We defined the current status and the future acidified status of the studied ecosystems to analyse the relative change in service provision. The latter is described as the output of the conceptual models presented in the above section, which projected a loss of habitats complexity due to the acidification impacts.

2.2.1 Provisioning services

Only few studies have addressed the direct effects of the acidification on fishes in the Mediterranean Sea. However the few available data -for the Mediterranean sea (Mirasole, 2017) and for other regions- reported that adult fishes are not directly impaired by ocean acidification. Indeed, it has been found that the physiological performance of the fishes allows them to cope with extracellular acidosis caused by ocean acidification (review in Lacoue-Labarthe et al., 2016). Early-life stages of some fishes seem to be more affected by direct effects of

hypercapnia, due probably to the non-maturity of their physiological systems and acclimation capacities (Portner and Farrell, 2008) while others do not. For example, recent data suggest that early life stages of cultured species such as the seabass, *Dicentrarchus labrax* (Moronidae) (Pope et al., 2014) and also adults of fished or farmed species as *Sparus aurata* (Sparidae) are resilient to ocean acidification. Studies performed at the vent sites (Mirasole, 2017) revealed slight changes in the community structure between control and acidified sites. Fish species-specific number of individuals between the two sites differed little, but species richness showed a decrease in the acidified site compared to the closer control site.

Seagrass meadows and coralligenous concretions are considered to have a fundamental role in maintaining populations of commercially and recreationally exploited fisheries species by indirectly supporting coastal food webs (Vizzini et al., 2002) and directly providing 'essential fish habitat' (*sensu* Auster and Langton, 1999). Their role is strictly associated with the complexity of the structures that they create and that are relevant for fish development and growth. The decline of the structural complexity of these biogenic habitats could influence the fitness of the target species of commercial interest. The loss of essential fish habitats may result in species gains and losses, and changes in community structure both at seagrass and coralligenous levels. Several studies have estimated the value of provisioning ES from seagrass meadows while, up to our knowledge, no one has estimated yet the value related to the coralligenous ecosystems.

Therefore, we analysed the impact of the acidification on the provisioning of ES as an indirect effect affecting the essential fish habitat of commercially important species.

2.2.2 Methods

Here, we valuate the food provisioning service offered by the *P. oceanica* and coralligenous habitats by applying a landing indicator and its economic value obtained through a market analysis. The possible loss of value due to the OA impact has been therefore valuated as a consequence of the loss of habitat complexity.

The results have been compared with those obtained in other studies, using different methods. Italian fisheries are among the most important fisheries in the Mediterranean, constituting, according to Food and Agriculture Organization of the United Nations statistics, roughly 30% of it all catches (Piroddi et al., 2015).

We assessed the demersal fisheries production in Italy for unit area of coralligenous and seagrass habitats developing an index of habitat use (H) for each species (i) of commercial

interest. Species were identified as being commercially targeted if they were listed on the General Fisheries Commission for the Mediterranean (GFCM) fisheries capture statistics (1950–2010) (Food and Agriculture Organisation 2012).

Firstly, we identified the species associated to coralligenous and *P. oceanica* meadows in the Mediterranean Sea. Then, we identified all the habitats (H) (i.e. lagoon, estuary, coarse sediment, deep mud, seagrass, shallow sand and mud, hard rocks and coralligenous) that are used by the selected species during their life cycles. This process was done by merging the results of a systematic literature review (Campagne et al., 2015; Guidetti et al., 2002; Jackson et al., 2001; Mangos et al., 2010 see Supplemtenary 1 for details) with those obtained from experts opinions.

Secondarily, a weight (W) was assigned to each species for each habitat (h): 0, if the selected habitat (h) is not used by the specie *i*; 0.5 if the selected habitat (h) is used during the juvenile or during the adult stage of the species *i*; and 1 if the habitat (h) hosts both the juvenile and the adult phases. Juvenile stage, according to Jackson (et al., 2015) includes egg development time, larval phase duration, and juvenile stages up to sexual maturity or adulthood. For each selected species we calculated the landing biomass (FAO, 2014) and then we calculated how much of the landing biomass (B_i) could derived from each habitat depending on the habitat use of each species. The index associates the landing biomass of each species (B) to each habitat (h) that supports a part or the whole species life-phase.

We defined the index as the biomass ($b_{i,h}$) of the species (i) associated to one selected habitat (h):

$$b_{i,\ h} = \frac{B_i}{\sum_H A_H \cdot W_{H,i}} \cdot A_h \cdot W_{h,i}$$

Where B_i is the landing biomass for each species, ($W_{h,i}$) is the weight of the area type h associated to the species i, A_h is the surface of the habitat h,

The landing biomass (B_i) of each commercially target species was obtained from the 3 years (2010-2012) capture production time-series of the FAO FishStat database (FAO, 2014), in order to take into account the intrinsic environmental and fishery efforts variability.

Seabed habitat type differentiation rests on the EU Marine Strategy Framework Directive and the EU-level marine habitat typology in Eunis and EUSeaMap.

The area for each habitat (A_h) was computed with QGIS from the EMODnet seabed habitat maps (version 2014) which provided detailed information on the distribution of coralligenous reefs and seagrass beds in the Italian coastal water. To classify the habitat typology, we have

followed the EUNIS classification and we have clumped the habitat into 6 main groups (i.e. coralligenous and mäerl formations, seagrass meadows, hard rock substrata, seagrass meadows, sandy habitat- see Appendix table 1). We have further added estuaries and lagoons since they have a pivotal role for many commercial species.

The scientific literature recognizes the existence of two main approaches, called the preference-based approaches and the biophysical approach, for the estimation of nature's value (TEEB, 2010). The preference-based approaches *"rely on models of human behaviour and rest on the assumption that values arise from the subjective preferences of individuals"* (TEEB, 2010).

Using a preference based approach, we computed the fisheries economic value by multiplying the landing data (FAO, 2014) with their market economic values. The market value of each species was obtained from the ISMEA database (www.ismea.it). Values included in the analysis were based on current market values representing the price at the time of the ISMEA assessment and it is the average value of different market places and processes of supply and demand (Unsworth et al., 2010). We estimated the current economic value of coralligenous and seagrass habitats in Italy as food providers and projected its future change -based on scenario of seawater acidification- through a value transfer technique.

2.2.3 Results

The mean national catches (FAO zone 37) from 2010 to 2012 accounted for 209,554 ± 13,347 tonnes for economic value of 1039.46 ± 99.06 millions of € (ISMEA). From the total list we have identified 38 demersal species that are related, at least is some stage of their lives, to the seagrass or coralligenous habitats (Table S2). Most of them are ubiquitous species, which are also linked to other habitats, such as lagoons, hard-rock substrates, shallow or deep sandy habitats, during their whole life cycle or during their juvenile or adult stages (see table S2). The total landing of the identified species were 46'727.33 ± 162.54 tonnes for an economic value of 394.13 ± 99.06 millions of €.

Almost half of the species linked to the seagrass habitat (19, see Table S2), spend both the juvenile and the adult stages associated to the seagrass habitat while the remaining part of their life cycles are not directly associated with seagrass meadows, but they move through onshore waters forming large schools. Among all the taxa, just few (i.e. Mugilidae, Mullidae, Scorpaenidae, and different typology of cephalopods) contribute to almost the 70% of the total

biomass and monetary value related to the seagrass meadows. These species are typically found swimming or hiding in seagrass meadows as juvenile and adults

Ten species were predominantly found linked to the coralligenous habitat. Among them we have found crustacean (*Palinurus elephas, Squilla mantis*) and other fishes (*Epinephelus marginatus*, Scorpenidae as well *Mullus barbatus M. surmuletus, Sepidae, Octopus* spp., *Seriola dumerili*) that account for 77% of the total landing value associated to the coralligenous and 65% of the total monetary value estimated for the coralligenous.

According to this analysis, seagrass and coralligenous ecosystems appear to provide the 24% of the total biomass of the commercial coastal species, and to the 30% of the economic benefits (Figure 8).

Their productivity in terms of biomass of food provided for surface unit of habitat is estimated as 81.74 ± 23.63 kg/ha for seagrass and 61.44 ± 14.46 kg/ha for coralligenous, with a unitary economic revenue of 71.11±15.50 €/ha/year for seagrass and 70.46 ± 14.30 €/ ha/year for coralligenous (Figure 8).

Figure 8: Estimated monetary values (orange points) of each coastal habitat derived from our estimated provision of fisheries resources (bars).
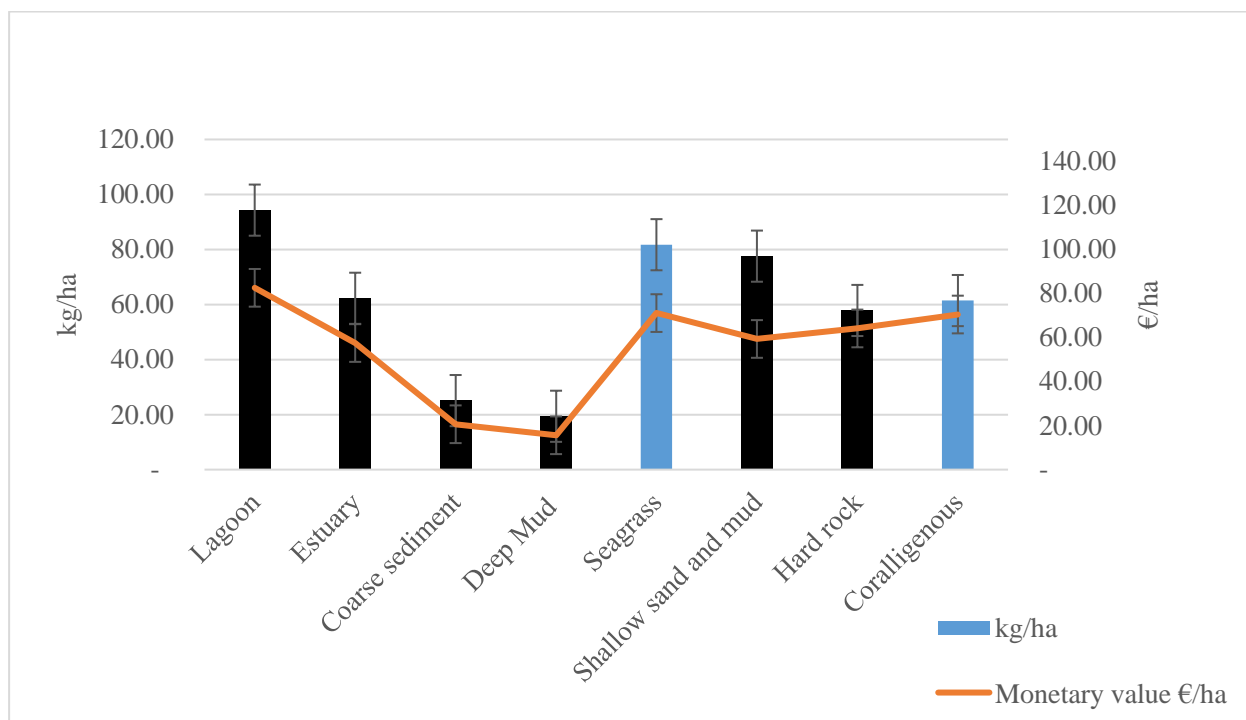
The value of the seagrass meadows provisioning services ranges between 71.11 ± 15.49 €/ha/year, while the value of the coralligenous provisioning services ranges between 70.46 ± 14.34 €/m²/year.

As shown in Figure 8, the results of this analysis highlighted the importance of the coralligenous and seagrass habitats for the commercial species. In comparison, their provisioning services values are comparable to those of other habitats, such as lagoons and estuaries, which are well recognised for their role as nursery spots for most of high important commercial species as seabream and seabass.

We have quantified the effect of OA in scenarios based on total loss in coverage of the coralligenous and the seagrass meadows and their evolution toward, respectively, hard rock and sandy habitats. The hypothetical loss of the two habitats induces a loss of demersal resource of 980 tons (-15%) of the current biomass with a maximum economic loss around 15 millions of euros (-20%) per year. In detail, we estimated that the loss linked to seagrass ecosystem is 6 millions, while the loss linked to coralligenous is up to 8.6 millions.

2.2.4 Discussion

OA, as a climate change related phenomena, has the potential to affect the economies of fisheries by decreasing the quantity and quality of marine fish cached (Sumaila et al., 2011). Indeed, considering the role that coralligenous and seagrass play as aggregation points, their loss due to OA could have multiple consequences on the fishing activities, also affecting travel time, which can lead to increase in fuel and ice cost depending on catch levels and patterns, and the management regime in place.

Seagrass and coralligenous habitats loss are likely detrimental to species that inhabits these environments. Organisms that associate directly with the complex substrata provided by these habitats, such as mesograzers, crustaceans, fishes that usually lived in the meadows or hidden in the coralligenous, and young of other species may be most impacted by habitat loss due to contraction of rearing habitat. Additionally, the potential loss of seagrass and coralligenous is also a concern for larger, more transient piscivorous species that may be visitors to seagrass and coralligenous habitats in the Mediterranean Sea- potentially limiting foraging chances and the export of associated secondary production via trophic transfer within mobile predators (Heck et al., 2008). Indeed, more than 80% of seagrass production was consumed by herbivores or

decomposed by detritivores, which have a role enhancing the food production for fishes (Cebrian et al., 1997), while coralligenous habitat significantly increased surrounding biodiversity and associated faunal biomass (Cerrano et al., 2009) producing the highest heterotrophic biomass when compared with the other benthic habitats (Franzese et al., 2017).

Some studies have estimated the economic value of seagrass and coralligenous habitats as 'fisheries' grounds following different strategies. Despite the low numbers of studies on this topic, our results fall within the range of the values assessed by these other studies giving a first rough validation of the index functioning.

While some studies focused on seagrass meadows, only Mangos et al. (2010) analysed the food provisioning services related to the coralligenous ecosystems.

Table 1: Comparison of the economic values of the provisioning service among different studies related to seagrass and coralligenous.

Study	Species		Units €/ ha^{-1} y^{-1}	Site
Unsworth et al., 2010	seagrass	fisheries' grounds	112.09	Indonesia
McArthur and Boland, 2006	seagrass	fisheries' grounds	87.82	South Australia
Blandon and zu Ermgassen, 2014	temperate seagrass	fisheries' grounds	162,684	Australia
Tuya et al., 2014	*C. nodosa*	fisheries' grounds +nursery	866 +95.75	Spain (Gran Canarias)
Mangos, 2010	*P. oceanica*	fisheries' grounds	23.79	Mediterranean
Campagne et al.,2014	*P. oceanica*	fisheries' grounds (water oxygenation)	35	France (Auction da Sete)
Jackson et al., 2015	seagrass	fisheries ground	34.6	Mediterranean
Our study	*P. oceanica*	fisheries' grounds	71.11	Italy
Mangos, 2010	Coralligenous	fisheries' grounds	10.32	Mediterranean
Our study	Coralligenous	fisheries' grounds	70.46	Italy

Mangos et al. (2010) estimated the value of benefits related to the natural resources provided by marine ecosystems in the Mediterranean Sea and considering only the behaviour of adult fish, they found that 3% of total catches in the Mediterranean are related to *P. oceanica* meadows and 4% are related to coralligenous reefs (Mangos et al., 2010), which are comparable with our results which considering both the adult and the juvenile life use of the habitat account for a total of 2% of total catches in the Italian area. McArthur and Boland, (2006) used the

catch-per-unit-efforts (CPUE) to assess the values of temperate and subtropical seagrass beds, extrapolating yearly estimates multiplied by the market price of the analysed fish species. This approach assessed the overall contribution of seagrass habitats to the Australian economy to 88 €/ha/y. Blandon and zu Ermgassen (2014) evaluated the increase of fish biomass in the presence of the seagrass in Australian water and found a value 2-3 order of magnitude larger than all the other studies that we have found. Even though, they considered data from the literature without taking into account fishing mortality rates and 90% of the value was assigned to exclusively one species making the results not easily comparable with ours. Moreover, fish species distribution is largely variable by seagrass species and geographic location and differences in the size and productivity of different seagrass species can influence ecosystem services provisioning. Such differences are an important component in explaining the difference in the ecosystem services provisioning shown in Table 1. Tuya et al. (2014) assessed the value of the direct extraction of fishery resources and the nursery function of *C. nodosa* meadow but their result is much higher (a hundred times) than our estimate. This can be explained by the fact that the largest economic value of the fishable fraction corresponded to pelagic, mobile, species (*Atherina presbyter, Boops boops, Sarda sarda, Sardinella aurita and Sardinella maderensis*) accounted for ca. 64% of the total monetary value. These species are not directly linked with seagrass meadows, but move through onshore waters forming large schools, therefore in our analysis these kinds of species have lower value compared to Tuya's work and this is probably the reason of such a different result comparing our study.

Jackson et al. (2015), through the application of the resident index, estimated that, despite covering <2% of the area, the direct annual contribution of *P. oceanica* to commercial landing values and to commercial and recreational fisheries is respectively, 4%, and 6%. Since our analysis is based on commercial fisheries we are not able to take into account the recreational fisheries and this lack may represent a source of underestimation of these habitat services values.

There are some caveats to our methodology. Firstly, an issue may arise from the fact that the free surface of the coralligenous habitats might be greater than that shown in the cartography due to the fact that coralligenous often grow on vertical walls rather than over horizontal areas. Therefore, the value of the coralligenous surface units could be higher than the one assessed by our study. Secondly, it can be argued that addressing the acidification scenario of the ecosystems, using the conceptual model, by hypothesising a 100% loss in habitat coverage is oversimplicistic. However, this methodology has the merit to highlight the value of these ecosystems and offer an initial estimate of service losses, providing direction for further

analysis. We are aware that the use of transfer techniques to estimate ecosystem services values under future scenarios may entail a degree of uncertainty since future generations may not hold the same preference in terms of consumptions of goods (i.e. fish species to consume). Moreover, the preferences and the values of ecosystem services may not remain constant over time leading a temporal source of generalisation error. Nevertheless, this is a methodology currently used in ecological economics (EEA, 2010).

Despite the precarious balance among sustainable resources exploitation and habitat degradation due to fisheries, the seagrass meadows and coralligenous habitats thanks to their numerous ecosystem functions and services, have important role for the coastal population. For example, artisanal fisheries, which production is mainly based on the species associated to the two habitats analysed in this work, constitute an important sector of primary production, and enhance social and economic cohesion by creating job opportunities and income security that are especially important for rural areas and islands (Giakoumi et al., 2013). In addition, recreational fisheries being an activity that takes place mainly along the coast, is strongly supported by coralligenous and *P. oceanica* meadows (Jackson et al., 2015). The presence of these habitats adds numerous socio-economic benefits that may be taken into account in evaluating the degradation cost of habitat loss.

It is noteworthy that, in addition to functioning as important nursery and foraging habitat for fish, shellfish, providing important goods to the society, seagrass and coralligenous are also important to oxygenate coastal waters and stabilize sediments, providing shoreline stabilization and erosion protection. These habitats are important carbon sequestration and nutrient cycling hubs, increasing potential economic value in terms of shoreline protection and climate regulation. The loss of the hydrodynamic barriers made by these complex structural habitats, leads to an increase in turbidity, reducing the light penetration and causing a further decline of seagrass and coralligenous environments and potential economic loss also in terms of cultural activities, such as tourisms and diving activities.

2.2.5 References

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2.2.6 Supplementary

Table S1: The mean of the national catches (FAO zone 37) from 2010 to 2012 accounted for 209.55 ±
13.35 tonnes for a value of € 1039.46 ± 99.06 (Mipfed-Irepa).

Year	2010	2011	2012
Landings (t)	222,500	210,324	195,839
Landings (millions €)	€ 1.102,76 millions	€ 1.090,33 millions	€ 925,03 millions
Data source	http://www.irepa.org/ relazione annuale 2010	http://www.irepa.org/ relazione annuale 2011	http://www.irepa.org/ relazione annual 2012
Target species Landings (t)	122,998	112,604	110,808

Table S2: The table reported the weight attributed to each commercial species considered in our
analysis based on the use of habitat.

Species	Common name		Lagoon	Estuary	Coarse sediment	Deep soft area	Seagrass	Soft areas	Hard substrate	Corall igenous
Boops boops	Bogue	Juvenile	0.5	0.5	0	0.5	0.5	0.5	0.5	0.5
		Adult	0.5	0	0	0	0.5	0.5	0.5	0.5
Conger conger	European conger	Juvenile	0	0	0	0.5	0.5	0.5	0.5	0
		Adult	0	0	0	0.5	0.5	0	0.5	0.5
Dentex dentex	Common dentex	Juvenile	0	0	0	0.5	0.5	0	0	0
		Adult	0.5	0	0	0	0.5	0	0.5	0.5
Dicentrarchus labrax	European seabass	Juvenile	0.5	1	0.5	0	0.5	0.5	0.5	0.5
		Adult	0.5	0.5	0	0	0.5	0	0.5	0
Engraulis encrasicolus	European anchovy	Juvenile	0.5	0.5	0	0	0.5	0.5	0	0
		Adult	0.5	0.5	0	0.5	0	0	0.5	0.5
Epinephelus marginatus	Dusky grouper	Juvenile	0.5	0.5	0	0	0.5	0	0.5	0.5
		Adult	0.5	0.5	0	0	0.5	0	0.5	0.5
Gobiidae	Gobies	Juvenile	0.5	0.5	0	0	0.5	0.5	0	0
		Adult	0.5	0.5	0	0	0.5	0.5	0	0

Lithognathus mormyrus	Sand steenbras	Juvenile	0.5	0	0.5	0	0.5	0.5	0	0
		Adult	0.5	0.5	0	0	0.5	0.5	0	0
Mugilidae	Mullets*	Juvenile	0.5	0	0	0	0.5	0.5	0	0
		Adult	0.5	0	0	0	0.5	0.5	0	0
Mullus barbatus	Red mullet	Juvenile	0.5	1	0.5	0	0	0.5	0	0.5
		Adult	0	0	0.5	0.5	0	0.5	0	0.5
Mullus surmuletus	Surmullet	Juvenile	0.5	0.5	0.5	0	0.5	0.5	0	0.5
		Adult	0.5	0	0	0	0.5	0.5	0.5	0.5
Oblada melanura	Saddled seabream	Juvenile	0.5	0	0	0	0.5	0	0.5	0.5
		Adult	0.5	0	0	0	0.5	0	0.5	0.5
Pagellus erythrinus	Pandoras	Juvenile	0.5	0	0	0	0.5	0	0	0
		Adult	0.5	0	0.5	0.5	0.5	0.5	0	0
Rajiformes	Rays*	Juvenile	0.5	0.5	0	0.5	0.5	0.5	0	0
		Adult	0.5	1	0.5	0.5	0.5	0.5	0	0.5
Sardina pilchardus	European pilchard	Juvenile	0.5	0.5	0	0	0.5	0.5	0	0
		Adult	0	0.5	0	0	0.5	0.5	0	0
Sargos	Sargo breams*	Juvenile	0.5	0.5	0.5	0	0.5	0.5	0.5	0.5
		Adult	0.5	0	0.5	0	0.5	0.5	0.5	0.5
Sarpa salpa	Salema	Juvenile	0.5	0.5	0.5	0	0.5	0	0.5	0
		Adult	0.5	0.5	0	0	0.5	0	0.5	0
Sciaena umbra	Croakers*	Juvenile	0.5	0	0	0	0.5	0	0.5	0.5
		Adult	0.5	0	0	0	0.5	0	0.5	0.5
Scorpaenidae	Scorpion fishes*	Juvenile	0.5	0	0	0	0.5	0	0.5	0.5
		Adult	0.5	0	0	0	0.5	0	0.5	0.5
Serranidae	Groupers*	Juvenile	0.5	0	0	0	0.5	0	0.5	0.5
		Adult	0.5	0	0	0.5	0.5	0	0.5	0.5
Solea solea	Common sole	Juvenile	0.5	0.5	0	0	0.5	0	0	0
		Adult	0.5	0.5	0	0.5	0	0.5	0	0
Sparus aurata	Gilthead seabream	Juvenile	0.5	0.5	0	0	0.5	0.5	0	0
		Adult	0.5	0.5	0	0	0.5	0.5	0	0.5
Spondyliosoma cantharus	Black seabream	Juvenile	0.5	1	0	0	0.5	0.5	0.5	0.5
		Adult	0	0	0	0	0.5	0.5	0.5	0.5
Trisopterus minutus	Poor cod	Juvenile	0.5	0	0	0.5	0	0.5	0.5	0.5
		Adult	0	0	0	0.5	0	0.5	0.5	0.5

Species	Common name	Stage								
Zeus faber	John dory	Juvenile	0	0	0	0.5	0.5	0	0.5	0.5
		Adult	0	0	0	0	0.5	0	0.5	0.5
Diplodus spp.	Seabream (saraghi) da ISMEA	Juvenile	0.5	0.5	0.5	0	0.5	0.5	0.5	0.5
		Adult	0.5	0	0.5	0	0.5	0.5	0.5	0
Platichthys flesus	European flounder	Juvenile	0.5	1	0	0	0.5	0.5	0	0
		Adult	0.5	0.5	0	0	0.5	0.5	0	0
Belone belone	Garfish	Juvenile	0.5	0.5	0	0	0.5	0	0	0
		Adult	0.5	0	0	0	0.5	0	0	0.5
Seriola dumerili	Greater amberjack	Juvenile	0.5	0	0	0	0	0	0.5	0
		Adult	0	0	0	0	0	0	0.5	0.5
Eledone	Horned and musky octopuses	Juvenile	0	0	0	0	0.5	0	0	0
		Adult	0.5	0	0.5	0.5	0.5	0.5	0	0
Loligo vulgaris	Common squids*	Juvenile	0.5	0	0	0	0.5	0	0.5	0.5
		Adult	0.5	0	0.5	0	0.5	0.5	0.5	0.5
Sepiidae	Cuttlefish	Juvenile	0.5	0.5	0	0	0.5	0.5	0.5	0
		Adult	0.5	0.5	0	0	0.5	0.5	0.5	0.5
Octopus vulgaris	Common octopus	Juvenile	0.5	0	0.5	0	0.5	0.5	0.5	0.5
		Adult	0.5	0	0	0	0.5	0.5	0.5	0.5
Brachyura	Marine crabs	Juvenile	0.5	0.5	0	0.5	0.5	0.5	0.5	0.5
		Adult	0	1	1	0.5	0.5	0.5	0.5	0.5
Palaemon serratus	Common prawn	Juvenile	0.5	0.5	0	0	0.5	0	0.5	0.5
		Adult	0.5	1	0	0	0.5	0	0.5	0.5
Crangon crangon	Common shrimp	Juvenile	0.5	1	0	0	0.5	0.5	0	0
		Adult	0.5	1	0	0	0.5	0.5	0	0
Penaeus kerathurus	Caramote prawn	Juvenile	0.5	0.5	0	0.5	0	0.5	0	0
		Adult	0.5	1	1	0.5	0	0.5	0	0
Homarus gammarus	European lobster	Juvenile	0.5	0	0.5	0	0	0	0.5	0.5
		Adult	0	0	0	0	0	0	0	0.5
Squilla mantis	Spottail mantis squillid	Juvenile	0.5	1	0	0	0	0.5	0	0
		Adult	0.5	1	0	0.5	0	0.5	0	0.5
Palinurus elephas	Common spiny lobster	Juvenile	0	0	0	0	0	0	0.5	0.5
		Adult	0	0	0	0	0	0	0	0.5

Table S3: Mean value and sd (second table) of catches and monetary value for the target species landed between 2010 and 2012. We considered the habitats classification in an area comprised from coastline to the 150 meters isobaths (that represents the average depth range of the considered species). The lagoon area was obtained from literature data related to the Italian coast.

		Lagoon	Estuary	Coarse sediment	Deep Mud	Seagrass	Shallow sand and mud	Hard rock	Coralligenous
Areal extension	km^2	1'967.43	2'430.00	2'430.00	79'258.76	9'937.66	18'804.66	2'847.81	4'923.02
Catches	kg y^{-1}	1'855'502.11	1'513'202.51	609'527.20	15'364'295	8'123'147.63	14'589'535	1'647'186.46	3'024'936.25
Exploited biomass	kg/ha	94.31	62.27	25.08	19.38	81.74	77.58	57.84	61.44
Monetary value	€/ha	82.59	57.51	20.61	15.60	71.11	59.36	64.14	70.46
Monetary value at Italian scale	€/y	16'249'662	13'976'115	5'008'491	123'651'219	70'668'998	111'626'429	18'264'824	34'688'713

Chapter 3 - Potential impacts of the OA effects on food web model

3.1 Introduction

Mediterranean Sea ecosystems are increasingly threatened by intense human pressures (Coll et al., 2012) that are acting synergistically with warming and acidification due to climate change (Giorgi, 2006). Current and future impacts on this densely populated semi-enclosed basin will likely threaten marine biodiversity (Danovaro et al., 2004; Garrabou et al., 2009; Kroeker et al., 2013) and their associated ecosystem services (Gattuso et al., 2015). It is crucial to better understand how marine ecosystems may respond to environmental changes and how the latter may impact ecosystems functioning, also because this has relevant implication on the socio-economic dimensions and human well-being.

Ecosystem models have an instrumental role in accurately identifying ecological relationships in the environment. Their introduction increased a lot scientists capability to understand complex marine ecosystems (Christensen, 2013) and they now are useful tools in ecosystem-based management. There are many type of ecological models that can be applied to marine ecosystems, including models that permit to analyse in common coherent framework processes occurring on different hierarchical levels of biological organization, and to assess the cumulative effects of direct and indirect interactions among multiple species (Rose et al . 2010, Peck et al. 2016). Such ecosystem modelling approach is very relevant, given direct impacts on one element of the food web may trigger cascading effects on the entire system. Furthermore, the very fact of considering multiple species introduces in the system non-linear dynamics, which might give rise to a number of complex dynamics, including regime shifts and hysteretic effects.

Ecopath with Ecosim (EwE) (Christensen and Pauly, 1992; Christensen and Walters, 2004) is a model of this type and it has been widely used over the last 20 years to describe food webs and ecosystem dynamics and to support the Ecosystem approach to management (Coll et al., 2015).

Portofino MPA food web

Our study focuses on the Portofino marine protected area (MPA) in the Ligurian Sea, northwestern Mediterranean Sea for which a food web model has been built by Prato et al., (2016) and made available on the Ecobase database. Using this food web model, we explored the potential community-scale effects of habitat loss due to OA by analysing the consequences of different scenarios of habitat alterations due to OA. Scenarios were identified by following the conceptual models presented in the previous chapters of this thesis (see Chapter. 2 and 3).

The food web model (Prato et al., 2016) has been developed using Ecopath and it represents the Portofino MPA for the period 2007-2014. The modelled surface covers 57 ha, and it is characterised mainly by hard bottoms (51% rocky habitat, 31% coralligenous habitat) with some *P. oceanica* meadows and shallow sands (overall 18% of the area).

The model includes 33 functional groups, where a functional group represents either a single species or a group of species. Functional groups composed by more than one species were labelled with a (+) (see Table S1 for further details). The functional groups are directly linked to one another through trophic relationship. The species groups of particular interest are described by taking into account life history relationship, called "stanza groups" in EwE (*Epinephelus marginatus* and *Sarpa salpa* to account for changes in their diet with age) (Prato et al., 2016). The model features three groups representing the primary producers (i.e. *Posidonia oceanica*, seaweed and phytoplankton), eight groups of invertebrates, one of cephalopods, two of zooplankton, and detritus (Prato et al., 2016), and represents all the functional groups relevant for our purpose (i.e. corals, *P. oceanica* meadows, commercially important species both as adults and juveniles).

P. oceanica meadow plays important ecological functions in the marine environment as habitat former (Orth et al., 2006). Indeed, *P.oceanica* forms high structurally complex meadows that are valuable habitats hosting a wide range of motile fish and invertebrate fauna (Mccloskey and Unsworth, 2015) ensuring species survival by offering protection from predators from juvenile phase to adult one, allowing the aggregation of individuals, helping the reproduction success, and providing foraging habitat for both juveniles and adults species .
Seagrass habitats are undergoing worldwide degradation as a result of anthropogenic activities (Short et al., 2011) and in the Mediterranean Sea, *P. oceanica* habitat has declined by 34% in the last 50 years (Telesca et al., 2015). In addition, OA is threatening this species leading to a change in the habitat complexity that could lead to the shift of high valuable ecosystem services to less valuable ones (Mccloskey and Unsworth, 2015).

Gorgonian species are part of the coralligenous habitat which ranks among the most important ecosystems in the Mediterranean Sea, being considered of great significance both for fisheries, carbon regulation (Martin et al., 2014), and tourist attraction (i.e. scuba divers). The coralligenous habitat is characterised by calcareous formations of biogenic origin primarily due to the red algae Corallinales and Peyssonneniales and secondarily by cnidarians, polychaetes and bryozoans (Ballesteros, 2006; Martin et al., 2014) that grow in dim light conditions. The coralligenous is known to host over 1600 species (Ballesteros, 2006) among which many commercially important species are known to depend on this habitat to reproduce, to feed and to live (Ballesteros, 2003). The gorgonians are among the major contributors in building the 3D complexity of the coralligenous habitat hosting the highest level of benthic species diversity in the Mediterranean Sea and creating microhabitats, which are used as shelters for different necto-benthic organisms (Cerrano et al., 2009; Ponti et al., 2014). The particular configuration of the coralligenous substrate enhances the aggregation of fish biomass attracting artisanal fishing with fixed nets and small purse sein, and recreational fishing (Prato et al., 2016).

Coralligenous environments are currently threatened by warming and acidification. The aim of this study is to upscale projections of impact of OA from direct species-level effects to the full ecosystem. Secondly, we plan to investigate how the changes in the ecosystem functioning could alter the services provided system. In this case study, we focused on the impacts on functional groups that give us provisioning services.

3.2   Material and Methods

In order to create a realistic model simulation of how a full ecosystem, such as Portofino MPA, responds to the impact of OA we collected information on direct and indirect impacts of OA, including those affecting the species interactions. Unfortunately, the dearth of information available, in particular those related to the impacts of OA on interactions among species, prevented us from deriving a fully quantitative description of all the changes in the trophic structure. In this case, we had to make additional assumptions.
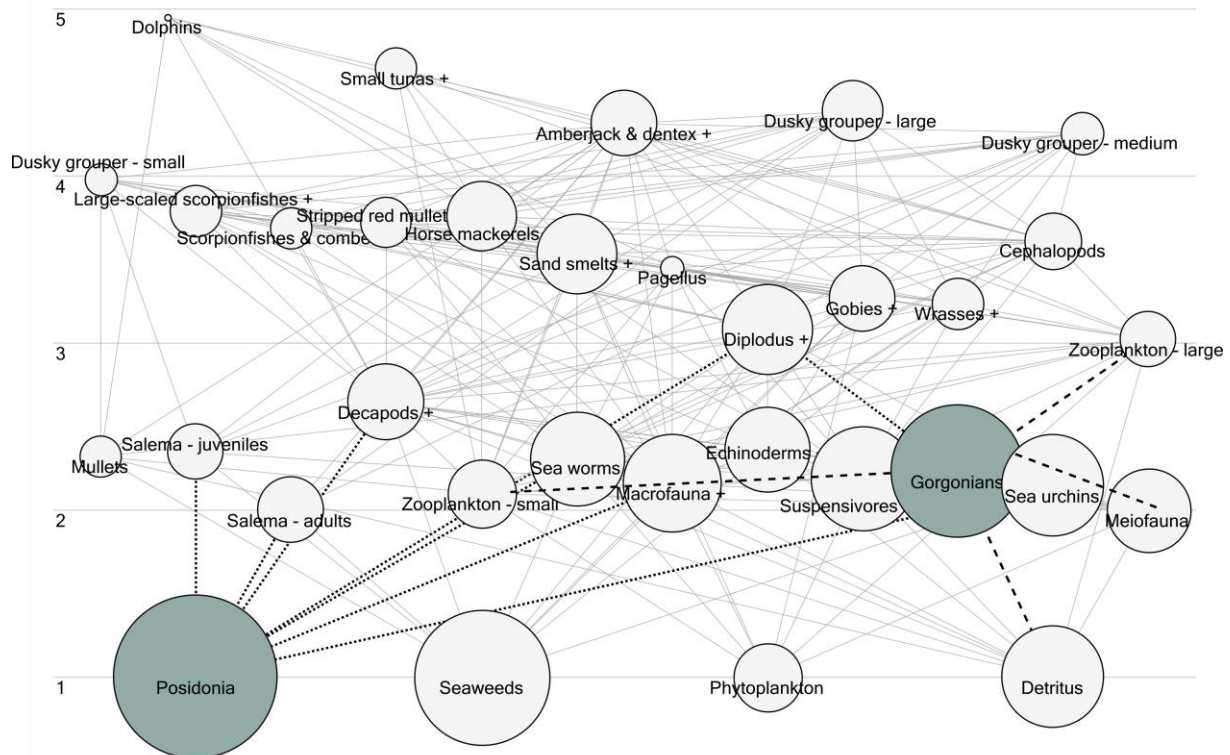
Figure 1: Food web of the Portofino MPA (Prato et al., 2016). All lines represent trophic interaction between functional groups. The HFSs are represented in blue.

Starting from the information already synthesised in the conceptual models (see Chapter 2), we designed 10 scenarios. More specifically, direct effects identified in the OA conceptual models (see chapter 2 of the thesis) were represented by directly removing and/or altering the habitat-forming species (HFSs) biomass from the model. In EwE this has been done by changing the 'so-called' forcing functions. Conversely, indirect effects were taken into consideration by changing the mass flows among selected compartments again following OA conceptual models in chapter 2. In EwE this can be done by changing the specific functions called mediation functions. The results of the latter set of simulations have been introduced in order to mimic the indirect effects of the loss of HFSs on functional groups through the loss of ecosystem functions and services linked to seagrass and coralligenous habitats (i.e. refugee, aggregation of prey).

EwE model

The model, built in Ecopath with Ecosim (EwE), simulates temporally the dynamic trophic interactions basing on a system of ordinary differential equations (Christensen and Walters, 2004; Walters et al., 1997), which describes the biomass variation of each functional group over time (t) as follows:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i \qquad \text{(Eq.0)}$$

where dB_i/dt represents the growth rate during the time interval dt of the group (i) in terms of its biomass B_i. g is growth efficiency; Q_{ji} is consumption of all prey j; Q_{ij} is consumption by all predators j; I is immigration rate; F is fishing mortality rate; M is another mortality; e is emigration rate. Ecosim dynamic is driven primarily by trophic interactions, which are based on foraging arena theory, whereby the rate of predation by predator group j on prey group i is dependent upon the rates of exchange (v) of prey between the so-called "invulnerable" pool (i.e., separated from the predator in time and space) and the "vulnerable" pool (Ahrens et al., 2012; Christensen and Walters, 2004; Walters et al., 1997). The core consumption equation of prey i by predator j (Q_{ij}) is:

$$Q_{ij}(B_i, B_j) = \frac{a_{ij}v_{ij}B_iB_j}{(v_{ji}+v_{ij}+a_{ij}B_j)} \qquad \text{(Eq. 1)}$$

where a_{ij} is the effective search rate for i by j, B_i is prey biomass, B_j is predator biomass, and v_{ij} and v_{ij} are the rates at which i moves between the vulnerable and invulnerable prey pools, respectively (Christensen and Walters 2004). Indeed, predator-prey interactions are assumed to take place primarily in restricted 'foraging arenas' where prey only become vulnerable to predation through their own requirements for resource acquisition (Walters et al., 1997).

The quantification of biomass changes due to habitat degradation is accomplished in EwE utilising forcing and mediation functions.

1) Forcing functions:

Forcing functions (S_{ij}) can be input in the model in order to introduce the effects of external variables on the trophic interactions. The forcing function in EwE can be used to directly influence primary production or to modify the Q/B ratio of the consumer groups in the model. In the second case, forcing function is defined as a multiplier used to modify the Q/B ratio of the consumer groups included in an underlying Ecopath file.

$$Q_{ij}(B_i, B_j) = \frac{a_{ij}S_{ij}v_{ij}B_iB_j}{(v_{ji}+v_{ij}+a_{ij}S_{ij}B_j)} \qquad \text{(Eq. 2)}$$

Forcing functions (FF) were introduced to simulate the perturbation of OA on sensitive functional groups' biomass.

Given uncertainty both in the spatial and temporal development of OA in the Mediterranean Sea and on how to model the response of functional groups to OA, we have followed the work of Busch and McElhany (2016). The authors have a change in forcing functions linearly proportional to the decrease of functional groups biomass. Species' responses to the increase in seawater CO_2 are not linear and even pH decrease is expected to vary according to geographic location, temperature variations and water circulation and stratification (Raven et al., 2005). However, there is still a high uncertainty regarding the shape of the functions which describe these responses. Therefore a linear assumption has been adopted as already highlighted by Busch et al. (2013). A series of simulations was performed by varying the values of the forcing functions (S_{ij}) for each HFSs (e.g. *P. oceanica* and gorgonians), in order to reach the expected biomass reduction of HFSs. In details, we have applied the functions which, by the end of 2100, lead to a HFSs biomass decrease of 10%, 30%, 50%, 70% and, 100%, thus generating 5 different scenarios. The scenarios have been projected in order to understand the HFSs' role in the interaction with the food web.
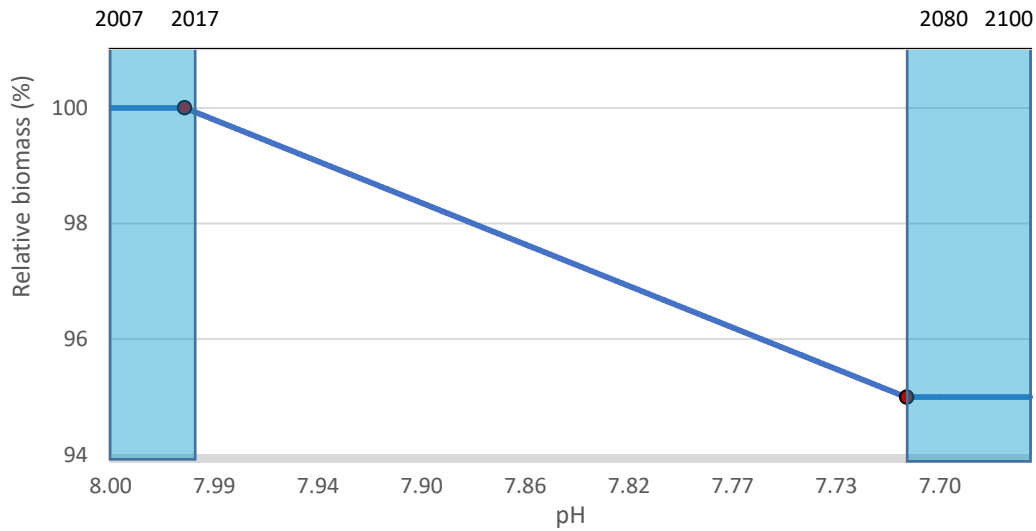
Figure 2: Shape of a forcing function applied to OA vulnerable groups (reduction of 10% of HFSs). The pH is on the x-axis and functional group pH sensitivity biomass is on the y-axis. The blue rectangle represents current conditions (on the left) and end-of-the-century conditions (on the right). The pH sensitivity biomass curves can be used to modify functional group biomass under scenarios of OA, potentially by multiplying baseline biomass in the model, for a functional group by the value on the curve that corresponds to local pH conditions (Busch and McElhany, 2016).

The "double-hockey stick" shape has been adopted assuming that, over the decade 2007-2017, pH at the reference condition is approximately around 8.0 and the forcing function, S_{ij}, is equal to 1. Thus, the biomass was identical to the current baseline model parameterisation. Given the uncertainties of the OA effects on HFS at the pH conditions expected for 2100, different response curves have been adopted which led to five different scenarios, Scenario 1-10%, Scenario 1-30%, Scenario 1-50%, Scenario 1-70%, Scenario 1-100%, with different degrees of HFSs biomass reduction (i.e. -10%, 30%, -50%, -70%, and-100%).

In figure 1 the case of 10% reduction in HFSs biomass is shown. At the base conditions of the models, the pH was approximately 8 (X-axis) and the biomass of the HFSs were 100%. At the end of the simulations (2080-2100) the pH would be approximately 7.7 and the biomass of the HFSs were reduced by 10% the current conditions.

2) Mediating functions in Ecosim

Mediation functions (M_{ij}) simulate the influence of a third (mediating) variable on predator-prey interactions. The mediation functions can be used to describe non-trophic interactions

between species or species and habitat within a food web modelling framework. For example, mediation functions have been applied by Plummer et al., (2013) to a system in which changes in eelgrass areal coverage modify the vulnerability of prey to predator through refuges provisioning or facilitating search efficiency by predators through aggregation of prey. Ma et al., (2010) have applied mediation functions to represent the decrease of vulnerability of juvenile crabs to predators in habitats with the increase of vegetation. Espinosa-Romero et al., (2011) have demonstrated how the benefits derived from the presence of kelp forests are manifolds, since the complex three-dimensional structures that they provide lead to an increase of feeding areas and improve the food availability for some predators, through prey retention. Ainsworth et al. (2008) have analysed how the removal of complex substrates (such as coral reefs) negatively impacted the juvenile fish and invertebrates that lost their refuges.

This analysis aims to improve the representation of ecological processes, specifically the mediating effects provided by habitat loss.

The work focused on the mediating effects of seagrass and corals, since the complex habitats that they create increase feeding areas through prey retention for some species. Complex habitat structures can also provide refuge for prey and nursery for juveniles reducing their risk to be predated and enhancing the food availability.

This approach aimed at investigating how the change in habitat species composition (i.e. seagrass and coral) can cause alterations in the behaviour of some species, which in turn may affect other species (Espinosa-Romero et al., 2011). After changing the biomass of HFSs via forcing functions, we applied mediation functions into the model that correspond to the non-trophic effects of seagrass and coralligenous on other species.

Two types of mediation functions (FF and MF) have been applied in the model, using multipliers to change the parameters of predator search rate a_{ij} (Eq. 3) and of prey vulnerability v_{ij} (Eq. 4) as a function of the biomass of the mediating group.

$$Q_{ij}\left(B_i, B_j\right) = \frac{a_{ij}M_{ij}v_{ij}B_iB_j}{(v_{ji}+v_{ij}+M_{ij}a_{ij}B_j)} \qquad (Eq.\ 3)$$

$$Q_{ij}\left(B_i, B_j\right) = \frac{a_{ij}v_{ij}M_{ij}B_iB_j}{(v_{ji}+v_{ij}M_{ij}+a_{ij}B_j)} \qquad (Eq.\ 4)$$

A reduced v_{ij} makes the group i subject to lower top-down control, and a decreased a_{ij} makes group j a less efficient consumer of the group i.

Three mediation functions have been applied to specific functional groups (Table 1) in order to evaluate the loss of habitat services due to the decreased habitat-forming functional groups (seagrass and corals). These functions represent three hypotheses of the propagation of the indirect effects within the food web model. The first function reduces the amount of refuge for small prey items and increased their vulnerability to predators (M1; Eq.3). The second function decreases the search rate of juveniles due to the loss of prey aggregation (M2; Eq. 4) and the third one decreases the search efficiency of predator species linked to the two habitats analysed (i.e. seagrass and coralligenous) (M3; Eq.3). The parameters for the linear mediation functions have been entered into EwE. The initial mediation value was set to 1 for M1 and M2 and 0.5 for M3 (see Figure 3). According to Harvey (2014), the latter value was chosen in order to damp the strength of the mediation effects on functional groups not strictly associated with the HFSs. Indeed, for example, the effects of the HFSs reduction might be lower on pelagic predators that can change feeding grounds moving to other sites. Simulations were then run in which HFSs biomass were decreased by 10%, 30%, 50%, 70% and 100% (the reduction were performed with the abovementioned forcing functions) leading to five different scenarios: Scenario 2-10%, Scenario 2-30%, Scenario 2-50%, Scenario 2-70%, and Scenario 2-100%. These scenarios enabled comparison of how the functional groups of the model responded to changes of HFSs at different magnitude under the three mediation functions.
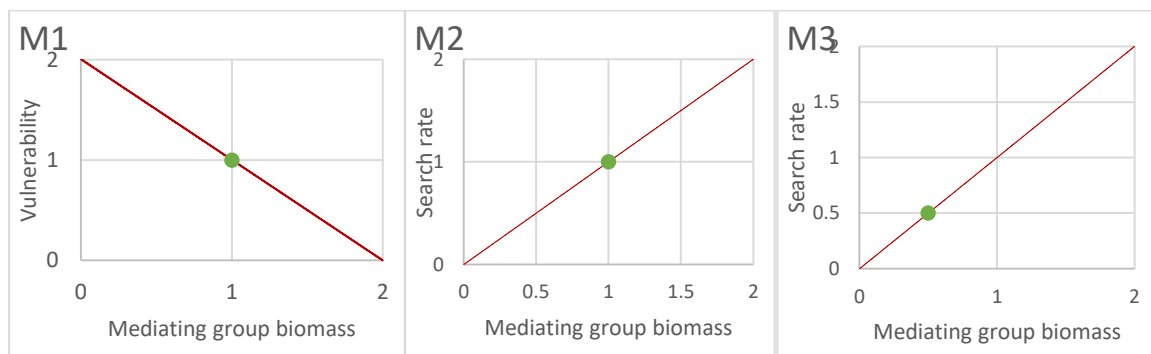
Figure 3: Mediation functions added to Ecosim model to affect specified relationships as a function of seagrass and corals relative biomass. Functions were applied to (M1) vulnerability of prey to predator due to the loss of refuge, (M2) the prey search rate for juvenile species, (M3) the search efficiency of predator species due to the reduction of prey aggregation. The green dot represents the initial mediation state.

These functions were applied to appropriate functional groups in the model as shown in Table 1.

Table 1: Assignment of mediation functions to functional groups in the Portofino MPA EwE model.

EwE group	Weight	Mediation function	Mediation parameter (prey, predator)
Decapods	*P. oceanica*; Gorgonians	M1	(+)v Decapods, all predators
Echinoderm	' '	M1	(+)v Echinoderm, all predators
Sea urchin	' '	M1	(+)v Sea urchin, all predators
Meiofauna	' '	M1	(+)v Meiofauna, all predators
Macrofauna	' '	M1	(+)v Macrofauna, all predators
Grouper small	*P. oceanica*; Gorgonians	M2	(-)a Scorpionfishes & combers, Grouper small
	' '	M2	(-)a Stripped red mullets, Grouper small
	' '	M2	(-)a Horse mackerels, Grouper small
	' '	M2	(-)a Diplodus, Grouper small
	' '	M2	(-)a Gobies, Grouper small
	' '	M2	(-)a Wrasses, Grouper small
	' '	M2	(-)a Mullets, Grouper small
	' '	M2	(-)a Salema - juveniles, Grouper small
	' '	M2	(-)a Decapods, Grouper small
Salema - juveniles	*P. oceanica*; Gorgonians	M2	(-)a Macrofauna, Salema - juveniles
Amberjack & Dentex	1/2 *P. oceanica*; 1/2 Gorgonians	M3	(-)a All prey, Amberjack & Dentex
Dusky grouper	' '	M3	(-)a All prey, Dusky grouper
Large-scaled scorpionfishes	' '	M3	(-)a All prey, Large-scaled scorpionfishes

Scorpionfish & combers	' '	M3	(-)a All prey, Scorpionfish & combers
Stripped red mullets	' '	M3	(-)a All prey, Stripped red mullets
Pagellus	' '	M3	(-)a All prey, Pagellus
Sand smelts	' '	M3	(-)a All prey, Sand smelts
Cephalopods	' '	M3	(-)a All prey, Cephalopods

These functions can be empirically defined, or they can be hypothetical (Plummer et al., 2013). We do not empirically know the true nature of seagrass and coralligenous mediation effects on the different predator-prey relationships (i.e. the shape and strength of these functions), hence we set the shape of all mediation functions to a linear function.

Finally, we ran the model for 100 years and recorded the functional groups biomass at the end of each simulation

Scenario results were synthesised in plots, in which we represented the final biomass for each group for all scenario simulations.

Fisheries

Prato et al., (2016) assessed the artisanal fishing catches within the MPA as 3.35 tons Km^{-2} yr^{-1} and the recreational fishing as 3.56 tons Km^{-2} yr^{-1}.

In the food web model, we assessed how the provisioning service of providing food would change due to the trophic and non-trophic interactions that we have imposed. Prato et al. (2016) identified 16 groups as providers of provisioning services essentially as commercially or recreational fisheries.

To assess the economic value for commercial fishing, we used market data from ISMEA database (www.ismea.it).Values included in the analysis were based on current market values representing the price at the time of the survey and it is the average value of different market and processes of supply and demand.

The relative biomass and the catches levels were calculated for the base model and compared to the forcing and mediation simulation results expected for the end of the century. Significant

differences between the base model and the imposed scenarios were assessed using a paired, two-sample means *t*-test.

3.3   Results

Scenarios with forcing functions (Scenario 1)

Results of the Portofino food web model scenarios with forcing functions, (namely Scenario1-10%, Scenario 1-30%, Scenario 1-50%, Scenario1-70%, and Scenario1-100%) were made by imposing a reduction of production and consumption rates for *P. oceanica* and gorgonians respectively in order to obtain a 10%, 30%, 50%, 70% and 100% reduction of HFSs biomass.

Firstly, we have analysed the reduction in HFSs biomass in two separate simulations, one for *P. oceanica* and one for gorgonians in order to determine the desired final biomass changes.

All the Scenario1 simulations, made by decreasing the coral habitat-forming functional groups, did not induce significant changes on the other functional groups biomass (t.test, p>0.05) due to the little trophic links to the other functional groups. Indeed, even a 100% decrease of gorgonians biomass will cause a slight decrease of 9.5% in the total biomass (see supplementary materials Table S 2). Instead, all the Scenario1 simulations made by decreasing the *P. oceanica* coverage induced a significant (t.test, p<0.001) overall decrease of the biomass of other functional groups (Table S 2).

Cumulative effects obtained by simultaneously imposing production and consumption reduction of HFSs, as previously determined, result in trophic effects that alter the final biomass changes (Figure 4). Therefore, the reduction imposed have to be interpreted as an approximate reduction of biomass by 10%, 30%, 50%, 70% and 100%.

The reduction of 30% of the habitat-forming functional groups determined an overall reduction of 27% of the total biomass of the food web with significant decreases (t.test, p<0.001) in many different groups. For example, the reduction in HFSs had negative direct trophic effects on *S.salpa* both as juveniles (-18%) and as adults (-31%), decapods+ (-18%), macrofauna+ (-19%), seaworms (-10%), and sea urchins (-22%) that fed directly and primarily on the seagrass meadows. The decreased biomass of the species mentioned above led to negative effects on others functional groups that loss their prey biomass. Hence, dusky groupers and wrasses+ decreased by almost 20% each, scorpionfishes (large scorpionfishes+ and scorpionfishes &

combers+) and pagellus by 16% each, stripped red mullets+ by 14%, and echinoderms+ by 13%, (Figure 4 and Figure 6- blue bars).

Figure 4: Scenario 1-10%, Scenario1-30%, Scenario1-50%, Scenario1-70%, and Scenario1-100%: Percent change in relative biomass due to the reduction of habitat-forming species (HFS) (see Table S 2 for details). In all radar plots, a value of 0 indicates no change in biomass, whereas deviations from 0 represent a proportional increase or decrease.

The biomass reduction for the abovementioned functional groups was even higher in the scenarios with higher reduction rate of HFSs (-50%, -70% and -100%). The direction of the changes in functional groups biomass was consistent across the 5 scenarios for the majority of

the functional groups. The magnitude of change increased linearly with the reduction of HFSs except for a slight increase of some pelagic organisms' biomass that increased in all the scenarios due to the increased of the zooplankton biomass. The increase in zooplankton biomass (scenario -30% HFS; 4%) was a trophic consequence of the reduction of their main predators, the polyps of the gorgonians. Hence, for example, a 30% reduction of HFSs led to an increase of small tunas (9%), horse mackerels (6%), and sand smelts (5%).

The trophic-dynamic presented in the model did not take into account other factors that in reality influence the relationships among functional groups within the model, for example, the fact that small tunas+, and sand smelts+ feed and sometimes to live on *P. oceanica*. Indeed, the sand smelts+ functional group are composed by *Atherina* spp., *Trachurus* spp., *Spicara maena, Spicara smaris, Chromis chromis, Anthias anthias, Boops boops, Oblada melanura* that are species often linked to the *P. oceanica* meadows and the coralligenous formations (Jackson et al., 2015; Mangos et al., 2010).

The following section focuses on the potential habitat impacts that may influence the functional group's biomass.

Scenarios with mediation functions (Scenario 2)

The second set of simulations, Scenario2-10%, Scenario2-30%, Scenario2-50%, Scenario2-70%, and Scenario2-100%, was made in order to evaluate the non-trophic effects, in addition to direct effects reproduced with the inclusion of the forcing functions. The non-trophic (mediating) effects induced by the decrease in habitat-forming functional groups (seagrass and corals) were taken into account. This analysis was carried out introducing the mediation functions, which represent in the model the changes in preys' vulnerability and in predators' search rate, according to the changes in the biomass of the two mediating groups (i.e. seagrass and corals). These functions describe the non-trophic functions of corals and seagrass. Again, a set of simulations was carried out by imposing a 10%, 30%, 50%, 70% and 100% decreased of HFSs biomass.
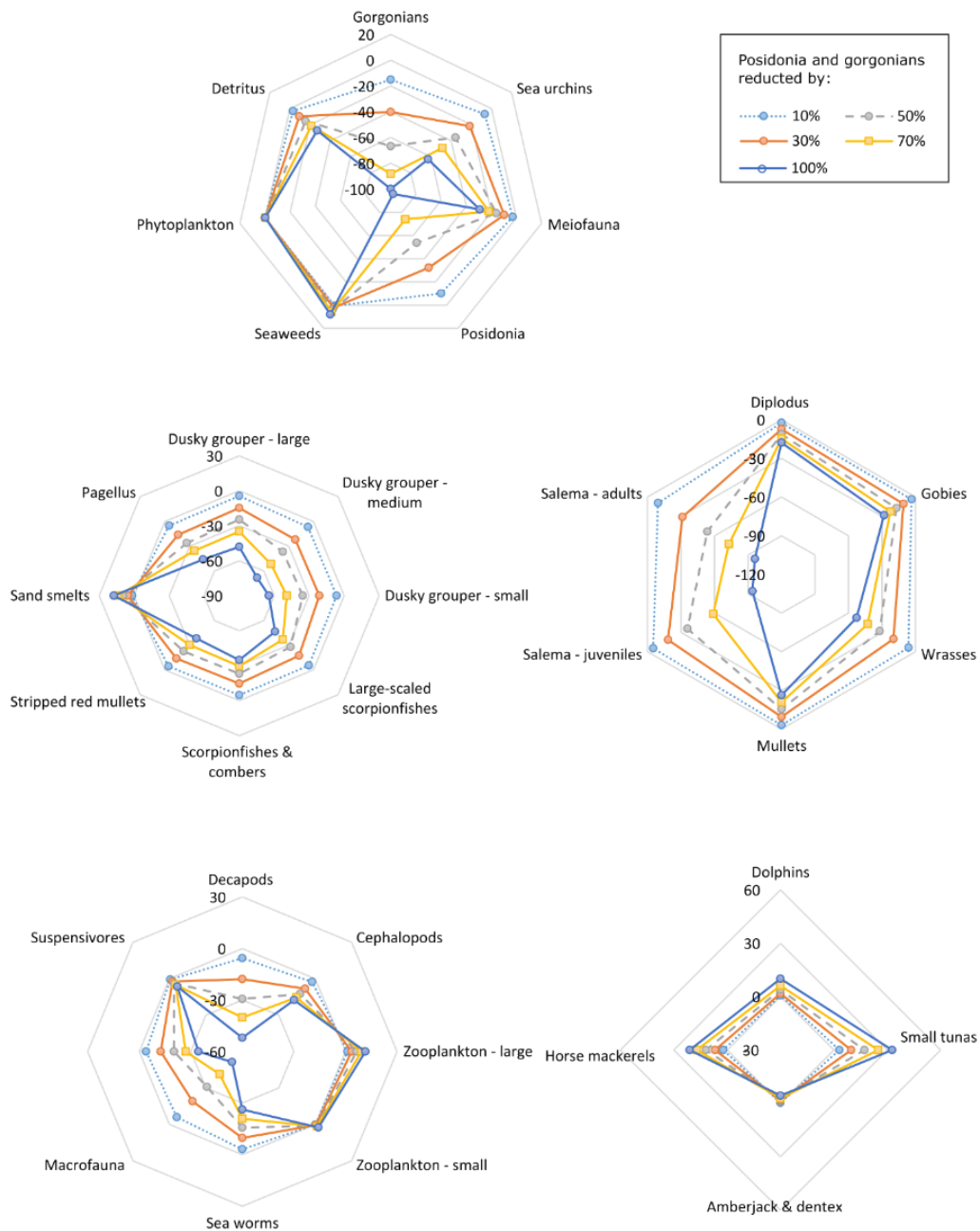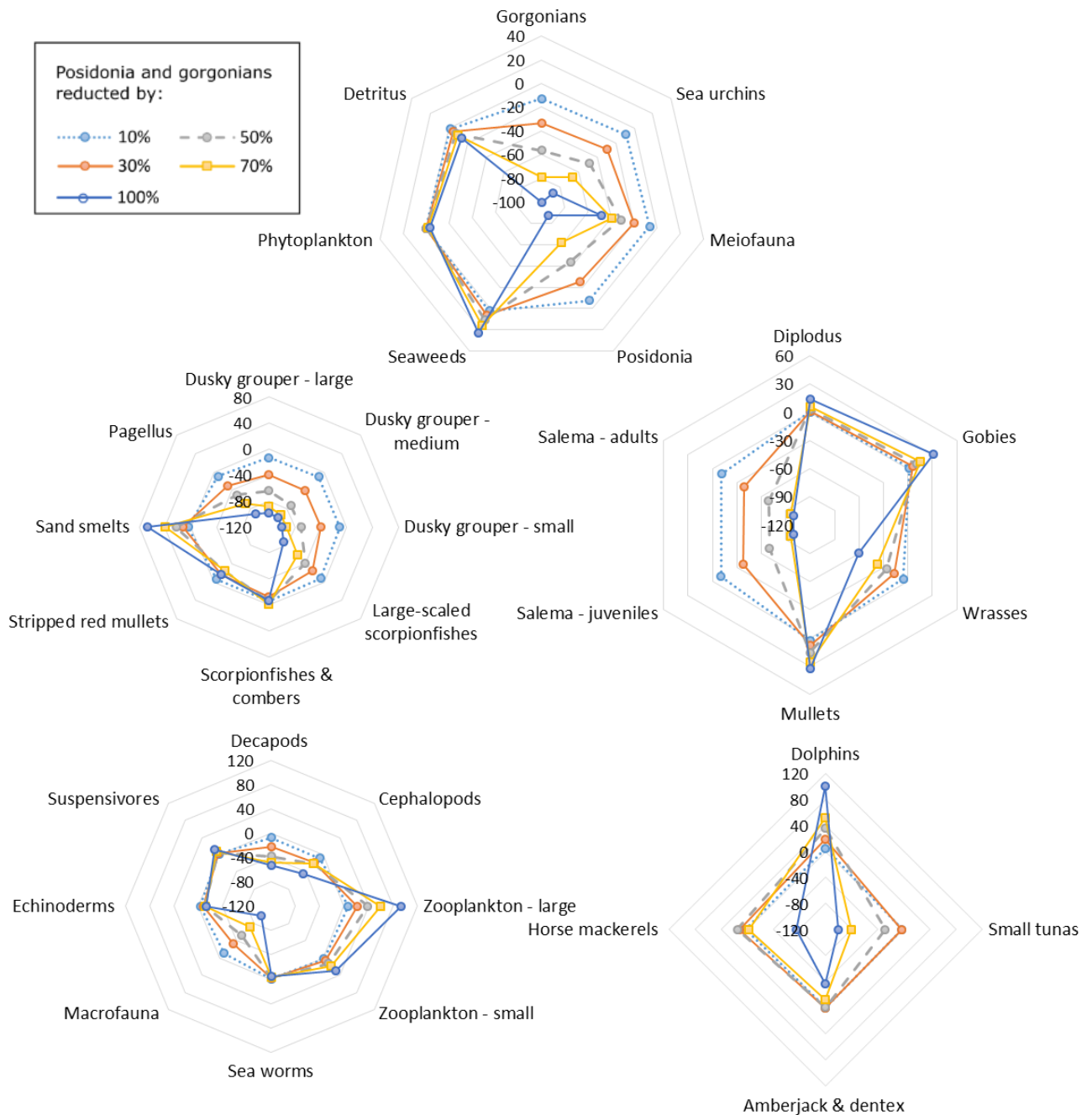
Figure 5: Scenario 2-10%, Scenario2-30%, Scenario2-50%, Scenario2-70%, Scenario2-100%: Percent change in relative biomass due to the reduction of habitat-forming species (HFS) with the inclusion of the mediation effects (see Table S6 for details).

A 10% decrease in HFSs as mediating groups caused widespread changes with a low overall magnitude (overall biomass reduction of 7%) (t.test, p<0.001). The 30% reduction of HFS led to a significant (p<0.001) reduction in the overall biomass of the functional groups (22%). The results for the other scenarios (i.e. -50%, -70% and -100% of HFSs) showed a 37% (p<0.001), a 52% (p<0.001), and a 71% reduction of the overall biomass (p<0.001) (Figure 5).

We focused our further analysis on the 30% reduction of HFSs scenario which led to a perturbation observable across multiple functional groups (e.g. pelagic fish, demersal fish, and invertebrates).
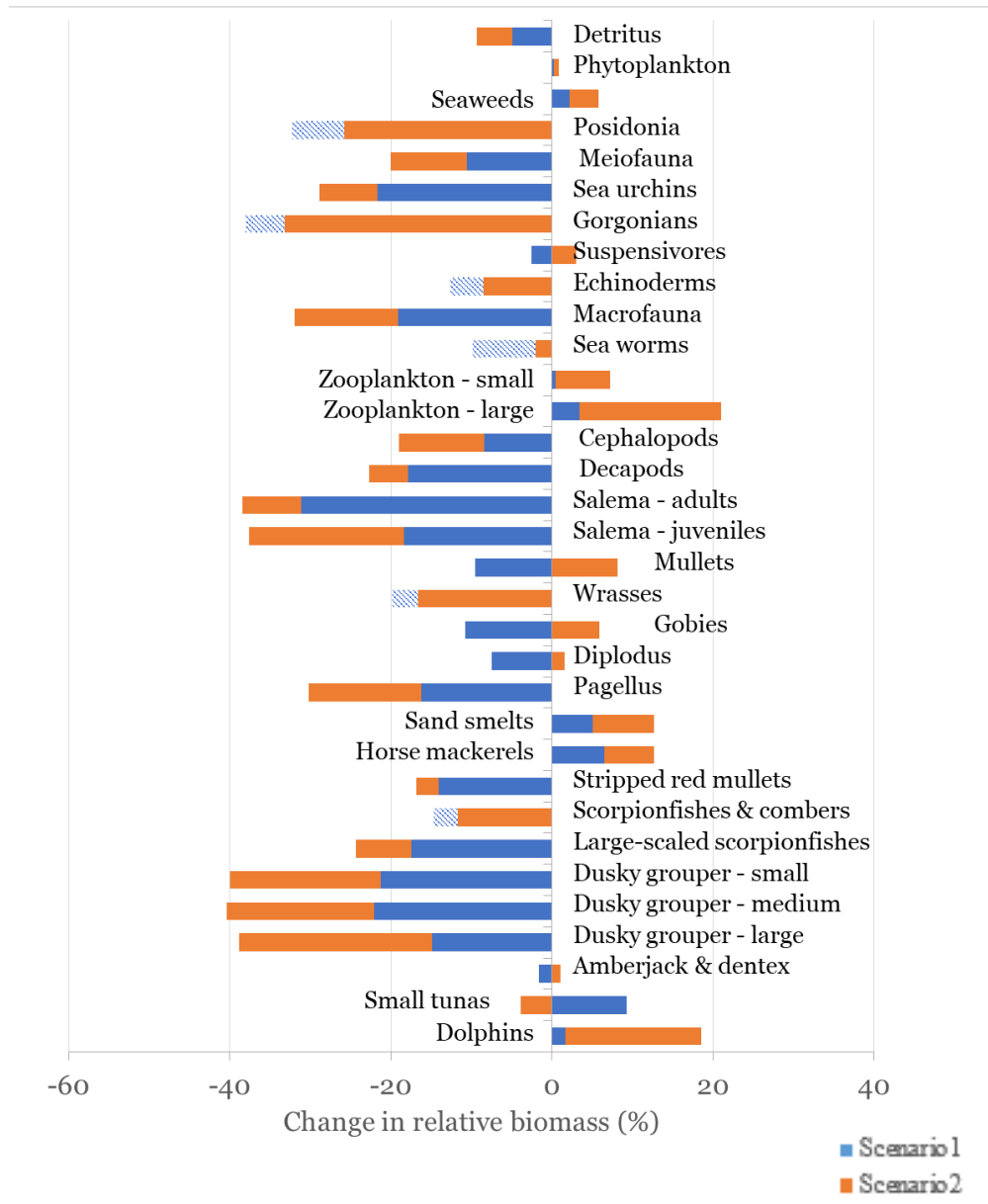
Figure 6: Functional groups with changes in relative biomass between initial conditions without changes in HFSs biomass and a simulated 30% decrease in P. oceanica and gorgonians biomass over 100 years. Changes in biomass resulting from trophic direct and indirect connection (made by applying FF; Scenario1-blue) or from groups targeted by direct and indirect non-trophic effects (made by applying FF+ MF; Scenario2 orange) are indicated. For the majority of the functional groups, the consequences of both trophic and non-trophic effects (FF+MF) are stronger than the trophic effects (FF) alone (blue + orange). The blue dashed forms denote the lower effects of the trophic and non-trophic effects (FF+MF) over the trophic effects (FF) alone. Relative changes in biomass for all the habitat reductions scenarios are in Supplementary Table S4 and Table S6.

The biomass of functional groups that were linked to HFSs through trophic and non-trophic effects (FF+MF) changed considerably, with the biomass of many groups decreasing (mean decreased 16%) and some groups increasing (mean increased 3%). In many functional groups, trophic and non-trophic effects (FF+MF) had negative effects that often were additive to the trophic effects alone (Figure 6). For example, the 30% reduction in HFSs trophic and non-trophic effects (FF+MF) resulted in decrease in dusky groupers (mean of multi-stanza groups -20%), stripped red mullets+ (-14%), pagellus (-16%), salema (mean of multi-stanza groups -25%), decapods+ (-18%), cephalopods (-9%), macrofauna+ (-19%), sea urchins (-22%), meiofauna (-11%), and detritus (-9%). In other cases, the trophic and non-trophic effects (FF+MF) were lower than the trophic effects alone (Figure 6) or even positive, due to the onsetting of top-down and bottom-up interactions. For example, the trophic and non-trophic effects (FF+MF) led to positive effects on functional groups by releasing them by the predator pressures (i.e. diplodus+, gobies+, mullets+ and suspensivores+ biomass increased) or by increasing of prey biomass such as zooplankton (+4%).

Fisheries

We evaluated €923 ha/year for the total annual landings value of commercial species within the MPA (Prato et al., 2016), based on current market values. The market values of each functional group were obtained as the average of the price of each species composing the functional groups (see Table S1). Economic values were derived from the ISMEA database (www.ismea.it). The values included in the analysis were based on market data of 2012 representing the price at the time of the survey and it is the average value of different marketplaces and processes of supply and demand.

The simulations carried out under the Scenario 1-30% (direct effect only) for 2100, and keeping the fishing effort at the present rate, suggests a 17% decrease of the catch of the commercial functional groups. In Scenario1, for the 16 functional groups listed by Prato et al. (2016), all but small tunas+, horse mackerels+ and sand smelts+ responded negatively to the decrease in *P. oceanica* and corals biomass. Instead, in Scenario2 (direct and indirect effects), all but diplodus+, gobies+, and mullets responded negatively. The reason is mainly due to the compensatory effects of Scenario2, in which the reduced biomass of predators leads to the release of the meso-predators from the trophic pressure that was not highlighted in the forcing function scenarios.
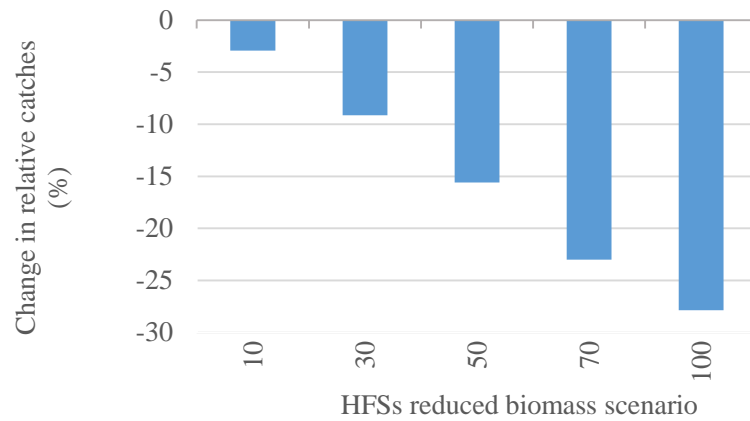
Figure 7: Percentage changes in catches biomass under Scenario2 (direct + indirect effects). In the figure are represented the important commercial species
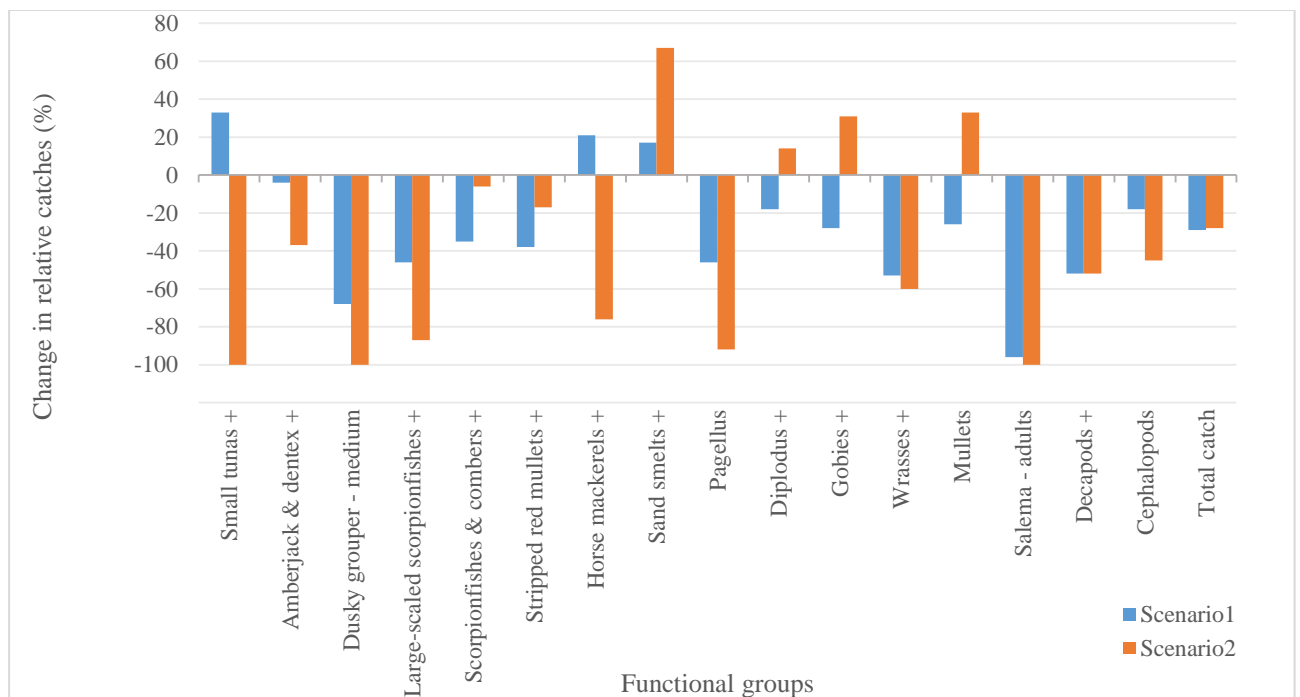
Figure 8: Percentage changes in catches biomass under scenarios representing trophic effects (FF- Scenario 1) and trophic and non-trophic effects (FF+MF- Scenario2). In the figure are represented the commercially important species under the 30% HFSs reduced scenario. (Scenario1 in blue and Scenario2 in orange)

In calculating the total commercial harvest ecosystem service value, we assumed that change in biomass does not affect harvest costs.

The simulation totally suggests an economic loss of about 247 €/h in Scenario1-100% and 308 €/ha in Scenario 2-100% (Table 2) in which all the *P. oceanica* meadows and gorgonians disappear.

Table 2: Monetary values associated with the commercially important species. It indicates the monetary loss due to trophic effects (FF- Scenario1) and trophic effects and non-trophic effects (FF+MF- Scenario2) respectively analysed with 100% reduction of habitat-forming species.

100% HFSs reduced scenario				SCENARIO1		SCENARIO2	
Group name	**Total catch (start)**	**Market price**	**Monetary value (start)**	**Total catch (end)**	**Monetary value (end)**	**Total catch (end)**	**Monetary value (end)**
	ton/km²/y	€/kg	€/ha	ton/km²/y	€/ha	ton/km²/y	€/ha
Small tunas +	0.21	11.80	25.37	0.29	33.66	0.00	0.00
Amberjack & dentex +	1.65	15.45	254.49	1.58	243.64	1.05	161.52
Dusky grouper - medium	0.08	18.70	14.18	0.02	4.51	0.00	0.01
Large-scaled scorpionf+	0.51	14.15	72.57	0.27	38.89	0.07	9.20
Scorpionfishes & combers +	0.32	16.31	52.64	0.21	34.31	0.30	49.23
Stripped red mullets +	0.10	12.20	12.65	0.06	7.82	0.09	10.53
Horse mackerels +	0.20	1.43	2.93	0.25	3.54	0.05	0.71
Sand smelts +	0.86	2.24	19.24	1.01	22.58	1.44	32.18
Pagellus	0.13	6.53	8.26	0.07	4.44	0.01	0.70
Diplodus +	3.34	8.05	269.14	2.75	221.41	3.80	306.09
Gobies +	0.06	3.62	2.09	0.04	1.50	0.08	2.75
Mullets	0.01	3.29	0.26	0.01	0.19	0.01	0.35
Salema - adults	1.88	5.85	110.19	0.07	4.29	0.00	0.00
Decapods +	0.14	20.90	29.04	0.07	13.93	0.07	13.83
Cephalopods	0.45	11.23	50.03	0.37	41.27	0.25	27.56
Total	**9.94**		**923.09**	**7.06**	**675.99**	**7.20**	**614.65**

3.4 Discussion

This study uses a combination of scenarios analysis to explore the potential effects of habitat loss due to OA by parameterizing within a mathematical food web model the direct and indirect effects of OA identified in the conceptual model of chapter 2. Different intensities of impacts were considered. Despite the growing empirical evidence of the OA effects on marine ecosystems and their component species, the prediction of the impacts of OA remains challenging, given the species-specific responses at local scales and the cascading effects of these responses (which can be additive, synergistic or antagonistic) on the entire ecosystem. Species habitat affinities, physiological preferences, life histories and interspecific interactions vary among systems and are rarely known in sufficient detail to make predictions. Despite the use of assumptions of linear relationship in the formulation of the effects of OA on the food web, the results of these ecological modelling application may be useful to demonstrate how changes in habitats extension can affect the community dynamics in terms of both, food web structures and flow of ecosystem services in a marine ecosystem.

Complex structured habitats offer protection to fishes and invertebrates both at juvenile and adult stages, and the loss of these functions may increase the vulnerability of some species to predation (i.e. preys' loss refuge). On the other hand, these complex habitats enhance the aggregation of prey, and their loss may lead to a decrease of the search rate of predators (i.e. loss of habitat aggregation point for prey). For example, it is documented that predation upon juvenile or invertebrate benthic species is significantly lower in seagrass than in unvegetated habitats (Espinosa-Romero et al., 2011, Pagès et al., 2012). Unfortunately, the model here used explicitly represents the ontogenetic phase shift from juveniles to adults only for dusky grouper and salema while for all the other groups the ontogenetic shifts are implicitly represented. Therefore, we were not able to identify completely the different effects of trophic and non-trophic impacts caused by the loss of HFSs on the functional groups of the model.

We assumed that the decrease of habitat-forming species will reduce the production of interested commercial species as a consequence of reduction of prey and for the loss of refuge for both adult and juvenile species. These assumptions are based on the main literature that identifies the seagrass meadows and the coralligenous as hotspots of biodiversity, refuge and nursery habitat for many commercially important species. For example, *P. oceanica* meadows are essential nursery areas for juvenile species of dusky grouper *E. marginatus* (Spedicato et al., 1995). Adult dusky grouper has a dominant role in structuring the food web (Prato et al., 2016) and its presence is influenced by complex habitats such as the coralligenous that

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represents shelter-rich sites highly favourite by the species (Harmelin and Harmelin-Vivien, 1999). The dusky grouper *E. marginatus* is a keystone species for the coralligenous habitat, and it is an important fisheries species of conservation concern (classified by IUCN as "endangered"; Cornish and Harmelin-Vivien, 2004). Therefore, the loss of HFSs could threaten the species presence.

Prato et al., (2016) have identified that three groups (i.e. dusky groupers, amberjack & dentex+, and large-scaled scorpionfish+), playing important keystone roles in the food web, held negative impacts on some functional groups through direct predation. The same groups also trigger positive consequences on other functional groups by reducing the pressure of meso-predation (Prato et al., 2016). Our results show that the habitat changes due to OA could threat these keystone species both reducing their foraging area and reducing their habitat, thus reducing the services that these habitats provide to them (i.e. the protection offered as nursery area). A slight decrease in medium and large dusky groupers biomass leads to large indirect effects on the food web that should favour cephalopods+ that are the groupers' favourite preys. Nevertheless, on the contrary of what we expected, scenarios representing both the trophic effects (FF) and trophic and non-trophic effects (FF+MF) indicate a cephalopods decrease, bottom-up induced, by the decrease in their preys (i.e. decapods+ and macrofauna+) that directly depend on *P. oceanica*.

The reduction in HFSs simulated together with the introduction of non-trophic effects (Scenario2) indicate that critical changes in the biomass of some functional groups sometimes dampen the impacts of the proposed scenarios of OA. For example, the reduction of HFSs - which were modelled by applying trophic effects (forcing functions) - was dampened by the addition of non-trophic effects – which were modelled by applying the mediation functions to simulate the indirect effects (Figure 6). This happens because Scenario 2, acting on the predator-prey relationship, leads to a higher reduction of the HFSs' predators (i.e. sea urchins, salema, decapods+ and especially diplodus+) which, in turn, favours some recovery processes for the HFSs.

The model is not able to represent completely the non-trophic interactions that would be needed, as it is shown by the increase in the sand smelts+ functional groups. The reason is due to the cascading effects of the trophic links within the web of unexpected strength. Indeed, a decrease of the gorgonian group that feed mainly on zooplankton will lead to an increase in the biomass of the zooplankton groups. Consequently, being the zooplankton the main food source of the

sand smelts+ there is an increase in the sand smelts+ biomass that is much stronger than the non-trophic effects imposed.

It is noteworthy to assess that these results are often counter-intuitive due to the complex interactions between bottom-up and top-down impacted trophic relationship. Our results highlight the importance of addressing the OA impacts in complex systems, including OA, by considering the whole food web (Bush et al., 2016). Indeed, competition and predation relationships are able to alter in complex ways the community responses to habitat degradation due to OA. Our study highlights how OA-induced changes in HFSs, such as *P. oceanica* and corals, could have substantial ecological consequences due to complex food web interactions.

Fisheries

Our results confirmed that the values of provisioning services are correlated to *P. oceanica* and coralligenous area. Climate change impacts, together with other anthropogenic pressures (i.e. fishing, pollution, and eutrophication), are threatening marine ecosystems, decreasing their resilience and their ability to provide benefits and well-being to the human society. Despite the difficulties of predicting the consequences of these impacts on the ecosystems, the modelling approaches can help to understand and predict ecosystem trends in the future scenarios. This kind of modelling exercises provide indications that could help to prevent and mitigate the climate change impacts.

The potential consequences caused by the loss of habitats and their functions/services (i.e. refuge and nursery) argues for empirical research to quantify the actual effect of habitat in coastal marine ecosystems.

The simulation analysis that is proposed here might overestimate responses to the impacts of the HFSs loss by accounting only partially the potential adaptive shifts in diet of the impacted functional groups. In fact, EwE allows to represent diet shifts in relation to change in biomass of prey and predators but firstly, diet shift parameters, clearly species-specific were set as default (Walters et al., 1997). Secondarily, EwE does not allow to introduce new functional groups in the diet.

In addition, the assumptions used for the application of the non-trophic effects (e.g. mediation functions) may be too simplistic leading to an overestimation of the effects of habitat loss.

However, this analysis might have underestimated some effects of HFSs reduction due to the underrepresentation of ontogenetic phases in the model. Increasing the number of functional groups split in age classes might allow to better represent the habitat services (i.e. nursery, refuge, food retention).

Another point that should be considered in future analysis is the fact that the model represents a high percentage of the production as export outside the system. This fact strongly drives EwE dynamics and might prevent to see some adaptation responses of functional groups. For instance, detritus accumulation (due to HFSs degradation) might be severely underestimated and all the detritus-based flows may be insensitive to functional groups changes.

Despite the widely recognised functions and services that coralligenous and *P. oceanica* provide, still few studies have tried to quantify the values of these habitats in supporting the ecosystem services (this is especially true for the coralligenous). Further researches are therefore needed in order to contribute to a holistic valuation of the Mediterranean marine coastal ecosystems. At the same time, it is important to understand the functional form and strength of the non-trophic interactions to comprehend and manage their influence in the marine ecosystems.

Moreover, further detailed data of the food web organisms' responses to OA together with the local-scale projections of ocean carbon chemistry are needed in order to allow for a more precise estimate of the OA and to better predict the functioning of future Mediterranean Sea ecosystem.

On the other hand, marine habitats display natural variability on various spatial and temporal scales and significant differences can be observed in the species-habitat relationship from site to site and through time. To address these objectives, more functional or process-oriented studies should be undertaken, in addition to long-term studies in a variety of Mediterranean localities (Charton et al., 2000).

However, predictions with complex models have the advantages to include complex ecological interactions (Serpetti et al., 2017). The model-driven scenario evaluation approach is an important tool to take into account future climate change and the potential impact on the food web whilst accounting for potential benefits loss for the human society. This work represents a step towards the improvement of predictions on the ecological and economic impacts on human systems that are necessary in order to contribute towards the definition of management mitigation strategies.

3.5   References

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3.6   Supplementary

Table S 1: Reference by species for fish groups in Portofino MPA Ecopath model (Prato et al., 2016)

Group names	Species name
Dusky grouper	*Epinephelus marginatus*
Amberjack+	*Seriola dumerili, Conger conger, Lophius piscatorius, Dicentrarchus labrax, Muraena helena, Scyliorhinus canicula, Dentex dentex, Sphyraena viridensis*
Scorpionfishes & combers	*Phycis phycis, Labrus merula, Labrus viridis, Sciaena umbra, Scorpaena scrofa, Pagrus pagrus, Zeus faber*
large scaled Scorpionfishes+	*Scorpaena notata, Scorpaena porcus, Serranus cabrilla, Serranus hepatus, Serranus scriba, Synodus saurus*
Stripped red mullet+	*Arnoglossus laterna, Bothus podas, Gaidropsarus mediterraneus, Gaidropsarus vulgaris,Trisopterus spp., Mullus surmuletus, Ophisurus serpens, Ophidion rochei, Parophidion vassali*
Wrasses	*Coris julis, Symphodus cinereus, Symphodus doderleini, Symphodus mediterraneus, Symphodus melanocercus, Symphodus ocellatus, Symphodus roissali, Symphodus rostratus, Symphodus tinca, Thalassoma pavo*
Gobies	*Deltentosteus colonianus, Deltentosteus quadrimaculatus, Gobius auratus, Gobius cruentatus, Gobius fallax, Gobius geniporus, Gobius paganellus, Gobius vittatus, Pomatoschistus minutus, Pomatoschistus quagga, Thorogobius ephippiatus, Thorogobius macrolepis*
Pagellus	*Pagellus spp.*
Diplodus+	*Diplodus puntazzo, Diplodus sargus, Diplodus vulgaris, Lithognathus mormyrus, Sparus aurata, Spondyliosoma cantharus*
Blennies+	*Blennius ocellaris, Diplodus annularis, Parablennius gattorugine, Parablennius rouxi*
Sand smelts+	*Atherina spp., Trachurus spp., Spicara maena, Spicara smaris, Chromis chromis, Anthias anthias, Boops boops, Oblada melanura*
Mullets	*Mugilidae*
Salema	*Sarpa salpa*
Decapods	Crabs, decapods
Suspensivores+	bivalves, suspensivores
macrofauna	macrofaunal invertebrates (amphipods, small crustaceans, gastropods, and brittle stars)
Echinoderms+	sea stars, sea cucumbers
Horse mackerels+	*Scomber spp., Sardinella aurita*

Table S 2: Simulation results of the application of single forcing functions compared with the combination of the 2 forcing functions

	Functional group	**Baseline** (t/km²)	10% loss P.oceanica	Gorgonians	P.oceanica & Gorgonians	30% loss P.oceanica	Gorgonians	P.oceanica & Gorgonians	50% loss P.oceanica	Gorgonians	P.oceanica & Gorgonians	70% loss P.oceanica	Gorgonians	P.oceanica & Gorgonians	100% loss P.oceanica	Gorgonians	P.oceanica & Gorgonians
1	Dolphins	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04
2	Small tunas +	1.23	1.25	1.24	1.27	1.31	1.27	1.34	1.37	1.30	1.44	1.43	1.33	1.53	1.52	1.39	1.63
3	Amberjack & dentex +	6.00	5.93	6.06	5.98	5.78	6.16	5.88	5.65	6.25	5.88	5.51	6.34	5.83	5.38	6.50	5.74
4	Dusky grouper - large	4.61	4.38	4.63	4.40	3.86	4.69	3.91	3.36	4.73	3.47	2.84	4.78	3.00	2.22	4.87	2.39
5	Dusky grouper - medium	1.26	1.17	1.26	1.17	0.98	1.26	0.98	0.79	1.27	0.79	0.60	1.27	0.61	0.39	1.28	0.40
6	Dusky grouper - small	0.62	0.58	0.62	0.58	0.48	0.62	0.49	0.39	0.62	0.40	0.31	0.62	0.31	0.21	0.63	0.22
7	Large-scaled scorpionfishes +	2.50	2.35	2.50	2.36	2.05	2.51	2.06	1.78	2.52	1.80	1.55	2.52	1.57	1.31	2.54	1.34
8	Scorpionfishes & combers +	1.18	1.12	1.18	1.12	1.01	1.18	1.01	0.91	1.18	0.91	0.84	1.17	0.83	0.78	1.17	0.77
9	Stripped red mullets +	2.14	2.04	2.14	2.04	1.83	2.15	1.84	1.64	2.15	1.66	1.47	2.16	1.49	1.30	2.17	1.32
10	Horse mackerels +	8.09	8.18	8.16	8.26	8.43	8.32	8.57	8.68	8.46	9.05	8.94	8.60	9.46	9.22	8.84	9.78
11	Sand smelts +	15.11	15.22	15.25	15.36	15.51	15.55	15.79	15.84	15.83	16.54	16.20	16.09	17.19	16.62	16.59	17.73
12	Pagellus	0.31	0.29	0.31	0.29	0.25	0.31	0.26	0.22	0.31	0.22	0.19	0.31	0.20	0.16	0.31	0.16
13	Diplodus +	29.70	28.99	29.71	28.99	27.51	29.73	27.51	26.28	29.75	26.34	25.28	29.77	25.35	24.35	29.79	24.43
14	Gobies +	6.00	5.79	6.01	5.80	5.34	6.03	5.35	4.95	6.04	4.98	4.61	6.05	4.65	4.26	6.08	4.31
15	Wrasses +	2.49	2.33	2.49	2.33	2.00	2.49	2.00	1.70	2.49	1.69	1.43	2.49	1.42	1.20	2.48	1.18
16	Mullets	1.17	1.13	1.16	1.13	1.06	1.16	1.06	0.99	1.16	0.99	0.93	1.16	0.92	0.87	1.16	0.86
17	Salema - juveniles	3.17	3.01	3.17	3.01	2.59	3.17	2.59	2.05	3.16	2.04	1.32	3.16	1.31	0.20	3.15	0.19
18	Salema - adults	6.10	5.53	6.09	5.53	4.20	6.09	4.20	2.85	6.08	2.83	1.68	6.07	1.66	0.25	6.06	0.24
19	Decapods +	12.61	11.90	12.61	11.90	10.34	12.62	10.36	8.89	12.63	8.91	7.52	12.63	7.54	6.01	12.65	6.05
20	Cephalopods	3.43	3.32	3.45	3.34	3.10	3.49	3.13	2.91	3.53	3.00	2.77	3.57	2.90	2.69	3.63	2.83
21	Zooplankton - large	3.12	3.13	3.14	3.15	3.18	3.18	3.21	3.22	3.21	3.32	3.28	3.25	3.40	3.34	3.31	3.48
22	Zooplankton - small	7.52	7.54	7.50	7.52	7.59	7.47	7.56	7.66	7.45	7.59	7.74	7.43	7.64	7.81	7.39	7.71
23	Sea worms	40.16	38.87	40.22	38.92	36.11	40.32	36.20	33.68	40.41	33.88	31.52	40.50	31.78	29.37	40.66	29.62

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24	Macrofauna +	49.72	46.68	49.75	46.71	40.10	49.83	40.19	34.21	49.89	34.35	28.98	49.96	29.15	24.00	50.07	24.14
25	Echinoderms +	21.38	20.50	21.42	20.53	18.60	21.49	18.67	16.92	21.55	17.06	15.40	21.62	15.59	13.83	21.74	14.03
26	Suspensivores +	74.23	73.52	74.40	73.68	72.05	74.73	72.26	70.78	75.02	71.44	69.68	75.30	70.55	68.58	75.82	69.49
27	Gorgonians	500.8	476.51	448.83	425.22	422.69	342.60	334.63	374.30	248.85	166.41	328.93	159.56	58.67	277.03	0.15	0.01
28	Sea urchins	64.95	60.51	64.96	60.53	50.72	65.00	50.86	41.71	65.04	41.77	33.23	65.07	33.32	23.91	65.14	24.03
29	Meiofauna	19.84	19.13	19.97	19.26	17.55	20.24	17.71	16.09	20.47	16.68	14.70	20.69	15.51	13.20	21.07	14.07
30	*P. oceanica*	3673.9	3305.60	3673.36	3305.25	2484.39	3672.62	2488.94	1706.12	3671.97	1704.75	960.62	3671.34	959.09	158.52	3670.06	157.93
31	Seaweeds	556.9	560.52	556.95	560.49	569.23	556.89	569.08	578.57	556.84	578.41	588.79	556.79	588.56	601.71	556.69	601.47
32	Phytoplankton	7.14	7.15	7.13	7.14	7.16	7.12	7.16	7.17	7.11	7.14	7.17	7.10	7.13	7.18	7.08	7.12
33	Detritus	65.25	63.34	65.25	63.34	59.13	65.26	59.18	55.20	65.26	55.19	51.50	65.27	51.47	47.61	65.27	47.57
	Total	5192.8	4787.54	5140.96	4736.65	3886.14	5035.56	3803.98	3036.91	4942.56	2830.95	2227.01	4854.00	1959.69	1355.06	4695.76	1082.28

Table S 3: Scenario 1

		10% HFS reduction			30% HFS reduction		50% HFS reduction		70% HFS reduction		100% HFS reduction	
	Functional group	Biomass (start)	Biomass (end)	Biomass (E/S)	Biomass (end)	Biomass (E/S)	Biomass (end)	Biomass (E/S)	Biomass (end)	Biomass (E/S)	Biomass (end)	Biomass (E/S)
1	Dolphins	0.03	1.01	0.03	0.03	1.01	0.03	1.04	0.03	1.06	0.04	1.10
2	Small tunas +	1.23	1.03	1.27	1.34	1.09	1.44	1.17	1.53	1.25	1.63	1.33
3	Amberjack & dentex +	6.00	1.00	5.98	5.88	0.98	5.88	0.98	5.83	0.97	5.74	0.96
4	Dusky grouper - large	4.61	0.96	4.40	3.91	0.85	3.47	0.75	3.00	0.65	2.39	0.52
5	Dusky grouper - medium	1.26	0.93	1.17	0.98	0.78	0.79	0.63	0.61	0.48	0.40	0.32
6	Dusky grouper - small	0.62	0.94	0.58	0.49	0.79	0.40	0.65	0.31	0.51	0.22	0.36
7	Large-scaled scorpionfishes +	2.50	0.94	2.36	2.06	0.83	1.80	0.72	1.57	0.63	1.34	0.54
8	Scorpionfishes & combers +	1.18	0.95	1.12	1.01	0.85	0.91	0.77	0.83	0.70	0.77	0.65
9	Stripped red mullets +	2.14	0.96	2.04	1.84	0.86	1.66	0.77	1.49	0.70	1.32	0.62
10	Horse mackerels +	8.09	1.02	8.26	8.57	1.06	9.05	1.12	9.46	1.17	9.78	1.21

11	Sand smelts +	15.11	1.02	15.36	15.79	1.05	16.54	1.10	17.19	1.14	17.73	1.17
12	Pagellus	0.31	0.95	0.29	0.26	0.84	0.22	0.74	0.20	0.64	0.16	0.54
13	Diplodus +	29.70	0.98	28.99	27.51	0.93	26.34	0.89	25.35	0.85	24.43	0.82
14	Gobies +	6.00	0.97	5.80	5.35	0.89	4.98	0.83	4.65	0.78	4.31	0.72
15	Wrasses +	2.49	0.94	2.33	2.00	0.80	1.69	0.68	1.42	0.57	1.18	0.47
16	Mullets	1.17	0.97	1.13	1.06	0.91	0.99	0.85	0.92	0.79	0.86	0.74
17	Salema - juveniles	3.17	0.95	3.01	2.59	0.82	2.04	0.64	1.31	0.41	0.19	0.06
18	Salema - adults	6.10	0.91	5.53	4.20	0.69	2.83	0.46	1.66	0.27	0.24	0.04
19	Decapods +	12.61	0.94	11.90	10.36	0.82	8.91	0.71	7.54	0.60	6.05	0.48
20	Cephalopods	3.43	0.97	3.34	3.13	0.91	3.00	0.87	2.90	0.84	2.83	0.82
21	Zooplankton - large	3.12	1.01	3.15	3.21	1.03	3.32	1.06	3.40	1.09	3.48	1.12
22	Zooplankton - small	7.52	1.00	7.52	7.56	1.01	7.59	1.01	7.64	1.02	7.71	1.03
23	Sea worms	40.16	0.97	38.92	36.20	0.90	33.88	0.84	31.78	0.79	29.62	0.74
24	Macrofauna +	49.72	0.94	46.71	40.19	0.81	34.35	0.69	29.15	0.59	24.14	0.49
25	Echinoderms +	21.38	0.96	20.53	18.67	0.87	17.06	0.80	15.59	0.73	14.03	0.66
26	Suspensivores +	74.23	0.99	73.68	72.26	0.97	71.44	0.96	70.55	0.95	69.49	0.94
27	Gorgonians	500.81	0.85	425.22	334.63	0.67	166.41	0.33	58.67	0.12	0.01	0.00
28	Sea urchins	64.95	0.93	60.53	50.86	0.78	41.77	0.64	33.32	0.51	24.03	0.37
29	Meiofauna	19.84	0.97	19.26	17.71	0.89	16.68	0.84	15.51	0.78	14.07	0.71
30	*P. oceanica*	3673.96	0.90	3305.25	2488.94	0.68	1704.75	0.46	959.09	0.26	157.93	0.04
31	Seaweeds	556.99	1.01	560.49	569.08	1.02	578.41	1.04	588.56	1.06	601.47	1.08
32	Phytoplankton	7.14	1.00	7.14	7.16	1.00	7.14	1.00	7.13	1.00	7.12	1.00
33	Detritus	65.25	0.97	63.34	59.18	0.91	55.19	0.85	51.47	0.79	47.57	0.73

Table S 4: Mediation functions M1 and M2

	Functional group	10% loss Biomass (start)	10% loss Biomass (end)	10% loss Biomass (E/S)	30% loss Biomass (end)	30% loss Biomass (E/S)	50% loss Biomass (end)	50% loss Biomass (E/S)	70% loss Biomass (end)	70% loss Biomass (E/S)	100% loss Biomass (end)	100% loss Biomass (E/S)
1	Dolphins	0.03	0.03	1.05	0.04	1.15	0.04	1.28	0.04	1.41	0.05	1.55
2	Small tunas +	1.23	1.32	1.07	1.50	1.22	1.68	1.37	1.86	1.51	2.06	1.68
3	Amberjack & dentex +	6.00	6.12	1.02	6.33	1.05	6.66	1.11	6.90	1.15	7.10	1.18
4	Dusky grouper - large	4.61	4.36	0.95	3.63	0.79	2.41	0.52	0.95	0.21	0.26	0.06
5	Dusky grouper - medium	1.26	1.07	0.85	0.56	0.45	0.12	0.09	0.01	0.01	0.00	0.00
6	Dusky grouper - small	0.62	0.52	0.85	0.30	0.49	0.10	0.16	0.01	0.02	0.00	0.00
7	Large scorpionfishes	2.50	2.39	0.96	2.17	0.87	2.04	0.82	1.85	0.74	1.47	0.59
8	Scorpionfishes & combers	1.18	1.15	0.97	1.13	0.96	1.19	1.01	1.14	0.96	0.95	0.80
9	Stripped red mullets +	2.14	2.03	0.95	1.76	0.82	1.58	0.74	1.39	0.65	1.17	0.55
10	Horse mackerels +	8.09	8.52	1.05	9.34	1.15	10.11	1.25	10.87	1.34	11.81	1.46
11	Sand smelts +	15.11	15.95	1.06	17.55	1.16	19.19	1.27	20.69	1.37	22.51	1.49
12	Pagellus	0.31	0.30	0.97	0.27	0.89	0.25	0.81	0.22	0.72	0.18	0.60
13	Diplodus +	29.70	29.65	1.00	29.14	0.98	28.61	0.96	27.90	0.94	27.25	0.92
14	Gobies +	6.00	6.08	1.01	6.16	1.03	6.24	1.04	6.23	1.04	6.14	1.02
15	Wrasses +	2.49	2.34	0.94	2.09	0.84	1.90	0.76	1.69	0.68	1.26	0.51
16	Mullets	1.17	1.17	1.00	1.18	1.01	1.18	1.02	1.17	1.01	1.14	0.97
17	Salema - juveniles	3.17	2.83	0.89	1.92	0.61	0.76	0.24	0.02	0.01	0.00	0.00
18	Salema - adults	6.10	5.37	0.88	3.57	0.59	1.48	0.24	0.07	0.01	0.00	0.00
19	Decapods +	12.61	11.10	0.88	7.67	0.61	4.62	0.37	2.17	0.17	0.31	0.02
20	Cephalopods	3.43	3.36	0.98	3.29	0.96	3.53	1.03	3.64	1.06	3.41	0.99
21	Zooplankton - large	3.12	3.25	1.04	3.51	1.13	3.78	1.21	4.01	1.29	4.28	1.37
22	Zooplankton - small	7.52	7.71	1.02	8.07	1.07	8.37	1.11	8.63	1.15	8.99	1.20
23	Sea worms	40.16	40.12	1.00	39.41	0.98	38.03	0.95	36.15	0.90	34.01	0.85
24	Macrofauna +	49.72	45.30	0.91	37.16	0.75	30.86	0.62	25.68	0.52	19.11	0.38

	Functional group	Biomass (start)	Biomass (end) 10%	Biomass (E/S) 10%	Biomass (end) 30%	Biomass (E/S) 30%	Biomass (end) 50%	Biomass (E/S) 50%	Biomass (end) 70%	Biomass (E/S) 70%	Biomass (end) 100%	Biomass (E/S) 100%
25	Echinoderms +	21.38	20.50	0.96	18.60	0.87	16.84	0.79	15.14	0.71	13.49	0.63
26	Suspensivores +	74.23	74.56	1.00	74.19	1.00	73.96	1.00	73.15	0.99	72.36	0.97
27	Gorgonians	500.81	431.80	0.86	332.46	0.66	187.56	0.37	74.26	0.15	0.01	0.00
28	Sea urchins	64.95	58.79	0.91	44.98	0.69	31.53	0.49	19.54	0.30	7.42	0.11
29	Meiofauna	19.84	18.26	0.92	14.23	0.72	10.83	0.55	7.21	0.36	3.32	0.17
30	*P. oceanica*	3673.96	3370.83	0.92	2646.83	0.72	1911.28	0.52	1167.55	0.32	261.02	0.07
31	Seaweeds	556.99	565.69	1.02	583.89	1.05	601.93	1.08	618.39	1.11	638.97	1.15
32	Phytoplankton	7.14	7.15	1.00	7.23	1.01	7.30	1.02	7.41	1.04	7.53	1.05
33	Detritus	65.25	64.26	0.98	61.75	0.95	59.04	0.90	56.25	0.86	52.88	0.81
	Total	5192.80	4813.86	0.93	3971.91	0.76	3075.01	0.59	2202.19	0.42	1210.48	0.23

Table S 5: Scenario 2

	Functional group	10% loss Biomass (start)	10% loss Biomass (end)	10% loss Biomass (E/S)	30% loss Biomass (end)	30% loss Biomass (E/S)	50% loss Biomass (end)	50% loss Biomass (E/S)	70% loss Biomass (end)	70% loss Biomass (E/S)	100% loss Biomass (end)	100% loss Biomass (E/S)
1	Dolphins	0.032	0.033	1.045	0.038	1.185	0.043	1.358	0.048	1.517	0.064	2.002
2	Small tunas +	1.229	1.194	0.972	1.181	0.961	0.875	0.712	0.234	0.191	0.000	0.000
3	Amberjack & dentex +	6.001	5.984	0.997	6.015	1.002	5.955	0.992	5.203	0.867	3.808	0.635
10	Horse mackerels +	8.086	8.322	1.029	9.109	1.127	9.342	1.155	7.885	0.975	1.965	0.243
4	Dusky grouper - large	4.607	4.014	0.871	2.817	0.611	1.647	0.358	0.564	0.122	0.048	0.010
5	Dusky grouper - medium	1.260	1.120	0.888	0.751	0.596	0.347	0.275	0.071	0.056	0.000	0.000
6	Dusky grouper - small	0.617	0.549	0.891	0.370	0.600	0.183	0.296	0.046	0.075	0.001	0.002
7	Large-scaled scorpionfishes +	2.496	2.313	0.927	1.888	0.756	1.476	0.591	1.043	0.418	0.317	0.127
8	Scorpionfishes & combers +	1.180	1.107	0.938	1.042	0.883	1.108	0.939	1.171	0.993	1.104	0.935
9	Stripped red mullets +	2.137	2.015	0.943	1.777	0.832	1.635	0.765	1.622	0.759	1.779	0.832

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#	Species											
	Sand smelts +	15.105	15.753	1.043	17.015	1.126	18.615	1.232	21.071	1.395	25.268	1.673
12	Pagellus	0.305	0.276	0.906	0.213	0.698	0.150	0.493	0.093	0.304	0.026	0.085
	Diplodus +	29.700	29.857	1.005	30.165	1.016	30.681	1.033	31.650	1.066	33.777	1.137
13	Gobies +	6.002	6.128	1.021	6.358	1.059	6.613	1.102	6.943	1.157	7.883	1.313
14	Wrasses +	2.488	2.352	0.945	2.074	0.833	1.832	0.736	1.547	0.622	0.995	0.400
15	Mullets	1.166	1.196	1.025	1.261	1.081	1.345	1.153	1.460	1.252	1.546	1.326
16	Salema - juveniles	3.171	2.832	0.893	1.978	0.624	0.960	0.303	0.111	0.035	0.000	0.000
17	Salema - adults	6.100	5.413	0.887	3.756	0.616	1.899	0.311	0.270	0.044	0.000	0.000
18	Decapods +	12.608	11.735	0.931	9.743	0.773	7.878	0.625	6.437	0.511	6.003	0.476
	Cephalopods	3.434	3.171	0.923	2.781	0.810	2.707	0.788	2.697	0.785	1.891	0.551
	Zooplankton - large	3.115	3.313	1.063	3.770	1.210	4.313	1.384	4.975	1.597	6.017	1.932
19	Zooplankton - small	7.518	7.677	1.021	8.060	1.072	8.490	1.129	9.040	1.202	9.853	1.311
20	Sea worms	40.163	39.903	0.994	39.346	0.980	38.996	0.971	38.839	0.967	38.169	0.950
21	Macrofauna +	49.716	44.529	0.896	33.838	0.681	23.999	0.483	14.169	0.285	1.489	0.030
22	Echinoderms +	21.383	20.704	0.968	19.570	0.915	19.017	0.889	18.973	0.887	18.631	0.871
23	Suspensivores +	74.234	75.013	1.010	76.438	1.030	78.071	1.052	80.135	1.079	83.303	1.122
24	Gorgonians	500.813	436.421	0.871	334.479	0.668	217.093	0.433	104.850	0.209	0.023	0.000
25	Sea urchins	64.952	59.112	0.910	46.230	0.712	33.737	0.519	22.021	0.339	8.201	0.126
26	Meiofauna	19.844	18.558	0.935	15.881	0.800	13.645	0.688	11.995	0.604	10.327	0.520
	P. oceanica	3673.963	3388.985	0.922	2728.476	0.743	2069.017	0.563	1408.547	0.383	474.876	0.129
	Seaweeds	556.988	566.752	1.018	589.311	1.058	614.229	1.103	642.577	1.154	682.601	1.226
27	Phytoplankton	7.139	7.141	1.000	7.135	0.999	7.102	0.995	7.025	0.984	6.903	0.967
28	Detritus	65.251	64.401	0.987	62.373	0.956	60.465	0.927	58.739	0.900	56.360	0.864
29	Total	5192.803	4837.871	0.932	4065.237	0.783	3283.466	0.632	2512.052	0.484	1483.229	0.286

Table S 3: Percentage changes in catches of commercially important species under the imposed scenarios.

Group name	CATCHES (%)									
	SCENARIO1					SCENARIO2				
	10	**30**	**50**	**70**	**100**	**10**	**30**	**50**	**70**	**100**
Small tunas +	3	9	17	25	33	-3	-4	-29	-81	-100
Amberjack & dentex +	3	-2	-2	-3	-4	0	0	-1	-13	-37
Dusky grouper - medium	0	-22	-37	-52	-68	-11	-40	-72	-94	-100
Large-scaled scorpionfishes +	-7	-17	-28	-37	-46	-7	-24	-41	-58	-87
Scorpionfishes & combers +	-6	-15	-23	-30	-35	-6	-12	-6	-1	-6
Stripped red mullets +	-5	-14	-23	-30	-38	-6	-17	-23	-24	-17
Horse mackerels +	-4	7	12	17	21	3	13	16	-2	-76
Sand smelts +	2	5	9	14	17	4	13	23	39	67
Pagellus	2	-16	-26	-36	-46	-9	-30	-51	-70	-92
Diplodus +	-5	-7	-11	-15	-18	1	2	3	7	14
Gobies +	-2	-11	-17	-22	-28	2	6	10	16	31
Wrasses +	-3	-20	-32	-43	-53	-5	-17	-26	-38	-60
Mullets	-6	-9	-15	-21	-26	3	8	15	25	33
Salema - adults	-3	-31	-54	-73	-96	-11	-38	-69	-96	-100
Decapods +	-9	-18	-29	-40	-52	-7	-23	-38	-49	-52
Cephalopods	-6	-8	-13	-16	-18	-8	-19	-21	-21	-45
Total catch	-3	-11	-17	-23	-29	-3	-9	-16	-23	-28

Table S 4. Predicted relative biomass after HFSs decreased by 30% over 100 years in the Portofino MPA with (in orange) and without (in blue) HFSs mediation functions. Biomass is relative to the base model (e.g., a value of 1 is equivalent to no change).
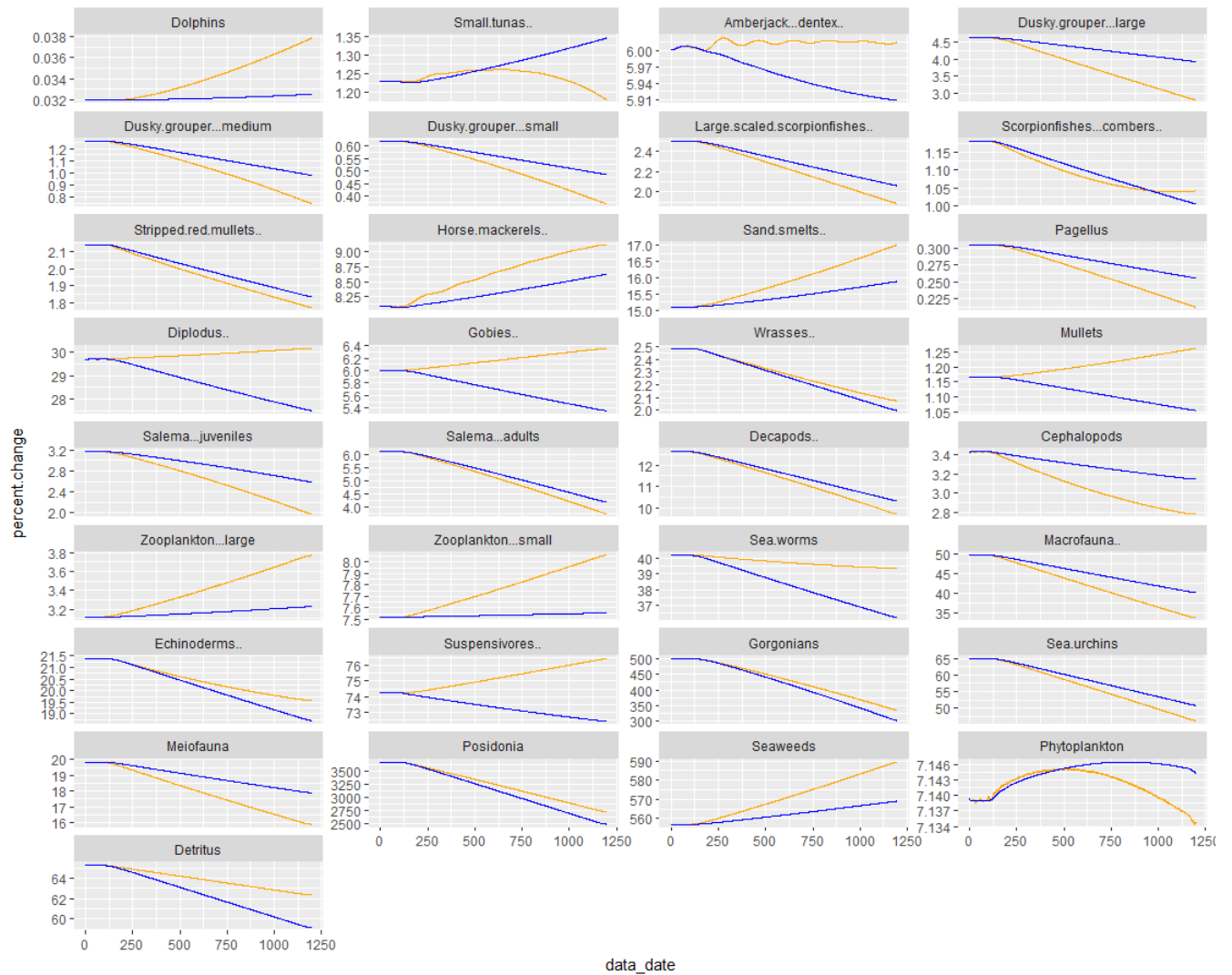
Chapter 4 - OA impacts on cultural ecosystem services: Case study of the divers in the Italian peninsula

4.1   Introduction

For the end of the 21st century, observed and projected ocean acidification (OA) and global warming impacts could have the potential to alter marine ecosystems and the provision of services and benefits supporting human well-being. In the last two decades, the ecosystem services (ES) framework has been adopted by the scientific community to understand the ways in which ES support human well-being and to improve the environmental decisions making, by providing information on the benefits of nature conservation and the consequence of ecosystems changes for human well-being.

Despite the high uncertainty of the impacts of climate changes on marine ecosystems in future scenarios (IPCC, 2014), integrating climate change drivers into assessments of ecosystem services provision is essential for designing context appropriate management strategies. Although our understanding of the ways in which ES support human well-being has increased in the last two decades, cultural ecosystem services (CES) have been relatively neglected by researchers and policymakers. This fact depends mainly on the difficulty to assess and to monetise non-material benefits that are closely linked with our emotional perception of the world, which is by definition intangible and subjective. Most economic valuations of the non-material benefits provided by marine CES have been based on market-related values arising from aesthetic and recreational opportunities (Jobstvogt et al., 2014). The quantification of environmental attributes in a monetary unit facilitates the prioritisation and comparison of the ecosystems services with the other services and benefits that are at stakes in the political agenda, raising awareness to policymakers (Lew , 2015). Hence, there is an urgent need of tools and methods to enable a better understanding and the inclusion of economic values associated with threatened marine ecosystems, such as coralligenous and *Posidonia oceanica* meadows, in the analyses of ecosystem-based management policies.

In this work, we focus on the cultural services provided by two Mediterranean ecosystems, coralligenous and *P. oceanica* meadows. These two habitats represent important biodiversity "hot-spots", highly threatened by current anthropogenic impacts and by future scenarios of

climate changes (Marbà et al., 2014; Martin et al., 2014). These ecosystems are able to generate highly valuable ecosystem services and benefits (BES). Following the ES theory (CICES V4.3, 2012) coralligenous habitats and seagrass meadows provide humans with several services belonging to provisional (i.e. food, raw materials, pharmaceutical molecules), regulating (i.e. carbon sequestration, nutrient recycling), and cultural ecosystem services (CES) (i.e. recreational activities, aesthetic inspirations) services. In order to analyse the CES provided by coralligenous and *P. oceanica* ecosystems, we have selected the scuba diving recreational activities as an indicator of the cultural services related to these habitats.

There are many typologies of CES, which have been listed and categorised under different frameworks, such as: the Common International Classification of Ecosystem Services (CICES V4.3, 2012), the Millennium Ecosystem Assessment (MEA, 2005), and The Economics of Ecosystems and Biodiversity (TEEB Foundations, 2010) initiative. Following the Millennium Ecosystem Assessment (2005), CES can be described as "the non-material benefits people obtain from ecosystem through spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experiences". This definition could be controversial because the categories are intangible and can overlap, e.g. recreation can include aesthetic and spiritual experiences (Jobstvogt et al., 2014). Hence, Common International Classification of ecosystem services (CICES) defined the CES as "the physical setting, locations, or situations that give rise to changes in the physical or mental states of people, and whose characters are fundamentally dependent on living processes".

Cultural services provided by coralligenous and seagrass meadows to scuba-divers consist of non-consumptive recreational use. The underwater seascape provided by coralligenous and *P. oceanica* provides numerous services (i.e. high biodiversity, fish abundance, complex habitats to explore, and water clarity) that enhance the quality and the enjoyment of underwater recreation. To a large extent, the economy of Mediterranean Sea countries rely on tourism, which accounts for the one-third of international tourism activity (EEA, 2000) and according to the UNEP/MAP, (2012), the Mediterranean region is the first world touristic destination. In 2011, the Mediterranean coast attracted 283 million international tourists, nearly 30% of the global tourism, generating the same year revenue of $224 billion in the Mediterranean (Campagne et al., 2015 and reference therein). Scuba-diving is one of the fastest growing marine-based activity in the world counting for 1 million of new trained divers per year (Davenport and Davenport, 2006). In the Italian peninsula, the coastal tourism and, in particular, the diving activities, are important economic sectors in terms of employment and benefits. Therefore, climate change driven ecosystem degradation (i.e. loss of iconic species from the

coralligenous, such as gorgonians and soft corals) is expected to negatively impact on the coastal economy. Indeed, scuba diving sector as a non-consumptive form of marine tourism largely depends on the quality of the marine environment.

Recent valuation studies (Rodrigues et al., 2015) have highlighted that relevant marine habitats such as the Mediterranean coralligenous assemblages, provide valuable CES, whose values are related to scuba diving tourist activity.

In order to value the cultural services ("output value" of the ecosystem), we used non-market analysis techniques that are useful tools to assess the potential economic impact on human well-being of future changes in environmental attributes (Louviere et al., 2000) in the absence of direct market values. The methodology belongs to the preference-based methods, which are currently the most commonly used methods to assess the economic value of ecosystem services (Kumar, 2010). These methods include both the stated preference and revealed preference approaches. Revealed preference methods (RP) are based on observing people's behaviour in markets, while stated preference approaches (SP) simulate a market and the demand for ecosystem services by means of surveys on hypothetical changes in the provision of ecosystem services. Stated preference methods are particularly relevant in this context, as they can elicit non-use as well as use values linked to the specific ecosystem service analysed.

In this study we used a choice modelling (CM) approach- belonging to the stated preference approach- that is a survey-based methodology for modelling preferences for goods, which are described in terms of their attributes and in terms of the levels that these attributes will take.

Respondents are faced with a series of alternative descriptions for goods, which differ in the attribute levels. Respondents are therefore asked to choose their most preferred one. The inclusion of a price attribute is determinant to recover indirectly the willingness to pay (WTP) for the selected good or service from the people 'choice.

The power of the choice model relies on not asking respondents directly for individuals' willingness to pay (WTP) or to accept compensation (WTA) for a certain environmental change; instead it consists in offering a choice of goods or services characterized by a bundle of attributes, just as consumers are accustomed to do in normal market.

Choice modelling (CM) has important advantages over other non-market valuation methods as it enables to collect large amounts of data from a single application (Hanley et al., 2001) and it allows for the estimation of the effects of changes in multiple resource attributes on consumer welfare (Louviere et al., 2000).

Literature review reports that the CM valuation of marine quality by divers was performed globally focusing on a wide range of attributes: Sorice et al., (2005) analysed divers' preferences for: 1) the presence of marine biodiversity, 2) the amount of an MPA open to diving, 3) availability of educational briefing, 4) presence of diving supervision, and 5) crowding in Texas; Schuhmann et al., (2013) estimated WTP for coral quality, fish diversity, turtle sightings, and crowding in Barbados; Gill et al., (2015) estimated WTP for fish abundance, viewing large fish and the presence of fishing gear in Caribbean; and Shideler and Pierce, (2016) estimated recreational divers' willingness to pay for grouper encounters in Florida. Rodrigues et al., (2015) is one of the first studies using the CE for the assessment of the impacts of sea warming and ocean acidification in the context of recreational scuba diving in the Mediterranean Sea. Rodrigues et al. (2015) employed the CM methodology to estimate WTP for changes in several attributes associated with the recreational use of coralline habitats, such as: the complexity of the underwater structure, the presence or absence of jellyfish, the level of crowding and the quality of gorgonian corals in Spain, where the different levels of the environmental status were associated to climate change pressures.

Following the Rodrigues et al., (2015) approach, we aimed at highlighting some of the societal implications of the degradation of coralligenous and seagrass meadows habitats due to climate change, focusing in particular on the implications to the Italian dive sector. Changes in diving quality were analysed by a choice experiment submitted to divers.

4.2 Methods

Choice experiment design

The questionnaire consisted of two sections: the first section aimed to collect personal and demographic data of the respondents to identify factors that could influence their responses, such as gender, age, level of education, and diving qualification. Additional questions explored the kinds of benefits that the scuba diving experience provided to them. The second section was a choice experiment that contained 12 multiple choice questions. We used the choice experiments to estimate the willingness to pay (WTP) of recreational tourist divers for different levels of habitat attributes (i.e. coralligenous and seagrass status) related to different levels of habitat alterations due to climate change impacts.

In the choice experiments, the respondents were asked to choose the most preferred alternative between two per times, where the alternatives differed in terms of attributes' level.

We used the literature review to identify the attributes that maximised the divers' utility and that will likely be impacted by the climate change. In particular we considered Wielgus et al., (2003), Gill et al. (2015) and Rodrigues et al., (2015) and we tested the consistency of the selected attributes and their respective levels administering the questionnaires to a pre-sample of tourist divers selected from 5 Italian sites with coral and seagrass habitats.

The selected attributes were the *"Number of tourists"* per Dive trip, *"Coral cover"*, *"Seagrass cover"*, and *"Price"* per dive (Table 2), while the chosen levels represented a spectrum of environmental conditions from good conservatory status to heavily damage, as detailed below.

1) *Number of divers* found on a diving trip: the crowding level was a relevant feature to value the quality of a dive as suggested by several studies (Wielgus et al. 2003, Gill et al. 2015, and Rodrigues et al., 2015).

2) *Coral cover*, expected status of corals: the corals - gorgonians were considered to be attractive features of coralligenous habitats of the Italian diving destination. Three levels were defined for this attribute: a) 100% corals in good quality; b) 50% corals have disappeared due to climate change, and c) 100% corals have disappeared due to climate change.

3) *Seagrass cover,* expected status of seagrass. Despite we were aware that this habitat was not among the favourite by the divers, the presence and the status of seagrass meadows (especially *P. oceanica*) were included in the questionnaires since this habitat is highly threatened by climate change and it is currently a conservation target of the marine policies (Jordà et al., 2012). Moreover, in the last few years, much effort has been made in the Mediterranean countries in order to improve the citizens awareness of the importance of the *P. oceanica* ecosystems. Thus, our analysis could provide insights into the effectiveness of the efforts in improving the citizen perception on the value of seagrass meadows and on the cultural values associated with this ecosystem.

4) *Price* of the dive: This attribute referred to the price of a single 50 minutes dive. This value included the boat trip, air and tank to dive, and dive insurance costs. The average price is € 40 for the high tourism season. For the CE, price levels were set at € 20, € 50, € 70 and € 90.

Table 1: list of attributes and levels relative to a diving experience in the Italian Sea.

Attributes	Levels				
Number of divers	5	15	25		
Corals cover	100%	50%	0%		
Seagrass cover	100%	50%	0%		
Price	€ 20	€ 40	€ 50	€ 70	€ 90

Starting from the attributes list -with their relative levels- we created a total choice set using the R software, ALgDesign package (Wheeler, 2004). A full factorial design with 3 three-level factors (*"Numbers of divers"*, *"Corals cover"*, *"Seagrass cover"*) and one four-level factor (*"Price"* -per-dive attribute) was created. In the full factorial design, the attributes (independent variables) were manipulated and all combinations of the levels of each attribute were included. In our case, where there are three three-level attributes and one five-level attribute, the full factorial design comprised 135 combinations of the levels of each attribute ($3^3 \times 5$).

An optimal set of thirty combinations of attributes was selected from the full factorial design of 135 combinations using the optFederov function in the AlgDesign package for the R statistical software (Wheeler, 2004). At this point, we generated a fractional factorial design from the full factorial design with the function optFederov.

The list of attribute combinations was then duplicated and each duplicate was randomised separately and joined to create the 30 random pairs of alternative version of a dive trip (as described by Aizaki and Nishimura, 2008).

We eliminated successively the internally inconsistent combinations and we obtained 24 alternatives that were considered to be cognitively manageable, whilst still permitting the estimation of non-linear main effects for each of the attributes. The pairs of alternatives were then blocked into two sets of six paired choices, each with a "neither" alternative for consistency with market decisions and were presented to divers. The presence of this latter choice option mimicked real market situations in which the diver is not forced to make a choice but can opt out (Rodrigues et al., 2015).

Table 2: Example of choice set

Caracteristic of the dive	Site 1	Site 2
Number of divers found on a diving trip	5	5
Expected state of gorgonians (red coral, black gorgonian, yellow gorgonian)	50% cover of corals due to climate change	0% cover of corals. Disappeared due to climate change
Expected state of seagrass meadows	0% cover of seagrass Posidonia oceanica due to climate change	100% cover of seagrass Posidonia oceanica, good status
Price of the dive (includes boat trip, air tank to dive and dive insurance)	50	40

All model estimation was conducted using the "survival" package (Therneau, 2015; Therneau and Grambsch, 2000) in R statistical environment (R Core Team., 2015) using the package "clogit" (Aizaki, 2012).

Model estimation-Theory framework of the econometric model

Statistical techniques for the analysis of discrete choices have been used with increasing regularity since the 90s, first with the development of the binomial logit techniques that were suitable for binary choice problems (Hoffman and Duncan, 1988). Afterwards, the multinomial logit technique and the conditional logit were implemented in order to address also the problem of the choice among three or more categories.

The CE technique is an application of the theory of value (Lancaster, 1966), combined with random utility theory (Manski, 1977; Thurstone, 1927). According to the Lancaster's theory of value (1966), the individuals obtain utility not from the goods but from the attributes that describe these goods (Hanley et al., 1998). In other words, the theory assumes that the consumer's utilities for good (U_{ij}) can be decomposed into attributes that characterised that good:

$$U_{ij} = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \beta_3 X_{i3} + \beta_4 X_{i4} + \ldots + \beta_n X_{in} \qquad \text{(Eq.1)}$$

where X_n represents an attribute of the good (in our case is an attribute of a diving trip) and β is a parameter which explains the contribution of each random variable to the overall utility of an alternative and is homogenous across individuals.

The foundation idea of the random utility theory (McFadden, 1974) is that when individuals are faced with alternatives, they will choose the alternative that gives them the greatest utility (U). Maximization of expected utility representation implies that two choices j and h involve comparison of expected utilities such that $U_j > U_h$. However, the analyst typically cannot observe all attributes that affect preferences. In our analysis, alternative choices are expressed as types of dive.

In its general representation, overall utility (*U*) has two components: (1) conditional utility (*V*), which is a function of the level of environmental attributes (X_{ij}) and is observable to the researcher (eq. 2), and (2) an unobservable, "random" component (ε), which contains variables that are predictors of preference formation in respondents, but which are not known to the researcher.

$$V_{ij} = \sum_{h=1}^{H} \beta_j X_{ij} \qquad \text{(Eq.2)}$$

Typically $U_j \neq V_j$ and V_j is linear in the parameters $X_j\beta$,

$$U_{ij} = V_{ij} + \varepsilon_{ij} = \beta_j X_j + \varepsilon_j \qquad \text{(Eq.3a)}$$

$$U_{ih} = V_{ih} + \varepsilon_{ih} = \beta_h X_h + \varepsilon_h \qquad \text{(Eq.3b)}$$

Where:

U_{ij}: total utility (U) for individual i choosing option j observable

V_{ij}: observable utility (V) for individual i choosing option j (is a linear additive function of the independent variables X with coefficient β)

X_j: the particular attributes (observable) of the good X in choice j

β parameter: is a weight measure that explains the contribution of each random variable to the overall utility of an alternative and is homogenous across individuals (Mariel et al. 2013).

ε_{ij}: unobservable utility (ε) for individual i choosing option j (is independently and identically distributed (i.i.d.) as extreme value).

The choice between alternatives (Eq. 4) will be a function of the probability (P) that the utility from alternative j is greater than the utility that could be derived from the other h alternatives within the choice set (C). That is:

$$P_{ij} = \text{Prob} \ (V_{ij} + \varepsilon_{ij} > V_{ih} + \varepsilon_{ih}) \ \forall j \neq h \in C \qquad \text{(Eq.4)}$$

As the complete utility of an alternative cannot be determined, we can only estimate the probability of choosing one option over another (Hoyos, 2010). The probabilistic odds that one alternative is selected over another is estimated using a standard multinomial logit model (MNL) also called conditional logit model. The MNL model can be derived by assuming the log of the odds ratio (the ratio of the success -in our case the dive trip selected- and the sum of the failure –in our case the other diving alternatives) equals an index function βX_j (Eq.5).

$$P_{ij} = \frac{\exp(V_{ij})}{\sum_h \exp(V_{ih})} \qquad \text{(Eq.5)}$$

By specifying the deterministic utility V_{ij} as linear in the parameters $\beta_1, \beta_2, \ldots \beta_n$ for each attribute in the model, the probability model becomes (Eq.6):

$$P_{ij} = \frac{\exp(\beta_j X_{ij})}{\sum_j \exp(\beta_j X_{ih})} \qquad \text{(Eq.6)}$$

The utility function for this model is specified in Eq.7:

$$
\begin{aligned}
U_{ij} = \quad & \beta_0 \cdot DIVE + \beta_1 \cdot \textit{Corals cover } 50_{ij} + \beta_2 \cdot \textit{Corals cover } 0_{ij} \ + \\
& + \beta_3 \cdot \textit{Seagrass cover } 50_{ij} + \beta_4 \cdot \textit{Seagrass cover } 0_{ij} + \\
& + \beta_5 \cdot \textit{Number of divers } 25_{ij} + \beta_6 \cdot \textit{Number of divers } 15_{ij} \ + \\
& + \beta_7 \cdot \textit{Price} + \varepsilon_{ij} \qquad\qquad\qquad\qquad\qquad\qquad \text{(Eq.7)}
\end{aligned}
$$

where *DIVE* refers to an alternative specific constant (1 if was selected the diving trip; 0 if it was selected the opt-out option); *"Coral cover 50%"* represents a dummy variable taking a value of 1 if the respondent chose the alternative with "50% degraded," and 0 otherwise; *"Coral cover 0%"* is a dummy variable taking a value of 1 if the respondent chose the alternative with 0% coral and 0 otherwise and so on for all the independent variables except for price.

Willingness to pay

The willingness-to-pay (WTP) for each attribute was derived from the MNL model using the coefficients from each attribute level and the coefficients for price. Estimated coefficients represent marginal utilities that are the increment of utility. When the coefficients are compared with reference levels they reveal the relative importance of attributes and their levels and reflect respondents' willingness to trade one attribute level for another.

The addition of the price attribute in the utility expression is essential in order to derive implicit price for marginal changes in attribute levels (Rodrigues et al., 2015), called the marginal WTP.

The marginal WTP for attributes/levels (non-monetary variable) is calculated as $-\beta_{nm}/\beta_{price}$; where β_{nm} is an estimated coefficient of the non-monetary variable and β_{price} is an estimated coefficient of the monetary variable.

$$WTP = -\frac{\beta_{nm}}{\beta_{price}} \qquad \text{(Eq.8)}$$

From the parameter estimates it is possible to derive welfare changes in monetary terms. These values are associated with changes in the level of an attribute compared with its reference level, provided that the remaining parameters are held constant. Welfare estimates designated as IP, or as a measure of WTP, reflect utility increases when the value is positive. This can be interpreted as WTP for a change in a certain attribute level. However, a negative value indicates a decrease in utility. This suggests that individuals require compensation through lower prices (Train and Weeks, 2005) in order to have the same level of utility as in the reference dive. We calculated the negative ratios of the parameters associated with each attribute level and price.

4.4   Results
Descriptive statistic

Over the period August 2016 August 2017, an online survey was sent to 18 diving centres and clubs in Italy. Among them, 9 responded to our request and delivered the questionnaire to their clients and/or members. 229 scuba divers responded using on-line surveys. The respondents were Italian, the average age of respondents was 45 years, and 68% of them were male (Table 3; $\chi^2 = 31.92$, df =1, p <0.001). The mean number of years of diving per diver was 13 years, ranging from 1 to 50 years; the divers owned mainly a superior dive licence (Table 3; $\chi^2 = 20.24$, df =1, p <0.001). The mean number of dive trips per each recreational diver (open, advance) was 15 per year, ranging from 1 to 40 dives per year. Divers holding a superior dive licence reported a mean of 53 dives per year, ranging from 5 to 250 (Table 3). The majority of paying recreational divers on dive trip in the analysis were visiting from another region (mostly northern Italian region 81%; $\chi^2 = 238.13$, df =2, p < 0.001) and spent on average between 200 and 1000 € for the diving trips lasting on average 7 days (min 1; max 30). On average, respondents spent 39 ± 22€ per a single dive (Table 3).

Over the half of the surveyed divers were full-time employed (60%; ($\chi^2 = 314.82$, df =5, p < 0.001) with an average annual gross income between 30.001 and 40.000 (53%).

Table 3:Descriptive data of the divers surveyed by the present study

Descriptive statistic		sample (229)
Gender	**%**	**n**
Male	68	157
Female	32	72
	Mean	SD
Age	45	13
Instruction	3.9	1.3
1 = Primary; 2 = Professional school; 3 = High school; 4 = Bachelor degree; 5 = Master degree; 6 = Higher university level		
Gross annual income level	4.09	1.99
1 = 0 – 10.000; 2 = 10.001 – 20.000; 3 = 20.001 – 30.000; 4= 30.001 – 40.000; 5= 40.001 – 50.000; 6 = 50.001 – 60.000; 7= 60.001 – 70.000; 8 = more than 70.000		
Amount paid for dive trip	39 €	22 €
Years of diving experience	%	n
1-5	24	56

6-10	19	43
11-15	18	40
16-20	16	36
>20	24	55
Employment status	**%**	**n**
Unemployed	3	7
Student	13	30
Part-time	8	18
Retired	6	14
Full-time employed	60	138
Other	9	21
Diver certification level	**%**	**n**
Beginners	15	34
Advanced	20	47
Superior	45	102
Superior -Technic	20	47
Change in the sea wellness since the beginning of the activity	**%**	**n**
Much worse	5	12
Worse	52	119
The same	20	46
Better	21	48
Much better	2	4

Most of the respondents (74%; χ^2= 51.88, df= 1, p < 0.001) have visited at least one MPA during their life and among them, more than 91% evaluated the experience as good or excellent (χ^2= 152.67, df= 1, p < 0.001).

The divers with more than 10 years of experience were asked to indicate their perception of the status of underwater environments. Almost the 60% of the respondents agreed that the underwater habitat conditions had worsened since the beginning of their diving activity (χ^2= 111.55, df= 2, p < 0.001). The main reasons were found in the decrease of the numbers and size of fish and corals (33%), the increase of plastic litters, ghost nets and pollution (29%), the increased abundance of stinging jellyfish, alien species and algae (9%). However, almost 12% of the respondents with more than 10 years' experience of diving acknowledged that the MPAs have significantly improved the environmental status through an increase in presence of marine biodiversity within the MPAs.

The respondents were asked to choose among three species the one that they would like to see during a dive trip. The responses were grouped by the level of expertise (i.e. beginners vs experts). No difference was found between beginners and experts in the choice of the emblematic species (χ^2 test, df=1, p >0.05) except for rock fishes and moray eels that appear to be more appreciate by beginners (χ^2 test, df=1, p <0.05). Overall, more than half of the participants have selected red corals (51%), groupers (42%), and seahorses (51%). The choice of red corals and groupers, which are emblematic species of the coralligenous, confirms the attractiveness of this environment. The appreciation for seahorses, often found in the seagrass meadows, is an evidence of the potential interest of the divers for the *P. oceanica* meadows, even if only 19% of the respondents have chosen to see the *P. oceanica* meadows during a dive trip. This result could be an evidence of the low awareness of the divers regarding the *P. oceanica* meadow that is considered a low attractive habitat even if the fauna hidden inside could be highly appreciated by the divers.
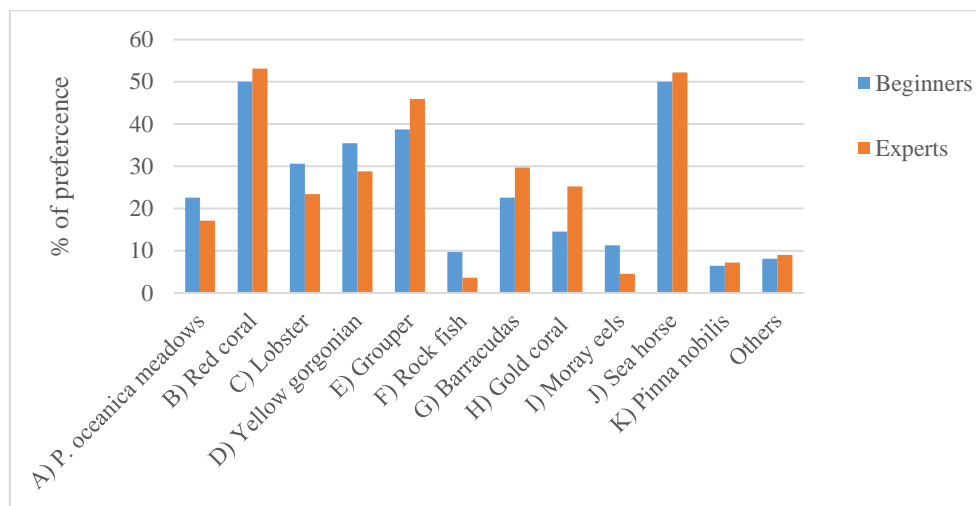
Figure 1: Percentage of preference by divers of emblematic Mediterranean marine species. The blue bars represent the beginners' divers (open and advance licence N= 80) and the orange bars represent the experts' divers (superior dive licence N= 149).

The respondents were asked about the importance of some features determining the choice of a dive experience. The most important factors that the respondents have selected are the beauty of the underwater landscape (important for the 91%; χ^2=77, df=1, p < 0.001), the abundance of marine fauna (90%; χ^2=73, df=1, p < 0.001), the well-being that they derived from the dive experience (85%; χ^2=58, df=1, p < 0.001), and the acquisition of new knowledge (84%; χ^2=77, df =1, p < 0.001) confirming the relevant role of the marine environment as providers of important CES. Significant preferences have been found also related to corals presence (66%; χ^2=11, df =1, p = 0.001) and to the beauty of coastal landscape (67%; χ^2=14, df =1, p < 0.001)

while no significant difference for the *P. oceanica* meadows has been found (44%; χ^2=1, df =1, p = 0.25).
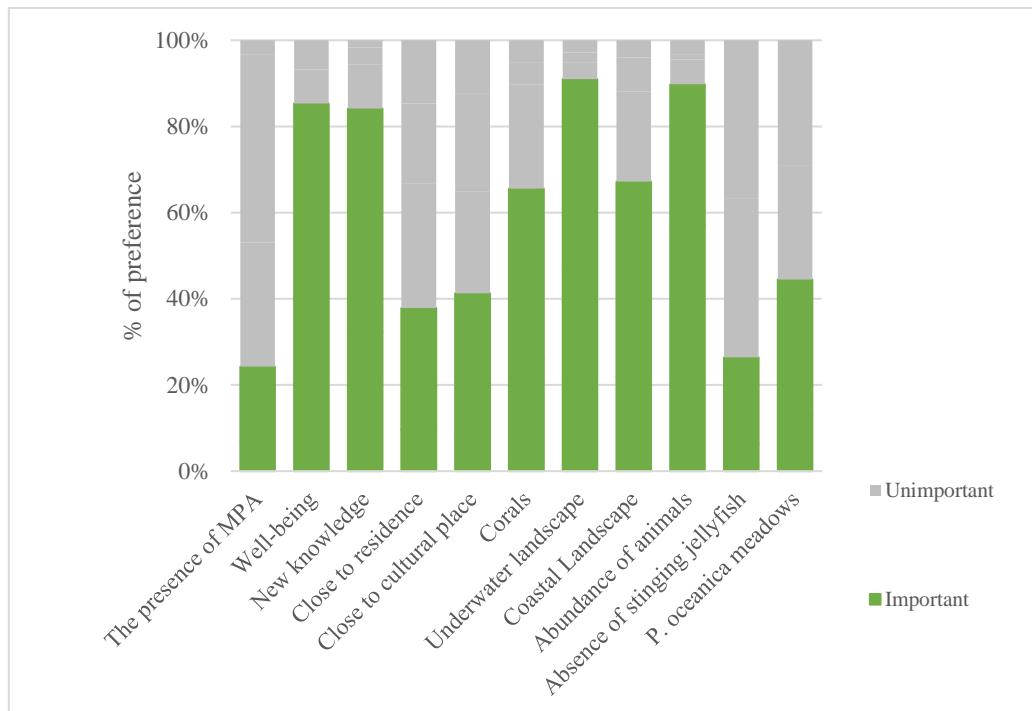

Figure 2: Divers percentage of preferences among different features determining the choice of a dive experience. The green bars represent the responses classified as Important and Very important, while the grey bars represent the responses classified as not important and very not important.

Choice experiment

The results of the choice experiment showed that the decision of taking a dive was chosen by 84% of the respondents in the choice simulation. Table 4 summarised the results of the MNL model.

All coefficients estimates are significant at 99% except for the attribute level "*Seagrass cover 50%*" that showed a 90% of significance, and the attribute level *"15 divers"* which was non-significant.

The coefficient of the variable Price is negative and significant indicating the respondents' preference for a cheaper product. The attribute levels "*Coral cover 50%*" and "*Coral cover 0%*" have significantly negative coefficients (p-value <0.05) indicating that respondents highly prefer habitats with a good coral coverage for their diving rather than the partial and the total degradation of the coral cover.

The results of the seagrass parameters show a slight preference of the divers (p=0.02) for habitat with seagrass meadows in good conditions "*Seagrass cover 100%*" and a significant rejection to choose degraded habitat "*Seagrass cover 0%*".

Table 4 MNL model results

	Conditional logit			
n	229			
Attributes	Coef	(SE)	Pr(>|z|)	
Dive	3.24	0.17	< 2e-16	***
Coral cover				
Coral 50%	-0.49	0.09	3.39E-08	***
Coral 0%	-1.58	0.13	< 2e-16	***
Seagrass cover				
Seagrass 50%	-0.28	0.12	0.02	*
Seagrass 0%	-1.16	0.12	< 2e-16	***
N of divers per trip				
15 divers	-0.48	0.11	0.00001	***
25 divers	0.11	0.13	0.36960	
Price	-0.02	0.00	< 2e-16	***
Adj R-squared	0.1216			
Likelihood ratio test	649.2			
AIC	4573.044			
BIC	4614.848			
Log likelihood	-2278.52			

Willingness to pay

The approximation of the mean willingness to pay (WTP) for the different levels of attributes suggested that the divers are willing to pay approximately 25€ less if the coral coverage decreases of 50%, and 80€ less if corals disappear entirely (Figure 3). The same occurred for

the seagrass coverage for which the respondents were willing to pay approximately 14€ and 60€ less in case of partial or total loss, respectively (Figure 3). Results also suggested that scuba divers were willing to pay less for dive trips that are highly crowded (25 divers).
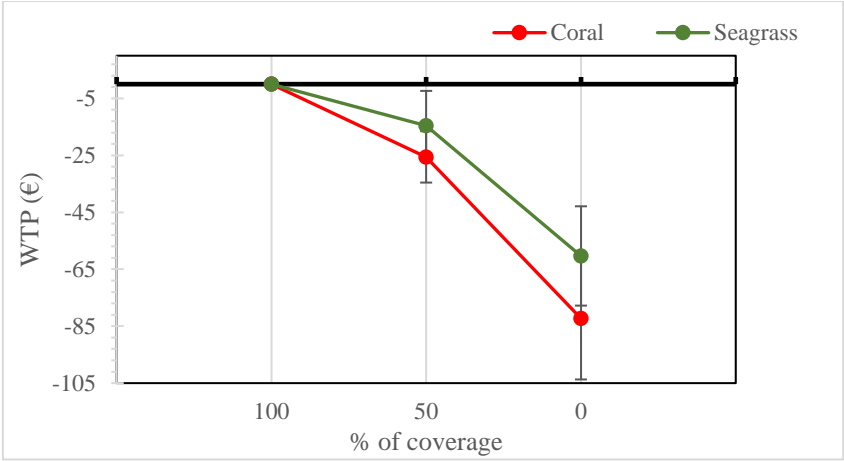
Figure 3: Estimates and 95% CI of the marginal willingness to pay (WTP) values (€) for divers on habitat degradation due to climate change

We have found that the respondents significantly prefer less crowded dives, instead of more crowded ones. These were the two extremes levels of this attribute, and they were described in the questionnaire, respectively, as "*5 divers*" and as "*25 divers*" per dives. The respondents instead were indifferent to the intermediate level, the "*15 divers*" dive, (Figure 4), in agreement with Rodrigues et al. (2015) that found that the attribute level "*15 divers*" were not significant in their CE. Indeed, scuba divers were willing to pay approximately 24.69 € less for dive trips with 25 other divers. The result was similar to the one reported by Rodrigues et al., (2015) that reported a willingness to pay of 24.87€ less if the dive trip is crowded.
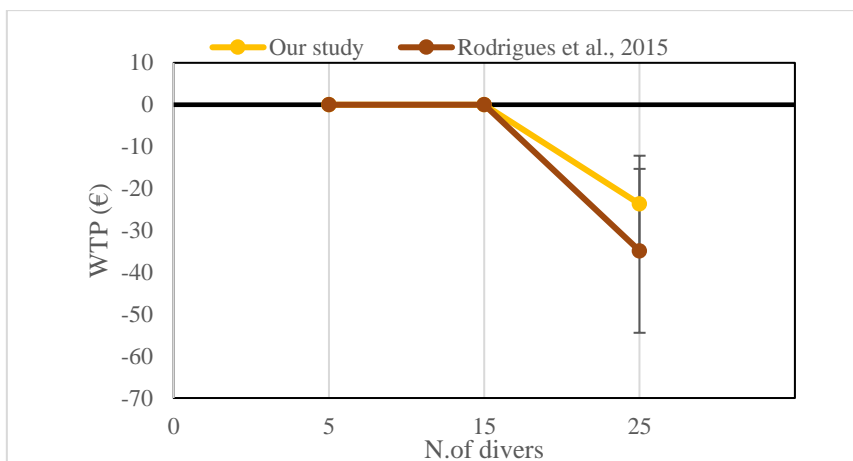
Figure 4: Estimates and 95% CI of the marginal willingness to pay (WTP) values (€) for divers in relation to the crowded level of the dive. Different colours shown the results of different studies.

Table 5 shows the marginal WTP for a dive with each attribute level compared to the reference levels (100% coverage of coral and seagrass and 5 divers per dive trip).

Willingness to pay

Attributes	MWTP (€)	2.50%	97.50%
Dive	168.407	142.915	193.9
Coral cover			
Coral 50%	-25.545	-34.567	-16.522
Coral 0%	-82.273	-103.712	-60.834
Seagrass cover			
Seagrass 50%	-14.571	-26.777	-2.365
Seagrass 0%	-60.338	-77.78	-42.896
N of divers per trip			
15 divers	-24.693	-37.216	-12.169
25 divers	5.866	-7.31	19.043
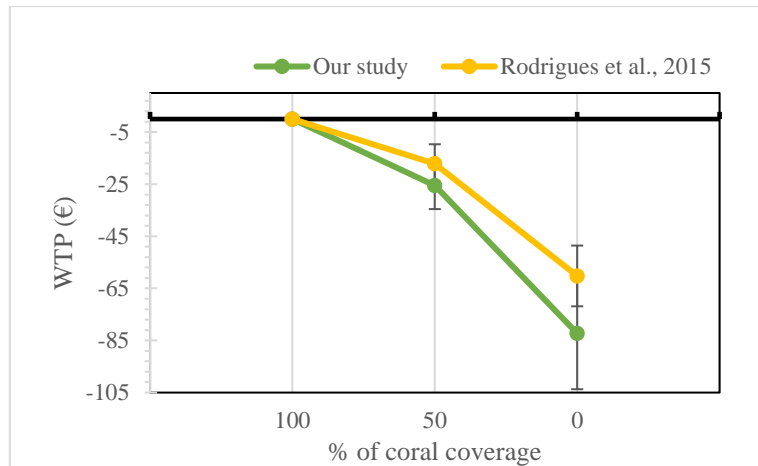
Figure 5: Comparison of our WTP results with Rodrigues et al., (2015) on coral cover data

4.5   Discussion

This paper attempted to describe the relationship between climate change and the value of cultural ecosystem services (CES) provided by coralligenous and seagrass meadows to Italian divers. Over the last two decades, the Ecosystem services (ES) framework has been adopted as a major tool to discuss social-economic-ecological interactions, in response to increasing pressure on ecosystems.

The cultural services provided by coralligenous and seagrass meadows habitats are classified as non-consumptive recreational benefits that are related to well-being, aesthetic inspiration, cultural identity, and spiritual experience. The stated preference techniques confirmed to be appropriate for this analysis being able to catch the multiple aspects of the recreational service.

The study demonstrated how valuable the Italian marine benthic ecosystems are at national levels, and how their loss could lead to economic losses. Mediterranean coastal underwater landscape attracts millions of scuba divers yearly and depends on the presence of healthy environments. The WWF 2017 report *"Reviving the economy of the Mediterranean Sea"* (Randone et al., 2017) estimated that marine tourism in the Mediterranean Sea generates US\$110 billion annually (~ €90 billion), representing, together with coastal tourism, the 92% of the annual economic output of all sectors related to the sea. Coastal and marine tourism are the major contributor to the economies of the Mediterranean area making this sea one of the most highly valued globally (Randone et al., 2017). The current threats imposed by human pressures on these habitats, exacerbated by climate changes, have the potential to degrade these

ecosystems and the flow of ecosystem services, among which the CES, provided by coralligenous and *P. oceanica* meadows.

Our results confirmed that the degradation of coralligenous and *P. oceanica* habitats related to climate changes may reduce the attractiveness of the Mediterranean Sea for scuba divers, by reducing the scuba divers' satisfaction, the consumers' surplus and would likely deteriorate the return visit rate. The results of this study suggested that the ecosystem services approach is a viable and comprehensive methodology to value biodiversity helping the promotion of efficient strategies for biodiversity conservation (Beaumont et al., 2008).

The WTP estimate obtained by the MNL model confirms the importance of structured and complex ecosystems as providers of benefits for scuba divers. With the present study, we found that the questioned Italian scuba divers have a strong predilection for coralligenous habitats, as expected (Rodrigues et al., 2015), but are sensitive to the loss of seagrass too. The decline in both coral coverage and seagrass coverage would result in significant economic losses to the recreational dive industry in the Italian peninsula, and likely across the whole Mediterranean. The conservation of high habitat quality will have a great economic impact on diving tourism and significantly influence the choice of a dive site destination. Despite the results obtained with this work, our analysis has evaluated the responses of people who voluntarily answered our questionnaire. This could mean that our sample was potentially biased towards scuba divers who were, likely, more interested and sensitive to environmental issues, hence limiting the generalisation of our results to the entire Italian scuba divers' category.

The study showed that part of the scuba divers in the Italian peninsula is aware of the importance to protect the environment and are conscious of the numerous threats that our sea is facing mainly due to anthropic activity (i.e. pollution, climate change, overfishing). Respondents stated a higher preference for diving in coralligenous environments but recognised as well the relevant ecological role of the seagrass meadows for supporting the good status of the sea. Our research showed that even if respondents are not interested in taking a dive over a seagrass meadows (Figure 2), they are particular aware of the need for protection and conservation of this habitat as they recognise the importance of *P. oceanica* meadows for regulating and provisioning services that they provide (i.e. water oxygenation, water clarity, nursery). However, scuba divers generally lack in a more in-depth knowledge about the great biodiversity associated with the seagrass habitats and indeed improving this knowledge would certainly lead to a higher valuation of these habitats in the human perception, therefore, increasing its recreational value. Seagrass awareness could be easily improved among scuba divers, since,

according to Sorice et al., (2006), divers are generally willing to receive 30 minutes presentation and description of the ecology and biology of the habitats they are going to see. This is also confirmed in our study by the high rate that the respondents gave to the importance to acquire new knowledge during a dive experience (Figure 2).

Warming and acidification are potentially associated with a higher abundance of stinging jellyfish. Our results (Figure 2) showed that 74% of the respondents are not concerned with the presence of stinging jellyfish contrary to the results of Rodrigues et al., (2015) that have found a reduction in scuba divers willingness to pay of 26€.

In our choice experiment, we have not taken into account the fish abundance because the literature has already assessed the primary role of this attribute for scuba divers, and our analysis confirmed that the fish abundance is the most important feature that determines the choice of a dive location (Figure 2). Fish abundance and biodiversity are generally higher in a complexly structured habitat like coralligenous and seagrass meadows due to the numerous functions that these habitats provide to marine organisms (i.e. nursery, a refugee from predators, provision of food). Given the correlation between fish abundance and complex habitats, our results may indicate further negative effects of climate changes on the attractiveness of Mediterranean Sea for scuba divers.

The potential loss of economic revenue may in turn have consequences at the local economy level and not only on the scuba divers' tourism revenues.

The Mediterranean marine habitats, such as coralligenous reefs and seagrass meadows have undergone a significant decline due to human impacts. Global and local projections indicate that under the business as usual scenario conditions, significant negative impacts are to be expected in the future to *P. oceanica* and coralligenous structuring habitats, and in the services that they support.

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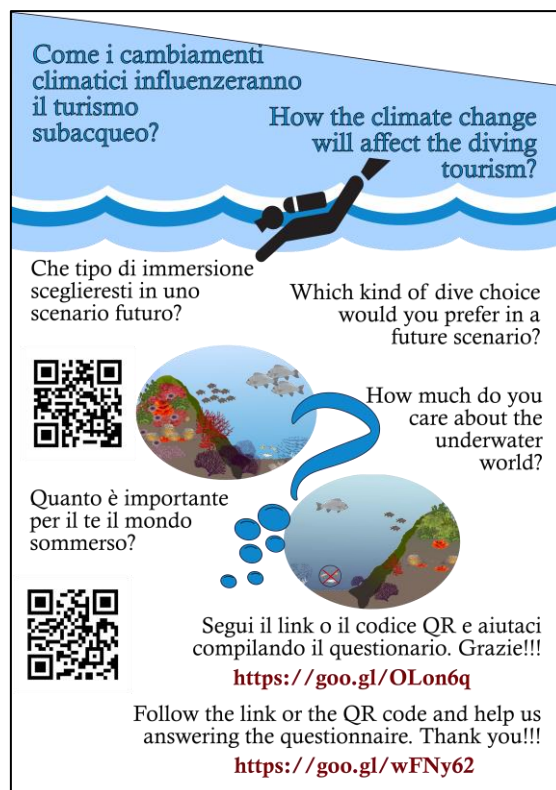
4.7   Supplementary

Figure S 1: Flyer of the questionnaire sent to the diving centres and club.

Conclusions

This work aimed at evaluating the possible impacts of the ocean acidification (OA) in the Mediterranean Sea and their socio-economic consequences at the Italian scale. In particular, the thesis focused on the potential effects of OA on two important and vulnerable habitats of the Mediterranean Sea, coralligenous reefs and *Posidonia oceanica* meadows. The research approach adopted in this thesis was the ecosystem services cascade framework in order to analyse the effects of OA in the Mediterranean Sea from organisms' responses to the ecosystems functioning levels.

OA is driven by the increased inputs of human-produced carbon dioxide (CO_2) into the sea, which cause a decline in seawater pH. At the present state of CO_2 emission, a 150% increase in the concentration of surface ocean H^+ is predicted by 2100. The potential effects of the OA phenomenon are expected to cause significant changes in the marine environment over the coming century. Thus, the deterioration of the marine natural capital, over time, will lead to a severe decline of the ecosystems services leading to broad consequences that cover the ecological, economic, and social spheres.

The work evaluated the responses of Mediterranean benthic organisms to OA in order to improve the quantitative estimates of the potential effects of seawater acidification in the near future. For this purpose, a meta-analysis of the OA Mediterranean studies was performed. Meta-analyses are statistical tools to evaluate the current state of knowledge through a set of formal methodologies designed to draw rigorous inferences from multiple studies.

The meta-analysis results provided evidence of different -both positive and negative- responses to ocean acidification in different groups of organisms highlighting the existence of direct effects. The quantitative results highlighted an increase in fleshy algae cover, a reduction of calcification by both algae and corals and a general increase in the photosynthetic activity of macrophytes. These results, integrated with those obtained from other studies, were used to develop two conceptual models of the coralligenous and *P. oceanica* ecosystems functioning and the respective alteration due to OA impacts. The models aimed at identifying ecosystem functions, services (ES) and benefits at current and future conditions.

The hypothesis represented by the models suggested that the OA would change many functions of the coralligenous and *P. oceanica* ecosystems through both the direct effects of OA and the instauration of indirect effects triggering habitats modification. The result was the loss of

coralligenous and *P. oceanica* habitats complexity leading to the shift of high-value ecosystem services to less valuable services.

The next step was to investigate in detail the ecosystem services provided by the two habitats and their variation due to OA impacts according to the results presented by the conceptual models. The work focused specifically on the provisioning and cultural services provided by the coralligenous formations and *P. oceanica* meadows.

Among the relevant services in the context of OA, fisheries provisioning and scuba-tourism have been identified, using the landing indicator to assess the provisioning service and a stated preference technique to assess the tourism's cultural service. These assessments were applied to the Italian seas and they have highlighted the potential degradation cost caused by seawater acidification.

An index has been developed to assess the food provisioning services of coralligenous and *P. oceanica* habitats. The index through a market analysis technique was used to assess the current status and its future value, under OA conditions. Using a preference-based approach, the current economic value of coralligenous and seagrass habitats in Italy –and its future changes under OA scenarios- has been estimated. According to our analysis, *P. oceanica* and coralligenous ecosystems appeared to provide the 24% of the total biomass of the commercial coastal species, and the 30% of the economic benefits in the Italian market. The hypothetical loss of the 2 habitats induced a loss of demersal resource of 15% of the current biomass with a maximum economic loss around 15 million of euros (-20%) per year.

Moreover, a more detailed site-specific analysis was developed for Portofino MPA applying an ecological simulation model built on Ecopath with Ecosim. Such ecosystem modelling approach has been very relevant, given direct impacts on one element of the food web may trigger cascading effects on the entire system. Furthermore, the very fact of considering multiple species has introduced in the system non-linear dynamics, which might give rise to a number of complex dynamics.

The ecosystem model was used to represent OA effects in a food web. This study has used a combination of scenarios to predict the potential effects of habitat loss on biomass and catches of target functional groups of the food web. The results confirmed that the values of provisioning services were correlated to *P. oceanica* and coralligenous area, showing in the worst-case scenarios (100% habitats loss and analysis of the effects at both trophic and non-

trophic levels) a loss in biomass (33%) and economic revenues (28%) of important economic species.

The value of a cultural service was derived by applying a non-market analysis technique. A choice experiment among Italian scuba divers was undertaken to value the impacts of OA on the recreational diving activities related to coralligenous and *P. oceanica*. The stated preference valuation performed through an online questionnaire was used to assess the cultural services of these habitats and the change in the divers' willingness to pay due to the habitats degradation related to the possible OA impacts. The results confirmed that the degradation of coralligenous and *P. oceanica* habitats related to OA may reduce the attractiveness of the Mediterranean Sea for scuba divers, by reducing the scuba divers' satisfaction, the consumers' surplus and would likely deteriorate the return visit rate.

This work has integrated novel and existing data and information in order to evaluate the ecosystems services provided by coralligenous and *P. oceanica,* in the Mediterranean Sea, in the present state and under future OA scenarios. The work confirmed the hypothesis that the alteration of habitats complexity may trigger key alterations to benthic systems, with potentially large effects on the ecosystems functions and consequently on the entire ecosystem services cascade. Nevertheless, the assessment of the ecological and socio-economic effects of OA on these two habitats has been proved to be very challenging.

Despite the growing amount of studies focusing on the OA, there is still high uncertainty regarding the organisms' response to OA. For this reason the understanding of OA and future coralligenous and seagrass' ecology might benefit from further experiments that focus on combined stressors (i.e. warming, overfishing, pollution), longer experiments duration, and differences that occur over varying spatial and temporal scales. Indeed, each of these factors may lead to non-additive, antagonistic, or synergistic effects that might have compensated or enhanced the effects of acidification on the organisms and ecosystems responses.

In this context, the studies should ideally be supported by mesocosm and field studies at appropriate natural laboratories (e.g. the vents sites) in which the physico-chemical parameters on an annual scale are carefully monitored and in which the confounding variables are identified. The vents sites represent ideally solution to analyse the response of OA but they are open systems, which ecology might be affected by surrounding area allowing, for example, recruitment and migration of organisms from non-acidified habitats.

In addition, further steps towards the scale-up of quantitative studies from individuals and populations to the community and ecosystem levels within a larger temporal frame that allows for the analysis of adaptive responses are recommended.

The results of this work so far suggested that OA may have significant negative impacts on *P. oceanica* and coralligenous habitats deteriorating the provisioning of ecosystem services and the human benefits associated with them.

Although the assumptions used in the construction of the conceptual models of OA responses may be criticised as too simplistic to accurately predict the responses of complex systems, these qualitative models provided conceptual frameworks wherein future scenarios can be explored representing also the necessary foundations for future research.

Finally, the assessment of the ecosystem services flows highlighted the importance of natural systems for the human well-being, and the degree of interdependence between the two systems. One of the strengths of this approach was to provide conceptual and empirical elements enabling communications among different disciplines toward the achievement of a sustainable use of marine resources and services.