Original Research Article

Direct and indirect impacts of marine acidification on the ecosystem services provided by coralligenous reefs and seagrass systems

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ARTICLE INFO

ABSTRACT

Increasing emissions of CO_2 and the resultant ocean acidification (OA) will have large implications for the marine ecosystems sustained by habitat-forming species and their related ecosystem services (ES), with potentially significant impacts on human well-being. Here, we provide an assessment of the direct and indirect impacts of OA on ES. The changes in the functioning of coralligenous reefs and *Posidonia oceanica* meadows promoted by OA were investigated by i) synthesizing current knowledge into conceptual models. The models were then used to, ii) assessing the impacts of exposure of the selected taxa at the acidification level associated with two CO_2 emission scenarios and iii) using the conceptual model outputs to project the cascading impacts from individuals to functions to ES.

The results highlight that the combination of the direct and indirect effects of acidification will alter many functions of both coralligenous and *P.oceanica* systems, triggering habitat modifications and the loss of highly valuable ES.

While the exact timing of the expected changes will depend on the severity of the emission scenarios, significant and hardly reversible changes can be expected as quickly as a few decades under the business-as-usual scenario, and many ecosystem services are at risk even under much more conservative scenarios.

1. Introduction

Nature provides a number of contributions to people and human well-being, ranging from more easily recognizable goods (such as food, timber, and raw materials) to possibly less evident but still very valuable services, such as pollination, recycling or cultural and recreational services. During recent decades, there has been a growing interest in the identification, assessment and valuation of these services, with the aim of stressing their importance to humanity and their vulnerability to anthropogenic pressures. In fact, while it is clear that human life relies on healthy natural environments and proper

ecosystem functioning, anthropogenic impacts on ecosystems and the exploitation of natural resources often occur at rates exceeding the carrying capacity of systems. Thus, increasing awareness of the vulnerability of ecosystem services to human activities might be an important step towards a sustainable future. As a result, several schemes have been produced to classify ecosystem services and logically connect pressures and impacts on ecological states and their related ecosystem services.

Global changes are major perturbation sources for ecosystem functioning, influencing ecosystem services both in terrestrial and marine ecosystems. However, along with warming, oceans are also experiencing the impacts of water acidification due to the increased dissolution of CO_2 in the seas, which alters the carbonate chemistry and lowers the pH of the seawater. This process, known as ocean acidification (OA), could have large consequences on many marine species and significantly alter the functioning of whole ecosystems, with potentially large economic and societal consequences. To date, studies and reviews have mainly focused on the physiological responses of marine species to OA (see, for example, Dupont et al., 2010; Hendriks et al., 2010; Kroeker et al., 2010; Zunino et al., 2017). Conversely, despite the growing request for holistic approaches in environmental policy and management, there is still a lack of synthesis and knowledge integration on the effects at the ecosystem scale, possibly because of the complexity and variety of the direct and indirect impacts to be considered for this purpose. Recent investigations have demonstrated that seawater acidification can potentially affect foundation species (Gaylord et al., 2015) and biogenic habitats (Sunday et al., 2016) as well as induce a homogenization of communities and a reduction of functional diversity at a landscape scale (Kroeker et al., 2013a). Changes in habitat complexity in marine environments represent key alterations for benthic systems with potentially large effects on ecosystem functions and, consequently, on a cascade of ecosystem services.

Here, we focused on the direct and indirect effects of OA on the ecosystem services (ES) provided by *Posidonia oceanica* meadows and coralligenous reefs, which are two endemic ecosystems of the Mediterranean Sea known to be vulnerable to OA (Jordà et al., 2012; Martin et al., 2014) that are commonly regarded as important sources of biodiversity and ecosystem services.

Impacts of OA on ecosystem services were investigated by reviewing and synthesizing current knowledge into conceptual models, which were then used i) to elucidate the impacts of exposure of selected taxa at the acidification level associated with two CO_2 emission scenarios and ii) to project the cascading impacts from individuals to functions to ES.

The manuscript is composed of three sections: the first section aims at developing conceptual models for coralligenous and *P. oceanica* ecosystems and their services based on the best available knowledge; the second section aims at analysing the responses of coralligenous and *P. oceanica* ecosystems to the direct and indirect impacts of OA; and the third section focuses on changes in their capability to provide ecosystem services under two different CO_2 emission scenarios. In particular we referred the so-called Representative Concentration Pathways (RCP) proposed by the International Panel of Climate Change, Assessment Report Five (IPCC, AR5) (IPCC et al., 2014), and considered ecosystem response to the low emission scenario (RCP 2.6) and to the business-as-usual scenario (RCP 8.5).

2. Methods

Conceptual models for *Posidonia oceanica* and coralligenous reefs have been drawn by collecting the available scientific literature, with particular reference to Mediterranean sites. This analysis considered all the manuscripts emerging from a systematic search conducted in the SCOPUS database by using the key worlds "*Posidonia oceanica*", "*corralligenous*", and "*acidification*". The information was integrated by additional sources suggested by experts during two workshops on the effects of ocean acidification on seagrass and coralligenous ecosystems organized within the Italian project Acid.it. The resulting information was organized, integrated and visually depicted in two conceptual schemes for each ecosystem: 1) a scheme summarizing the interdependencies and functional relationships among ecosystem components; and 2) a cartoon describing the major effects of OA as a comparison between pristine and acidified systems. In particular, the conceptual models identified i) the major systems components (SCs) and their interactions, synergies and feedbacks; ii) the functions that the SCs created; and iii) the effects of OA on each of the abovementioned SCs and functions.

The assessment of how and to what extent OA cascades on the capability of the two systems to provide ES was performed again based on a review of the existing literature. In this case, we collated and analysed the results of the exposure of organisms and ecosystems at the acidification level associated with two RCP scenarios (IPCC et al., 2014) and used the output of the conceptual model to project the cascading impacts from the individuals to the functions of the services.

We chose the business-as-usual scenario (BAU), RCP8.5, and the mitigated emission scenario, RCP2.6. These scenarios projected, respectively, an increase in atmospheric CO_2 concentration of about 930 ppm and 420 ppm in 2100 (Meinshausen et al., 2011), which corresponds to a decrease of, respectivley, approximately 0.4 and 0.1 pH units at the end of the century (IPCC et al., 2014). If information on the impacts of OA on the analysed function or service was available only for the BAU scenario, the expected effect at RCP2.6 was derived by a linear interpolation between the BAU scenario and present day (Meinshausen et al., 2011) conditions. In any case, studies performed at pH changes larger than 0.5 were not considered. For this analysis, ES were classified following the Millennium Ecosystem Assessment (MEA) framework (MEA, 2005), and for each ecosystem, we selected at least one service for each MEA category, namely, the supporting, provisioning, regulating and cultural services. The assessment of the OA impacts on ES, therefore, integrates quantitative information on the effects of OA on organisms, the role of the organisms in ecosystem functioning and the relationship between functions and service. The results were categorized based on the strength of the impact in semi-quantitative impact classes, as shown in Table 1.

Table 1

The effects of OA on key organisms in *P. oceanica* and coralligenous ecosystems are represented as either a mean percentage increase (+) or a percentage decrease (−) in a given response (abundance and calcification) under the two IPCC scenarios, RCP2.6 (mitigated emission scenario) and RCP8.5 (business-as-usual scenario). The * symbol indicates that the value was obtained by linear interpolation. To produce a qualitative assessment of OA impacts on ES, the quantitative data in the table were categorized based on the strength of the impact according to the legend below.

		RCP2.6	RCP8.5	References
Calcifying algae	Abundance	−20*	−79	Zunino et al. (2017)
	Calcification	−15*	−58	Zunino et al. (2017)
Corals	Calcification	−6*	−22	Zunino et al. (2017)
	Abundance	−12*	−47	Kroeker et al., 2013b
Seagrass	Abundance	−25*	−99	Chefaoui et al. (2018)
Fleshy macroalgae	Abundance	110*	143	Zunino et al. (2017)
Echinoderm	Abundance	−20*	−79	Zunino et al. (2017)

Legend			
0	±1/±34%	±35/±67%	±68/±100%
Undetectable	Moderate	High	Very high

3. Results and discussion

3.1. Identification of the services provided by seagrass meadows

Seagrass meadows play important ecological functions as habitat and ecosystem formers, providing important ecosystem services (*i.e.,* supporting, provisioning, cultural and regulating services) and sustaining the well-being of societies by providing many benefits. Highly structured seagrasses such as *Posidonia oceanica* host a broad range of motile fish and invertebrate fauna and provide valuable habitats compared to other seagrasses. Indeed, ecosystems hosting high habitat complexity guarantee species survival, offering protection from predators to juveniles and adults and facilitating the aggregation of individuals, thus improving their reproductive success. Seagrass beds play a fundamental role in maintaining populations of commercially exploited species (both fish and invertebrates; Jackson et al., 2015) by providing permanent habitats and allowing completion of their life cycles. Moreover, they serve as a temporary nursery area for the development of juvenile stages (Fig. 1A - number 3), a feeding area for various life stages and a refuge from predation, indirectly supporting coastal food webs (Fig. 1A - number 6), and water oxygenation (Fig. 1A − number 7).

For example, P. oceanica meadows host more than 400 species of algae and thousands of animals during in-life phases. Heck (2003) performed a review of the extensive literature to test the importance of seagrass meadows as nursery areas for juvenile fish and invertebrates. They found that the abundance, growth and survival of juveniles were generally higher in stable seagrass meadows compared to unstructured habitats (Fig. 1A − number 3)

Seagrass meadows, *P. oceanica* in particular, are highly productive ecosystems with a net primary production equivalent to 14.8 tons CO_2 ha yr^{-1} (Duarte et al., 2013) that accumulates almost 30% of the fixed organic matter below-ground. The below-ground layer, called matte, is composed of rhizomes, roots and sheaths reaching up to 6 m in height. The matte constitutes a long-term carbon sink that contributes to mitigating CO_2 emissions, thus providing an important regulating service (Fig. 1A − number 9).

Moreover, the matte of *P. oceanica* stabilizes sediment, while the leaves enhance the deposition of sedimentary particles and attenuate swells and waves (Fig. 1A − number 9, 8). The consequences are clear water and the protection of the coast from erosion (Fig. 2). The coastal protection service is even reinforced by the massive shedding of leaves in autumn, which produces "banquettes", solid structures that prevent beach erosion.

Moreover, *P. oceanica* meadows produce a considerable quantity of oxygen (*i.e.,* P. oceanica at a 10 m depth produces more than 14 L of oxygen per day per m^2, Bay, 1978), and this function is relevant to enhancing the quality of the water column and the maintenance of ecosystem properties (Fig. 1A − number 7).

Another important service that seagrasses provide to humans is the bioremediation of wastes by the trapping and storing of nutrients, thus filtering land inputs to coastal waters. Recently, Lamb et al. (2017) discovered that the presence of seagrass meadows reduced the relative abundance of potential bacterial pathogens to humans and marine organisms by 50%.

3.2. Conceptual models of the seagrass response to OA

The effect of OA on seagrass meadows presented in the analysed literature has been summarized and visually captured in two models that describe i) the complex interactions between the structuring elements of these ecosystems and ii) the direct and indirect effects of OA on these ecosystems. The combination of the direct and indirect effects of the acidification defines a scenario of changes and provides indications about the nature of OA impacts.

The seagrass conceptual model is represented in Figs. 1 and 2, where the pristine and acidified states are shown in panels A and B, respectively.
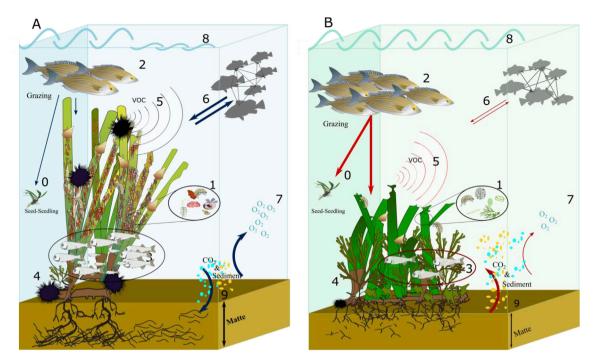
Fig. 1. Schematic representation of the *P. oceanica* ecosystem under current (A) and acidified scenario (B). The thickness of an arrow indicates the strength of a process. Red arrows in figure B indicate processes affected by OA. Numbers indicate functional groups or processes that might be altered by the OA scenario. Number (0) shows *P. oceanica* seeds and seedlings that will be advantaged under OA conditions. The number (1) represents the epibiont community that changes from calcareous organisms (A) to fleshy microalgae and epiphytic diatoms (B). Number (2) indicates the increased grazing pressure by herbivorous fish (e.g. *S. salpa*) and the consequent reduction in the height of the meadows and the above-mentioned seeds and seedlings advantages. Number (3) refers to the fact that loss of habitat complexity, that will inhibit the refuge and aggregation functions, and alter the nursery functions and compromising the provision of the habitat services (number 6). Number (4) points to the relationships between the negatively affected sea urchins and the positively affected fleshy algae. The sea urchins' reduction allow the spread of the fleshy algae among the seagrass shoots. Number (5) refers to the chemical stimuli promoted by the volatile organic compounds (VOC) produced by mechanical damage (e.g. grazing) of seagrass leaf or its epibionts (see the Appendix, Fig. S1 for details). In (B) OA leads to a reduction/alteration of VOC and of their functions as grazing activities deterrent. Under OA scenario (B) the loss in the height of the canopy will reduce the oxygenation of the water (number 7), the attenuation of waves and currents (number 8), and the consequent service of coastal protection. Number (9) represents the long-term carbon sink within the matte, and contribute to the water clarity due to sediment trapping.

The results of the acidification studies performed both in mesocosm and at natural vent sites suggest that seagrass will benefit directly from OA, increasing its photosynthetic rate. However, for *P. oceanica,* the proof is limited and not uniform, suggesting that the benefits for *P. oceanica* productivity over the next century may be minimal. Indeed, the available data on significant changes in photosynthetic rates refer to studies in which the pH change was larger than that expected for the end of the century in the BAU emission scenario. In contrast, no difference in *P. oceanica* photosynthesis (Cox et al., 2016, 2015; Hendriks et al., 2017) or in the electron transport rate or shoot density were found in the conditions expected by the end of this century (pH$_T$ 7.7). Donnarumma et al. (2014) and Garrard et al. (2014b) reported that the increase in the shoot density at the acidified sites at Ischia Island was possibly related to the increase in the light radiation intensity due to the reduction in leaf length because of herbivorous pressure. In contrast, Guilini et al. (2017) at Panarea Island and Cox et al. (2015, 2016) in mesocosm studies at Villefrance did not find any significant difference in shoot density between control and acidified sites. On the other hand, Hernán et al. (2016) found that seeds and seedlings of *P. oceanica* might benefit from acidification due to the enhanced photosynthetic activity and carbon fixation during the early life stage of the plant (seed biomass under high pCO$_2$ was almost 2-fold higher than under control conditions- Fig. 1B- number 0). These positive effects would help plant dispersal and provide the potential for adaptation under future OA scenario. Nevertheless, these seedlings were preferred by herbivorous which could potentially counteract some of the positive effects of OA increasing the already high mortality rates of the early life stages of *P. oceanica* (Hernán et al., 2016). Considering all these results, we opted to adopt the hypothesis related to the loss in habitat complexity of *P. oceanica* meadows.

The cartoons (Fig. 1) highlight that in pristine conditions seagrass leaves and roots host a large variety of epibiont organisms (see Fig. 1A - number 1), micro- and macroalgae, and both fleshy-filamentous and calcareous algae (*i.e.*, coralline algae). In turn, the epibionts support a diverse community of mesograzers (small invertebrate grazers: decapod crustaceans, gastropod molluscs, and polychaetes, including fish that are targeted by artisanal fishers). Seagrass leaves host a community of filter feeders, suspension feeders and detritus feeders and the meadows host several secondary consumers, tertiary consumers and higher-level consumers (Boudouresque et al., 2012; Giakoumi et al., 2015) (Fig. 1A - number 6). The loss of
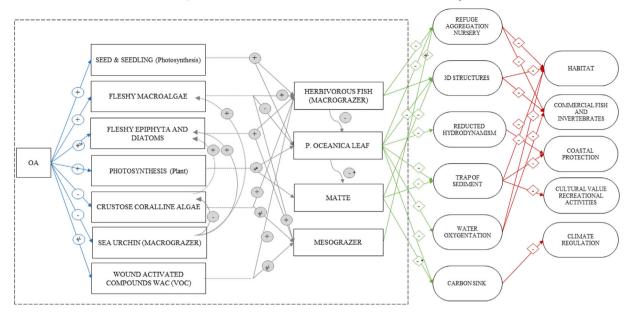
Fig. 2. Conceptual model of OA impacts on *P. oceanica* meadows. The blue arrows represent the direct effects of OA on the ecosystem components. The effects can be positive ($+$), negative ($-$), or create alterations with contrasting effects ($\pm$). The * indicate high uncertainty. The grey arrows indicate the indirect effects of OA and the labels in grey circles indicate the cumulative effects of both the direct and indirect effects. On the right, the green arrows depict the impacts on the functions and the red arrows the impact on the associated services.

such a complex habitat will also reduce the community of important species at both juvenile and adult stages because of the reduction in prey and the loss of refuges (Fig. 1B - numbers 3, 6) (Fig. 2).

Culturally, the seagrass meadows in the Mediterranean Sea are important, especially for recreational fisheries. Moreover, Jackson et al. (2015) demonstrated that the degradation of seagrass will have a disproportionate negative economic impact on fishery sectors with smaller inshore fisheries.

Scientific studies suggest that seawater acidification leads to a consistent loss of crustose coralline algal epiphytes living on seagrass leaves (Martin et al., 2008; Apostolaki et al., 2014, Fig. 1B − number 1), promoting an increase in fleshy algae and diatom communities (Fig. 1B - numbers 1, 4 and Fig. 2). The changes in epiphytic composition may increase the palatability of leaves and the related grazing pressure (Apostolaki et al., 2014, Fig. 1B − number 2) that is further enhanced by reductions in the phenolic content leaching from seagrass leaves (Fig. 1B - number 5). Phenolic compounds are volatile organic compounds (VOCs), among which there are wound-activated compounds (WAC) (Zupo et al., 2015), that act as natural deterrents of grazing activities (Fig. 2), controlling grazer preference and grazing rates in a range of consumers, including the macrograzer community composed of fishes and sea urchins (Arnold et al., 2012 - Fig. 2). Moreover, WAC compounds are dispersed in water after mechanical damage to leaves or to the epiphyte community, acting as an attractant for some invertebrates that need to maximise the search for food and as a repellent for other invertebrates for which mimicry and defence from predators represent the most important behavioural constraints (Jüttner et al., 2010; Fig. S1).

Seawater acidification yields a chemical alteration of WAC compounds and a consequent change in the behavioural responses of the associated species (Zupo et al., 2015) up to the community level due to the change in the prey-predator interactions (Fig. 2).

The cover of epiphytic diatoms of seagrasses greatly increases up to 6-fold under acidified conditions (Johnson et al., 2013, Fig. 1B - number 1), and the consequent altered production of VOCs (induced by acidification; Fig. 1B - number 5) could lead to deep change in the communities associated with seagrass meadows. The biomass of epibionts is controlled by grazing gastropods, and these populations have been found to decrease at low pH (Hall-Spencer et al., 2008; Johnson et al., 2013) (Fig. S1 [see *Littorina littorea*]) and Fig. 2). These invertebrate grazers together with sea urchins (*i.e., Paracentrotus lividus*) play a pivotal organizing role in facilitating seagrass dominance by consuming their competitively superior epiphytic (Duffy et al., 2003) and algal communities (Asnaghi et al., 2013, Fig. 1B - number 4; Fig. 2). The increasing abundance of fleshy algae and diatoms (Fig. 1B − numbers 1, 4 and Fig. 2) is likely to inhibit light availability for the plant, thus promoting the regression of seagrass (Pergent et al., 2014). Vizzini et al. (2017) found that fewer trophic groups contribute to the community structure of seagrass ecosystem (composed by *Cymodocea nodosa* and *Zoostera noltii*) at the CO_2-enriched site constituting a food web shorter and trophically simpler. The OA scenario according to the results of Vizzini et al. (2017) might be dominated by herbivores/detritivores and herbivores (98%), while filter-feeders would account for only 1.1% and omnivores/detritivores and carnivores would be almost absent (0.4% and 0.1% respectively).

The above-mentioned reduction and alteration of the epiphytic community (mostly composed of calcareous algae that are threatened by acidified conditions (Martin et al., 2008) and the reduction in phenolic contents will increase the palatability of plant and seedling leaves for herbivorous fishes (Fig. 2; Arnold et al., 2012; Hernán et al., 2016). *P. oceanica* has a shoot lifespan estimated to be up to 50 years (Gobert et al., 2007) and a slow growth strategy; thus, it is unable 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 can reach 57% of the leaf production (19% and 33% by urchins and *Sarpa 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 and Beaumont, 2014) in acidified conditions, which 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 leaf production (Prado et al., 2008). In addition, a higher abundance of *S. salpa*, more than double, was estimated under acidified in situ conditions (Mirasole, 2017). To counterbalance grazing pressures, an increase in the translocation of photosynthesis products into below-ground compartments has been hypothesized, which leads to an increase in the growth of roots and rhizomes (Hall-Spencer et al., 2008; Russell et al., 2013), at least until the leaves can sustain physical damage and sedimentation rates. A loss of *P. oceanica* meadow biomass could thus reduce the production of oxygen, coastal protection from erosion, the stabilization of the sediment and water clarity (Fig. 1B - numbers 7, 8, 9; Fig. 2). The loss of meadow complexity could result in the loss of seagrass carbon sequestration capacity in the short term, even if the long-term sink capacity, which represents carbon sequestration from a few decades to several millennia (Serrano et al., 2012), will be maintained if the below-ground matte is not destroyed.

Our assumption about the loss of habitat complexity is reinforced by the increased presence of alien species, particularly herbivorous fish (e.g., Siganidae) that may compete with Mediterranean species (e.g., *S. salpa* and *Sparisoma cretense*) and increase the herbivory pressure. The invasion of alien species (e.g., *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).

In a meta-analysis performed 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 algal communities that are generally advantaged by water acidification (Asnaghi et al., 2013) and higher CO_2 availability (Fig. 2). Based on a literature review (Apostolaki et al., 2014; Caronni et al., 2015; Garrard and Beaumont, 2014), the conceptual model shows that urchin 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) (Fig. 2). However, as shown in the conceptual model in Fig. 2, the negative impacts of the OA might be mainly linked to the indirect effects of the OA rather than on direct effects.

The acidification impacts and the consequent changes in habitat complexity could lead to the shift from high-value ecosystem services provided by complex seagrass meadows (i.e., *P. oceanica*) (Mccloskey and Unsworth, 2015) to less valuable services (see Fig. 5).

Ocean acidification is coupled with other anthropogenic stressors, notably ocean warming (Marbà and Duarte, 2010). Warming has been predicted to result in the complete extinction of *P. oceanica* meadows by the year 2049 (Jordà et al., 2012) or, according to Chefaoui et al. (2018) a reduction of 70% by 2050 due to the strong regulating effect of temperature on this
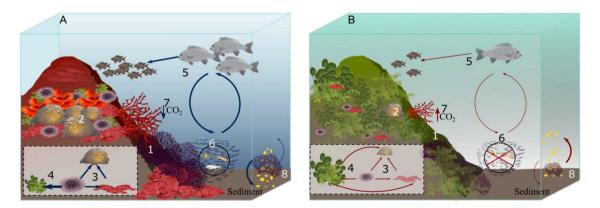

Fig. 3. Schematic representation of the coralligenous ecosystem under current (A) and acidified scenario (B). The thickness of an arrow indicates the strength of a process. Red arrows in figure B indicate processes affected by OA. Numbers indicate functional groups or processes that might be altered by the OA scenario. The number (1) represents azooxanthellate corals (gorgonians and the precious *Corallium rubrum*) and number (2) zooxanthellate corals (e.g., *Cladocora caespitosa*). These components of the ecosystem are important as organisms aggregating points (number 5) and nurseries (number 6). Coralligenous algae and sea urchins play important roles, allowing the creation of recruitment spaces (for example for corals, number 3) and keeping the growth of fleshy algae under control (number 4). Under acidified condition (B) the reductions in abundance of corals (number 1,2), coralligenous algae (number 3) and sea urchins (number 4) lead to fleshy algae dominance, which have direct and indirect benefits from OA. Ephemeral fleshy algae do not provide high levels of habitat complexity. The consequences could be the loss of the aggregation points (number 5) and of the nursery function (number 6). Number (7) points to changes in carbon sequestration related to the building of calcareous structures and number (8) to the reduction in the sediment trapping and stabilization due to the reduction of the habitat complexity.
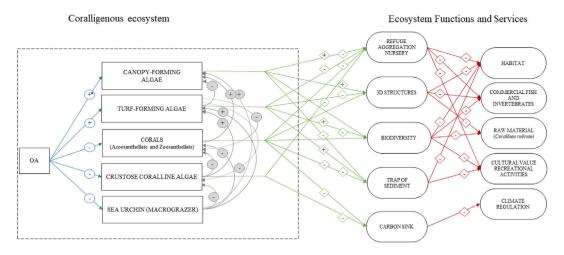
Fig. 4. Conceptual model of OA impact on coralligenous system. The blue arrows represent the direct effects of OA on the ecosystem components. The effects can be positive (+) or negative (−). The grey arrows indicate the indirect effects of OA and the labels in the grey circles indicate the cumulative effects of both the direct and indirect effects. On the right, the green arrows depict the impacts on the functions and the red arrow the impact on the associated services.
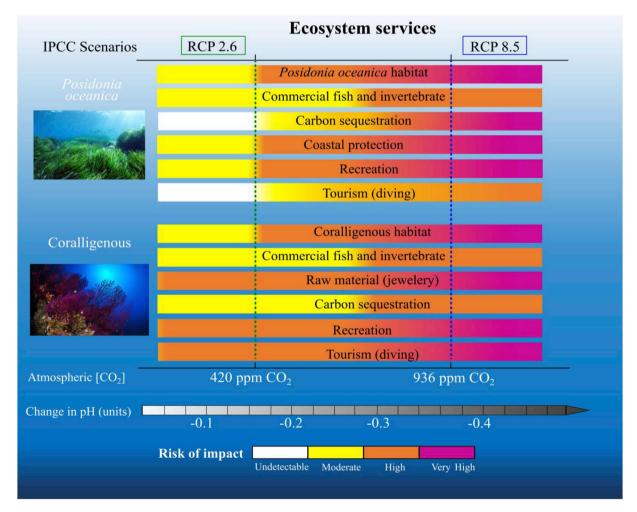

Fig. 5. *P. oceanica* and coralligenous ecosystem services risk impacts due to the increase in pCO2 (x-axis) according to the RCP2.6 and RCP8.5 (IPCC et al., 2014) pCO$_2$ scenarios. The services expected to be highly impacted/lost by the degradation of the ecosystem are shown in orange and purple, respectively. In yellow, we show the services expected to be reduced moderately, whereas the undetectable changes are left in white (see the appendix for details). Due to the lack of quantitative valuation, the uncertainties linked to the categorization must be considered high.

species (Zupo et al., 1997). Therefore, the hypothesis that increased CO_2 availability would enhance seagrass production and help alleviate thermal stress is not fully supported (Cox et al., 2016). In addition, as many authors have highlighted, the continuous 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; Marbà et al., 2014).

3.3. Identification of the services provided by coralligenous reefs

Coralligenous reefs are considered one of the most diverse and representative marine benthic ecosystems in the Mediterranean Sea. Due to their importance, they have been classified as special areas of conservation by the European Habitat Directive, (92/43/EEC), the Bern Convention, and the Barcelona Convention Action Plan with the Protocol for Special Protected Areas (SPA/BD). In 2008, the "Action plan for the conservation of coralligenous and other calcareous concretions in the Mediterranean Sea" (Unep-Map-Rac/Spa, 2008) was developed. Scientists have identified several types of coralligenous morphology (Falace et al., 2015), ranking among the most important hotspots of biodiversity in the Mediterranean. In this study, we use a general definition of coralligenous reefs described as mesophotic biogenic structures produced by the growth and accumulation of calcareous encrusting algae (Ballesteros, 2006). Crustose calcareous algae have an important role in structuring ecosystems both as builders and as inducers of larval settlement of hard corals (Tebben et al., 2015, Fig. 3A - number 3). Corals, both azooxanthellate and zooxanthellate (Fig. 3A - number 1, 2), as living structures protruding from the seafloor, increase the morphological complexity of the environment, providing structural resources for other species ("habitat engineer" *sensu* Jones et al., 1994). Corals' shapes allow the intercept of settling propagules, and their relations with the substrata provide favourable habitats for both larval and adult settlement, increasing food sources and contributing to the species richness (Paoli et al., 2016).

Coralligenous concretions support biodiversity by providing habitats, feeding grounds, recruitment, refuges and nursery sites for many invertebrates (Spotorno-Oliveira et al., 2015) and fishes both at the juvenile and adult stages (Fig. 3A — number 5, 6). According to some recent estimates, coralligenous concretions are known to host over 1600 species (Ballesteros, 2006), including many commercially important species, among which is the precious red coral, *Corallium rubrum* (Ballesteros, 2006) (Fig. 3A —number 1).

The ecosystem created by a coralligenous community is known as a place where fish aggregate for feeding, which is the case of many large predators, such as *Dentex dentex, Seriola dumerili* and *Sphyraena viridensis* (Vacchi et al., 1999). In addition, coralligenous concretions are well known by fishers because they facilitate the aggregation of fish, especially during the spawning of such species as *Epinephelus marginatus* and *Spondyliosoma cantharus* (Sahyoun et al., 2013).

Corals and coralline algae, due to their calcareous skeletons, are among the major contributors to CO_2 fluxes, acting as a carbon dioxide sink in geological times and as carbon sources on a human timescale (Martin et al., 2014) (Fig. 3A —number 7). They take carbon from seawater where it is available as dissolved ions and fix it into their skeletal structures. When these skeletal structures disaggregate, they become important sources of inorganic carbon (Paoli et al., 2016). Coralligenous concretions create spectacular seascapes built by gorgonians that are among the preferred diving sites in the Mediterranean Sea (Paoli et al., 2016).

3.4. Conceptual models of coralligenous responses to OA

As in the case of seagrass (previous sections), the impact of OA on coralligenous reefs has been summarized in two conceptual models that describe i) the complex interactions between the structuring elements of these ecosystems and ii) the direct and indirect effects of OA on these ecosystems.

The conceptual model that we propose is a synthesis of different typologies of coralligenous reefs and considers the concretion made by coralline algae and coral aggregations (Fig. 3A).

In coralligenous environments, 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 for their survival (Fig. 3A - number 3, 4).

Macroalgae compete with corals for fundamental resources and have a range of detrimental effects on them. With respect to present-day conditions, future acidification will favour fleshy/filamentous algae (Fig. 3B — number 3, 4) (Zunino et al., 2017) and have direct and indirect negative impacts on coralline algae, corals and sea urchins (Figs. 3B and 4). Coralline algae have an important role to ensure a recruitment area for coral larvae (Fig. 3A; Fig. 4). Sea urchins, which have a projected decrease in abundance of 79% (Zunino et al., 2017) due to OA (Fig. 4), are key organisms that play an important role in controlling the equilibrium among different algal communities (Fig. 3A - number 4). The loss of sea urchins and calcareous algae (Fig. 3B - number 3) combined with the advantages that fleshy algae may have (Fig. 3B —number 4) due to acidification may trigger a phase shift towards fleshy algae-dominated environments (Asnaghi et al., 2013) (Figs. 3B and 4). Filamentous algae, especially those belonging to the eco-physiological group of turf algae (i.e., algae that provide little to no three-dimensional seascape structure compared with kelp/canopy-forming macroalgae) can lead to lower coral fecundity, inhibit coral recruitment and the formation of high habitat complexity (Linares et al., 2012; Strain et al., 2014) (Fig. 3B - number 4). Under OA scenario turf appears to gain a competitive edge over more complex and structuring macroalgae due to the fast-growing and high adaptability under acidified conditions (Connell et al., 2018).

Moreover, the negative effects of OA on coral calcification and indirectly on coral recruitment (by a reduction of the available substrate for recruitment) may lead to a reduction in habitat complexity (Fig. 4). Indeed, the estimated reduction in the calcification rate of calcareous organisms (Zunino et al., 2017) could become substantial if extrapolated through the lifespan of long-lived species such as corals. Recent field studies in Mediterranean Sea vents have demonstrated that low pH strongly inhibits the presence of calcareous corals (Cigliano et al., 2010; Dias et al., 2010; Hall-Spencer et al., 2008; Rodolfo-Metalpa et al., 2010). These studies indicate that seawater acidification at the levels predicted for the 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 OA and climate change-related disturbances (i.e., warming, severe storms, and coral bleaching) would affect the growth and survival of tropical scleractinian corals, likely shifting the corals' habitat towards structurally simplified coral communities (Fabricius et al., 2014). Similarly, a reduction in complexity associated with temperate coral reefs may cause a shift in the associated community of consumers and thus the modification of the ecosystem services that coralligenous assemblages provide (Fig. 5).

3.5. Impact of OA on ecosystem services

According to the literature, *P. oceanica* is expected to completely disappear under the business-as-usual scenario (RCP8.5) (pH: 0. 4 units) (Chefaoui et al., 2018; Gattuso et al., 2015) expected for the end of the century (Table 1). Therefore, according to Gattuso et al. (2015), we categorized the impact on seagrass meadows as moderate (yellow) under a mitigated scenario (RCP 2.6) and very high (purple) under a BAU emission scenario (RCP 8.5) (Table 1).

The *P. oceanica* provision service of commercial fish and invertebrates is expected to be moderately impacted under the RCP2.6 scenario and highly impacted under the RCP8.5 scenario, mainly because few species are linked to this habitat for their full life cycles (Jackson et al., 2015) (Fig. 5).

Nevertheless, we were not able to quantify how the other functions of the ecosystem, for example, water oxygenation, maintenance of the food web and the refuge and aggregation functions, will affect this service. Therefore, the impact shown in Fig. 5 could be much worse.

A moderate impact on the carbon sequestration service is expected under the RCP2.6 scenario, having hypothesized the maintenance of the buried sediment within the mat. In case of the total disappearance of the seagrass meadows, the matte will also be threatened, thus returning the carbon that had been sequestered. Several studies have determined the extent of wave attenuation by *P. oceanica* meadows. Infantes et al. (2012) assessed that meadows attenuate low waves by 50%. Seagrass meadows significantly affect littoral geomorphology, providing biogenic sediments, controlling beach slope, and attenuating hydrodynamic energy (Tigny et al., 2007). Therefore, even a partial loss of the height or the area covered by the seagrass meadows may have a moderate impact on coastal protection, a service that is expected to be lost in the RCP8.5 scenario (Fig. 5).

As for the cultural services provided by *P. oceanica* meadows, even though seagrasses are not a favourite site for underwater tourism, they are considered important for the maintenance of good environmental status, and therefore, their protection is important for human well-being (Zunino et al., in preparation; Campagne et al., 2015) (Fig. 5).

Following the conceptual models, under the RCP8.5 scenario, we expect a very high impact on coralligenous ecosystems, with coralline algae and coral abundance reduced by about 80% (Zunino et al., 2017) and 50% (Kroeker et al., 2013b), respectively. The interpolated values at the condition expected for the mitigated scenario (RCP2.6) are −20% for the algae and −12% for the corals. Additionally, the calcification is reduced by 58% for the coralline algae and by 22% for the corals. The interpolated values in the mitigated scenario (RCP2.6) are −15% for the coralline algae and −6% for the corals (Table 1). In contrast, the increasing abundance of fleshy macroalgae, which are competitors of corals and coralline algae, will have a detrimental effect on the coralligenous habitat. Therefore, according to the precautionary principle, we should expect a very high impact in the BAU scenario (purple) and a moderate impact in the mitigated scenario (yellow) (Table 1).

An impact on food provisioning is also expected, ranging between moderate under the RCP2.6 scenario to very high under the RCP8.5 scenario, since, analogously to the seagrass meadows, a few species were found to be linked to coralligenous habitats for their full life cycles (Mangos et al., 2010) (Fig. 5). The loss of the aggregation functions of the coralligenous ecosystem may affect both artisanal and recreational fishing activities. The provisioning of raw materials, such as the valuable red coral, is expected to be jeopardized because the species is directly threatened by climate change impacts (Cerrano et al., 2013; Galli et al., 2017) (Fig. 5). The losses in both the abundance and calcification of coralligenous algae will have a direct consequence on carbon storage, and the losses are expected to alter the carbon sequestration service that might be impacted moderately (under the RCP2.6 scenario) or highly (in RCP8.5) (Fig. 5). The cultural services provided by coralligenous algae are related to well-being, aesthetic inspiration, cultural identity, and spiritual experience. The underwater seascape provided by coralligenous algae, representing one of the more fascinating habitats of the Mediterranean Sea, provides numerous services (i.e., high biodiversity, fish abundance, complex habitats to explore, and water clarity) that enhance the quality and enjoyment of underwater recreation. The degradation of coralligenous habitats related to climate change may reduce the attractiveness of the Mediterranean Sea for scuba divers (Rodrigues et al., 2015 and Zunino et al. (in preparation) (Fig. 5).

4. Conclusion

The synthesis and integration of a large but fragmented amount of information on OA effects on coralligenous reefs and *Posidonia oceanica* meadows enabled us to provide a qualitative and sometime semi-quantitative assessment of the impacts

of OA on the main ecosystems services provided by those systems, which might be useful in the valuation of their related contributions to human well-being. Despite the growing number of studies focusing on OA, there is still high uncertainty regarding the response of many organisms to OA. Furthermore the available information is often fragmented and few studies focused on the task of comparing and integrating available knowledge to derive information on potential responses at the ecosystem level.

The integration of the available knowledge into conceptual models helped us to track, integrate and visualize the cumulative direct and indirect OA effects on these valuable systems. The results highlight that OA will alter many functions of both coralligenous and *P. oceanica* systems, have a negative effect on these habitats, and deteriorate a variety of ecosystem services and their related human benefits.

The exact timing of the expected changes will depend on the severity of the emission scenarios (the higher the emission the shorter the time), but under the business-as-usual scenario significant and hardly reversible changes can be expected as quickly as a few decades, and many ecosystem services are at risk even under a much more conservative scenario.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00625.

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