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Changes of energy fluxes in marine animal forests of the Anthropocene: factors shaping the future seascape

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Abstract

Climate change is already transforming the seascapes of our oceans by changing the energy availability and the metabolic rates of the organisms. Among the ecosystem-engineering species that structure the seascape, marine animal forests (MAFs) are the most widespread. These habitats, mainly composed of suspension feeding organisms, provide structural complexity to the sea floor, analogous to terrestrial forests. Because primary and secondary productivity is responding to different impacts, in particular to the rapid ongoing environmental changes driven by climate change, the present paper presents some directions about what could happen to different MAFs depending on these fast changes. Climate change could modify the resistance or resilience of MAFs, potentially making them more sensitive to impacts from anthropic activities (i.e. fisheries and coastal management), and vice versa, direct impacts may amplify climate change constraints in MAFs. Such changes will have knock-on effects on the energy budgets of active and passive suspension feeding organisms, as well as on their phenology, larval nutritional condition and population viability. How the future seascape will be shaped by the new energy fluxes is a crucial question that has to be urgently addressed to mitigate and adapt to the diverse impacts on natural systems.

Introduction

Marine animal forests (MAFs) (*sensu* Rossi *et al.,* 2017a) acquire energy via autotrophy (symbiotic algae), heterotrophy, or some combination of both (mixotrophy, Caron, 2016). In shallow waters, especially in the nutrient-poor tropical seas, a larger proportion of the energy input to most of the scleractinians, sponges, and gorgonians that comprise MAFs is provided by autotrophy. Some of these benthic suspension feeders have morphological adaptations to maximize light absorption by their symbionts (Enríquez *et al.,* 2005; Brümmer *et al.,* 2008). As depth increases, light becomes scarcer and photosynthesis cannot solely provide the same metabolic support (Roth, 2014). Hence, heterotrophy dominates, and is the rule in most of the MAFs that form ocean seascapes below 50-60 m depth (Rossi *et al.,* 2017b; Schubert *et al.,* 2017). Ongoing climate change is rapidly reducing the availability of both sources of energy to shallow MAF (autotrophy and heterotrophy, Rossi *et al.,* 2017b; Hughes *et al.,* 2018a,b), and is acting synergically with increasing pressures on MAFs in the Anthropocene deriving from multiple anthropogenic drivers. These drivers include eutrophication, overfishing, marine pollution, warming, and changes in ocean acidity (Rossi, 2013), operating at multiple spatial and temporal scales. Climate change effects will act both on large spatial and temperature scales (e.g. rising temperature, acidification, sea level rise), chronically transforming the distribution, trophic functioning and biodiversity of benthic communities; and at local scales, with punctual acute and disruptive impacts (e.g. heat waves, tropical cyclones, strong storms).

We argue that the MAFs in our oceans are thus in a transition state, shifting from the natural range of variation, found prior to the industrial revolution, to an unpredictable state that may or may not stabilize during decades or centuries.

Seascape before the first transition

Prior to the industrial era, large areas of coastal and offshore seabed sustained complex MAFs (Figure 1), mainly composed of benthic suspension feeders (Turner *et al.,* 1999; Airoldi and Beck, 2007; Harasti, 2016; Thurstan *et al.,* 2017). Industrial bottom trawling and gillnets fishing, excessive harvesting, pollution and coastal mismanagement wiped out or severely reduced the structural complexity and functioning of many of these MAFs, which played an essential role in biogeochemical cycles (Jackson, 2001). Some of these impacts can be considered chronical and non-reversible, taking into account medium and even large recovery periods, (e.g., centuries, millennia), while others are reversible but with a long-lasting effect (e.g, decades). The forests of the sea (both animal and vegetal) are now a remnant of what they once were, with a corresponding loss of their ecosystem services (Worm *et al.,* 2006). A very rough (and probably underrated) estimate of current marine cnidarian biomass is around 0.1 Gt of carbon (a very small proportion of the 550 Gt C of the overall biosphere biomass, Bar-On *et al.,* 2018). There are no historical estimates of this value, but we assume that it was much higher (Thurstan *et al.,* 2017). Consequently, their influence on the organic and inorganic carbon cycles has drastically declined and, with it, their role as carbon sequesters (Harvey 2004; DeVries *et al.* 2019).

Similar to the effects of agriculture and other land uses on terrestrial ecosystems, short-term or episodic (pulse) disturbances can homogenize marine habitats and thus decrease community complexity (Watling and Norse, 1998; Puig *et al.,* 2012;). This is caused primarily by adverse impacts on long-lived, slow reproducing, habitat-forming species, which commonly form the structural component of MAF communities. For example, bottom trawling in the continental shelf or in deep areas (even only a few trawls) destroys soft and hard bottom assemblages which cannot recover in short-medium elapsed times (Thrush &Dayton, 2002). In shallow coral reefs, high intensity El Niño events, lasting for days or few weeks, may affect huge communities, which require decades to recover recovery (Bianchi *et al*., 2017; Hughes *et al*., 2018b). Such species are often unable to rapidly recover from major structural disturbances. Together with the short-time scales between pulse disturbances, such as trawling, and the fact that human-induced pulse disturbances tend to occur over much larger spatial scales than natural pulses (Thrush & Dayton 2002), they can have disproportionally large long-term effects on MAF communities. As a result of anthropogenic disturbance (e.g. the Anthropocene) MAFs are evolving towards rapid cycling systems (Thrush and Dayton 2002; Rossi 2013), i.e. less diverse, less resilient, much younger and low-biomass MAFs, with faster energy turnover processes are replacing long-lived complex structures. In other words, long-lived structures are substituted by fast-growing ones (such as gorgonians, polychaetes, etc., Rossi, 2013), which may be better adapted to frequent disturbance (Ladd *et al.* 2019). As a result, having transformed nutrients cycling (N, O, P, C, etc.) and carbon retention capability of these communities, we face an acceleration of biogeochemical cycles.

Once passed this first transition, from long-lived highly complex structures to simplified ecosystems, the problem will be the source of energy. Heterotrophic and autotrophic inputs are already changing due to increasing sea temperatures, sea level rise (SLR), extreme floods or droughts and ocean acidification, leaving serious concerns and unknowns about what a second transition of the seascape will look like, or when it will occur (Poloczanska *et al.,* 2018). The relevance of MAFs may be thus higher than previously thought, albeit much diminished relative to the pre-industrial age (Rossi *et al.,* 2017a).

Facing the second transition

At the time of writing, Mauna Loa Observatory in Hawaii has registered a CO_2 concentration above 410 ppm (IPCC, 2018), far surpassing critical limits for coral reefs put forward only 10 years ago (Veron *et al.,* 2009). The earth system transformation or time reduction of biogeochemical responses due to climate change is happening (fast changing environmental conditions) (Reay *et al.,* 2008), and part of the long-lived structures (terrestrial and/or marine) that may partially mitigate their effects (as natural carbon sinks) are strongly diminished or missing. The shift in ecosystem functioning is thus continuing, but now MAFs have another problem that was not present during the first transition: the acquisition of energy.

Most tropical coral reefs depend on light harvesting (autotrophy) are suffering from recurrent bleaching due to sea temperature rises and episodic heatwaves, impacting their symbiotic algae living in the tissues (Hoegh-Guldberg *et al.,* 2018; Hughes *et al.,* 2018a). Mortality of habitat-forming symbiotic corals results in the degradation of formerly complex and highly biodiverse ecosystems, with a concomitant loss of functionality. Scleractinian corals are being replaced by macroalgae, octocorals, zoanthids or sponges (Norström *et al.,* 2009; Bell *et al.,* 2013; Cruz *et al.,* 2016) that have the advantage of being more flexible in their trophic strategies (switching from autotrophy to heterotrophy, depending on the environmental conditions, Fabricius et al., 1995; Rossi *et al.,* 2018). The synergistic effects of multiple stressors (Figure 2) in a rapidly changing environment make the energetic performance of the autotrophy-dependent anthozoans sub-optimal, and may threaten their dominance and survival (Ruzicka *et al.,* 2013). We thus appear to be facing the transformation of one of the most biodiverse and complex systems that has ever existed on Earth (Hughes *et al.,* 2017a,b). It is unlikely that these habitats will recover their past biodiversity and structure should conditions stabilize. The problems related with light harvesting and temperature shifts may be, however, an opening for opportunists and alien or "immigrant" species that thrive in the new conditions. In a global-change context, due to perturbations, such as bio invasions (Libralato *et al.,* 2015; Rizzo *et al.,* 2017), eutrophication (Cloern, 2001) and ocean warming (Churst *et al.,* 2014), plankton communities might respond differently and their production could have different fates at higher trophic levels (D'Alelio *et al.,* 2016). In the Mediterranean Sea (an area highly impacted by tropicalization trends, Bianchi, 2007), tropical alien scleractinians and soft corals may effectively reproduce (thus producing viable new recruits) in a warmer and more transparent sea. These tropical organisms may be benefited from the new conditions related to the climate change. At the same time, these conditions may induce latitudinal shifts in the distribution of those species that may effectively migrate on time (Bianchi 2007).

SLR is expected to increase coastal erosion, mixing and circulation, and hence, increase turbidity due to the amount of suspended sediment. This will decrease light availability for photosynthesis and increase sediment-induced stress (Storlazzi *et al.,* 2011) in MAFs composed of mostly symbiotic corals. Thus, SLR undermines the corals' ability to grow and thrive in future seascapes of drowned reefs. Consequently, many scleractinians will be unable to grow fast enough to keep up with predicted SLR, leaving tropical coasts and some oceanic islands exposed to increasing erosion and flooding risk. Only a few reefs will have the capacity to track SLR projections under futures scenarios of climate change by 2100 (Perry *et al.,* 2018), leaving tropical coasts and some oceanic islands exposed to increasing erosion and flooding risk.

But climate change will impact MAFs far beyond the surface layers: the transformation of primary and secondary productivity patterns (microphytoplankton, zooplankton and seaweeds/seagrasses). MAFs depend on this production as filter feeders (Rossi *et al.,* 2017b). All the ongoing transformation of our oceans due to climate change will affect food availability, the MAFs capability to capture particles, retain the associated energy and invest it in new recruits. For example, ocean warming will potentially result in longer periods of water column stratification; thus, affecting primary productivity, diurnal plankton migrations and possibly leading to discontinuities in prey availability for MAFs (Doney, 2006). Also, a slowdown in water circulation and reduced upwelling due to freshwater input at higher latitudes in the North Atlantic is expected (Curry *et al.,* 2003). We are still trying to understand how will the general and local patterns of ocean circulation change, being the current models clearly uncertain in several areas and showing spatially heterogeneous trends (e.g.,. the Mediterranean sea, Adloff *et al*., 2015). We must consider that MAFs will be largely impacted by these future changes. Since MAF-forming organisms are sessile, they depend on currents and sinking biogenic particles to feed that are expected to be drastically reduced by increased ocean stratification. Thus, the potential reduction in plankton production in the surface (i.e., Steinacher *et al.,* 2010; Bopp *et al.,* 2013), accompanied by a reduced export flux of particulate organic carbon to the deep sea (Jones *et al.,* 2014), will have severe impacts on MAFs. This will come together with increased nutritional requirements to buffer negative effects of ocean acidification and increased temperatures (Edmunds, 2011; Castillo *et al.,* 2014; Towle *et al.,* 2015; Büscher *et al.,* 2017).

In recent decades, overall phytoplankton productivity has already declined in response to climate change, with seasonal shifts observed in several areas (Henson *et al.,* 2013; Laufkötter *et al.,* 2015; D'Alelio *et al.,* 2016). Also, changes in bloom formation (much earlier and persistent in some cases), species dominance and total biomass size have been described in different areas. Phytoplankton growth depends on temperature and the availability of light and nutrients, including nitrogen, phosphorus, silicon and iron. In more stratified waters, especially those of tropical and subtropical systems (including the warm temperate seas), higher temperatures may assist phytoplankton growth, but nutrient availability will be limited by a lack of mixing. Furthermore, the temperature-driven increase in primary productivity might be more than compensated by an increase in respiration and catabolism, with net results of increased dissolved organic and inorganic matter, rather than biomass (Lazzari *et al*., 2014). The loss of productivity in these tropical and subtropical areas is expected to be offset by a higher productivity poleward. A slight decrease in annual primary production of 0.4% (0.10 Pg C year^{-1} of an ocean average of 50 Pg C year^{-1}) might result in similar C preservation, and an unknown quantity of C sunk, sedimented or available for MAFs (Keil, 2017). Taking into account that models estimated declines of up to 20% of the productivity in some regions during the next 60 years (Roxy *et al.,* 2016) the effect on MAFs could be dramatic.

Other effects may be related to salinity change. The increasing salinity of the Mediterranean Sea, for example, particularly in the intermediate and deep layers, is related to the general increases in seawater temperature and evaporation rates in this basin (Rixen *et al.,* 2005; Vargas-Yáñez *et al.,* 2010; Borghini *et al.,* 2014). This process is accelerated by decreases in river flow to the sea due to the construction of water reservoirs (Vargas-Yáñez *et al.,* 2017) and decreased precipitation (Viola *et al.,* 2016). Changes in salinity are critical for ocean mixing depth and current circulation, and therefore for the dynamics of nutrient transfer. Such changes can alter the structure of the communities of planktonic primary producers and the trophic chains that feed on them (Learmonth *et al.,* 2006). Although this process may be spatially heterogeneous (Adloff et al. 2017), changes in salinity and density are critical or ocean mixed layer depth and thermohaline circulation, therefore for the dynamics of nutrient transfer and spatial connectivity. Circulation dynamics are also affected by warming-induced stronger stratification, changes in the winter mixing layer depth and a poleward displacement. Another example can be deduced for the North Atlantic general circulation pattern. Since the mid-twentieth century, a weakening of the Atlantic Ocean overturning circulation has been detected (Caesar *et al.,.* 2018). This change has a major impact on climate but might also reduce the deep oxygen concentrations and the energy supply (in terms of nutrients and organic matter flux) into the deep ocean, with unpredictable biological consequence benthic marine ecosystems.

One of the least investigated factors is the effect of change in rainfall patterns on MAFs, especially in the animal-dominated coastal seascapes. Rainfall commonly controls the estuarine water flow processes and the transfer of materials (nutrients and organic matter) from the mainland to the sea. The Intergovernmental Panel on Climate Change (IPCC, 2018) is expecting shifts in the pattern of rainfall worldwide, including reduced rainfall and intense droughts in some regions, while in others increases in precipitation and floods are predicted. Reduced rainfall and extreme droughts will decrease the fluvial contribution to the ocean and affect the input of carbon for sessile suspension feeders, composing the coastal MAFs.

Climate change appears to be altering also the productivity of macroalgae and seagrasses, which has consequences for the availability of plant detritus. Unsworth *et al.* (2008) suggested that the primary productivity of seagrass meadows has already diminished, so the available detritus has declined (Maxwell *et al.,* 2017). Warming and ocean acidification will continue to affect macroalgal productivity in different ways (e.g., decrease in calcification rates in coralline algae, increased biomass in fleshy algae; Comeau and Cornwall, 2017; Duarte *et al.,* 2018). Calculations show that for some suspension feeding organisms detritus may represent more than 50-90% of their food inputs (Gili and Coma, 1998), though it represents a low-quality food source (Rossi and Gili, 2009). Changes in its availability may be a key to understand which suspension feeding organisms will be affected by such detritus flux change.

Greenhouse gas–driven ocean warming is also lowering the oxygen concentrations in both the open ocean and coastal waters, with negative consequences in the distribution and abundance of animal populations and associated biogeochemical cycles (Breitburg *et al.,* 2018). As oxygen depletion becomes more severe, persistent and widespread, a greater fraction of the ocean is losing its ability to support high-biomass and diverse animal assemblages. Warming also raises metabolic rates, thus accelerating the rate of oxygen consumption. Therefore, decomposition of sinking particles occurs faster and their remineralization shifts toward shallower depths (Brewer *et al.,* 2017). Under such conditions, energy is recycled faster. Changes of the microbial loop also affect marine food webs and hence, the efficiency of organic carbon transfer (Howes *et al.,* 2015; Keil *et al.,* 2016). Guidi *et al.* (2016) suggest that specific plankton communities, from the surface and deep chlorophyll maximum, correlate with carbon export at 150 m depth. Thus, changes in the microbial loop and the degradation speed of organic matter will synergistically affect deep MAFs.

Pelagic secondary production also suffers climate change-related impacts, either directly through changes in the environmental conditions or indirectly through changes in phytoplankton productivity (Howes *et al.,* 2015), and trophic efficiency of pelagic food webs (Fanelli *et al.* 2013). Zooplankton occupies a key position in marine ecosystems, serving as the primary trophic pathway for the transfer of primary productivity to higher trophic levels. Given that zooplankton is an important food source for sessile filter feeders (Gili & Coma, 1998) and that it drives carbon transfer to benthic habitats, changes in these communities would have significant impacts on the benthic seascapes due to shifts in benthic-pelagic coupling (Griffiths *et al.,* 2017). Overall, zooplankton communities are predicted to shift toward dominance by smaller-sized individuals (microozooplankton) and to alter dominance patterns in favor of species with lower metabolic demands, in response to global warming and stratification of waters (Richardson and Schoeman, 2004; Daufresne *et al.,* 2009). Pelagic secondary production is already changing in temperate coastal areas (Smetacek and Cloern, 2008), affecting the potential quality of food transferred to other organisms. It is likely that a change in the size distribution within zooplankton communities, stimulated by increases in sea surface temperature, as well as shifts in their prey availability and composition, will cause ecosystem shifts in MAFs. These shifts will trigger changes in energy fluxes related to the MAFs due to the potential transformation of the available food, as observed for deep waters (Fanelli *et al.* 2013). In fact, resource availability more than hydrographic conditions seems to explain the assemblage variation of benthic fauna in certain areas (Fanelli *et al*.,. 2013).

Further, climate change impacts work synergistically with other disturbances reducing the availability of food for suspension feeders (Kunhz *et al.,* 2014; Yesson *et al.,* 2016). For example, trawled sediments at 500 m depth are characterized by a significant decrease (5–52%) in labile organic matter content, reduction in the organic C turnover rates and by a significant reduction in meiofaunal abundance, biomass and biodiversity (Pusceddu *et al.,* 2014). Loss of these deep habitats would lead to decline or disappearance of the enduring animal forests and their ecosystem services, but also their role as an essential part of the biogeochemical cycles. In general, the future soft bottoms are expected to favor smaller benthic organisms, lowering the energy transfer and sediment mixing (Keil, 2017). Adding both direct and indirect impacts will cause negative feedback on MAFs, particularly for suspension feeders especially sensitive to cumulative impacts.

The impact of changing C fluxes on the energetic budget of MAFs

Let us discuss some examples of what could be the questions to be addressed in such future seascape panorama. Lowering the water column productivity in the tropical and subtropical zone, and conditioning the *Symbiodinium* host to other than scleractinian species in many areas, what will be the future of the seascape in coral reefs? Which suspension feeding species could substitute the efficient light harvesting scleractinians? Bell *et al.* (2013) suggest that sponges may become the dominant organisms inhabiting some tropical shallow-water reefs when the effect of global climate change and ocean acidification becomes established. Sponges, gorgonians and scleractinian corals are major components of MAFs and respond differently to a fast-changing marine environment (Figure 3). For example, direct and indirect responses of the sponge holobiont (Roughgarden *et al.,* 2018) and its constituent parts (host and symbionts) to changes in temperature and pH are generally less extreme than the effects of these factors on a coral holobiont. Overall, the predicted shifts in the Anthropocene (decrease of pH, increase of turbidity and sedimentation in coastal waters, increase of seawater temperature) favors heterotrophic sponges instead of mixotrophic scleractinian corals. Whilst sponges have already increased in abundance as sensitive corals have declined in the Caribbean, Atlantic and Indo-Pacific (Bell *et al.,* 2013), soft corals are also becoming more abundant in certain areas (Ruzicka *et al.,* 2013; Lenz *et al.,* 2015; Schubert *et al.,* 2017). The flexibility of autotrophic versus heterotrophic contributions to the host's energy budget may be a key to understand why they are becoming dominant under certain circumstances (Fabricius et al., 1995; Rambsy *et al.,* 2014; Schubert *et al.,* 2017; Rossi *et al.,* 2018). However, some tropical shallow-water reefs, dominated by stress-tolerant corals, may be more resilient to global environmental change. This occurs where the temperatures are naturally elevated and/or environmental conditions are historically suboptimal (e.g., through high turbidity or sedimentation). These natural features provide an "environmental filter" potentially liable to harbor thermal-resistant taxa and disturbance-tolerant corals (Sanders and Baron-Szabo, 2005; Morgan *et al.,* 2016).

At greater depths we find the mesophotic ecosystems – (MEs, 30-150 m depth). These are diverse benthic ecosystems that occur generally along the continental shelves, seamounts and oceanic islands (Khang *et al.,* 2017). The MEs are composed of a mosaic of distinct seascapes and may be dominated by algae (rhodolith beds or coralline algal reefs) and/or sessile suspension feeders. These seascapes include MAFs, such as scleractinian-dominated ecosystems (deep coral reefs), sponge grounds, octocoral, and black coral forests (Soares *et al.,* 2019). MEs will be affected by many of the same changes in energy fluxes due to local and global human stressors, as experienced by shallow communities (Rocha *et al.,* 2018; Soares *et al.,* 2019). However, these deeper ecosystems (especially in the lower mesophotic zone, 70-150 m depth) are more dependent on the heterotrophic input than their shallow-water counterparts (Houlbréque and Ferrier-Pagés, 2009).

Although these systems will not be directly affected by changing light levels, temperature increase is a possible scenario in these systems, and a global average warming of 1°C change may be a real constraint for the productivity of these systems in a near future (Khang *et al.,* 2017). This assumption, however, is region-dependent. Some areas of the planet have well-mixed water columns, where higher sea surface temperatures can reach down to 60 m depth. At this depth, MEs are still dominated by mixotrophic scleractinian corals (Sinniger *et al.,* 2013) that may be less resilient than shallow reefs, considering the increase of multiple human impacts (Rocha *et al.,* 2018; Soares *et al.,* 2019), combined with being vulnerable due to slow growth rates, limited genetic connectivity, and low reproductive performance (Shlesinger *et al.,* 2018). Heterotrophic taxa (i.e., non-symbiotic corals, octocorals, sponges, and black corals) are more common in the deeper zone (70-150 m depth) (Semmler *et al.* 2017). The benthic species in this zone will be affected by changes in the carbon export (from primary and secondary productivity) to the sea floor. We hypothesize that shifts in energy fluxes will significantly affect the health status of mesophotic species depending on the ecoregion and the species bathymetric distribution. Moreover, the effects will be most likely species-specific, considering the different strategies of carbon budget management among sessile suspension feeders.

In deeper areas, where a high proportion of the biomass of MAFs is concentrated (e.g., submarine canyons, paleochannels, sea mountains, cold water coral reefs, Henry *et al.,* 2017), the particulate flux could decrease in some areas by up to 55% (Sweetman *et al.,* 2017), probably altering 80% of the communities. In deep areas, were the particulate organic carbon flux may be limited (POC flux 1-2 g C m^{-2} $year^{-1}$; Watling *et al.,* 2013), a reduction of available organic matter may be critical for respiration, reproduction, growth and other metabolic pathways of the species. Cold water corals will be exposed to changes in currents and surface productivity, as well as oxygen impoverishment and pH changes (Sweetman *et al.,* 2017). For example, it has been suggested that in areas like the Northern Adriatic Sea and the Gulf of Lions (Mediterranean Sea), dry-extreme cold winds (the main driver of cold water cascade, bringing sediments, oxygen and food to the MAFs) may be reduced, producing a direct effect on the viability of deep water populations (Taviani *et al.,* 2016; De Clippele *et al.* 2018). Hypoxia can also have dramatic consequences for their metabolism, altering the input-output equilibrium, which will be reflected in their survivorship (Gooday *et al.,* 2010). Biodiversity declines as O_2 declines, but also as food availability gets scarcer and thus, the basic maintenance of the structuring organisms is no longer given due to the imbalances in energy inputs-outputs (Rossi *et al.,* 2017b). This scenario is a real possibility in deep seas all over the world, but the mechanisms involved are not yet well understood (Sweetman *et al.,* 2017).

Another example of potential repercussions of changes in energy fluxes in MAFs exists in the warm temperate seas. The Mediterranean Sea is possibly one of the clearest examples of drastic and rapid changing seascapes in shallow waters. Recent mass mortalities, affecting suspension-feeding organisms, occurred due to anomalous high sea surface temperatures and water stratification (Garrabou *et al.,* 2009). However, the centre of the problem may be the lack of an adequate trade-off between food input and energetic costs for metabolic maintenance (Rossi *et al.*, 2006; Galli *et al.,* 2016). Changes in the timing of peaks in primary productivity at key moments may limit the capacity of MAFs to store energy, after which they may then face prolonged warm conditions in non-optimal conditions (e.g., long water mass stratification periods in summer, Rossi *et al.,* 2006). The lack of an adequate lipid storage, gathered in the normally productive late winter-early spring period, may be crucial to explain mass mortality events (Rossi *et al.,* 2017b). Moreover, extreme events, such as frequent and prolonged heat waves, may impact the survival of low-motility organisms, favouring the transformation of marine snow in marine mucilage, but also triggering selective zooplankton mortality, which diminishes the carbon availability for suspension feeding animals (Danovaro *et al.,* 2008; Marbà *et al.,*. 2015). It might be noted that recent studies highlight how in the near future marine heat waves will be more frequent, more severe and reaching deeper layers in the water column (Galli *et al*., 2017).

Nutritional condition and recruitment: a key factor to understand future seascapes

Climate change and particularly temperature can deeply influence organisms' metabolism. Reproduction, considered as one of the keys factors to understand the distribution and resistance of species in the face of environmental change (Adjeroud *et al.,* 2017), would be one of the most affected processes. Reproductive events and success are related not only to temperature, but also to the available autotrophic or heterotrophic inputs (Rossi *et al.,* 2017b). Changes in temperature, primary productivity and water stratification, due to the ocean warming, are thus affecting trophic chains in sensitive world areas (Milisenda *et al.,* 2017; Rossi *et al.,* 2017b), inducing a mismatch between functional groups and trophic levels (Edwards and Richardson, 2004). Energy storage, essential for the offspring viability (and concentrated in high-productive seasons), may be slightly changing (Rossi *et al.,* 2017b). The lack of food affects directly the number of eggs or larvae produced (Gori *et al.,* 2013), being a potential factor to be considered in the general understanding of seascape changes. We know that larval growth rates can increase associated to faster metabolic activity (Munday *et al.,*. 2009), which depends on the amount of energy stored in the offspring. The source of this energy is the mother colony or individual that will invest such macromolecules depending to the availability of the organic matter (Rossi *et al.,*. 2017b).

Phenology of the species (i.e. the timing of key seasonal events) will also affect the viability of new generations (Rossi *et al.,* 2019). In fact, more than 60% of studied species in aquatic systems have responded to ocean warming by advancing their reproductive phenology (Greve *et al.,* 2005; Poloczanska *et al.,* 2018). Since reproductive events have evolved to occur at optimal times of food availability to maximize the survival of the next generation (Forrest and Miller-Rushing, 2010; Rossi *et al*., 2019), these phenological shifts can reduce reproductive success of species and affect their population in the long-term (Schaper *et al.,* 2012). As an example, spawning and release of larvae in summer implies that lecithotrophic larvae of anthozoans in the Mediterranean Sea settle and metamorphose a few weeks before phytoplankton concentration rises in the early fall (Rossi and Gili, 2009), supplying moderate to high amounts of food. Within the context of global change (see the previous considerations), there is a risk that the period of trophic crisis (Rossi *et al.,*. 2006) might be significantly prolonged to the point that the capacity of the energy reserves in lecithotrophic larvae would not last until the arrival of favorable feeding conditions in the early autumn. This situation could be even worse if the spawning of these species would be triggered earlier by the increase ~~of~~ in temperature (Rossi *et al.,* 2019). Despite the potential severe consequences of the undermining of reproductive success for the long-term persistence of species populations, little is known of the importance of prey phenology to population persistence. This lack of studies on benthic suspension feeders in the literature is especially problematic not only due to their ecological importance, but also because research suggests that shifts in phenology will occur faster in marine environments (4.4 days per decade) than in terrestrial ecosystems (2.3–2.8 days per decade) (Parmesan, 2007; Poloczanska *et al.,* 2018).

Larval nutritional condition and species phenology will affect the potential seascape composition in a near future, (e.g., decades), but population connectivity has to be also considered from another point of view: hydrodynamic features and larval dispersal (Andrello *et al.,*. 2015). As previously explained, climate change will modify water current velocity patterns, which could affect the dispersal routes of larvae and connectivity (Brochier *et al.,*. 2013). In a recent study, Andrello *et al.* (2015) suggested that larval dispersal distances in the Mediterranean Sea may decrease by 10%, thus increasing by 5% the retention effect Sea. This is important because it implies a higher concentration of larvae in smaller areas and a significant decrease in connectivity in certain areas and periods (Andrello *et al.,.* 2015). A decrease in larval dispersal distances and a higher retention in certain areas would probably decrease the gene flow (Watson *et al.,.* 2011), affecting also the viability of the MAF populations.

The ability to transform the energy input into viable offspring, the hydrological conditions that will change connectivity, and the phenological changes in prey life cycles and reproductive timing of MAF species are important knowledge gaps that demand prioritization, if we want to foresee the consequences of the ongoing seascape transformation.

Conclusion: Seascape future depends on the first and second transition

It is clear that changes in the autotrophic or heterotrophic inputs of suspension feeding organisms due to climate shifts will partly set the future seascape due to a complex balance in which “winners” and “losers” will be identified (Berggren *et al.,* 2009). The first transition (the degradation or loss of complex benthic structures, currently underway; Jackson, 2001) is likely to accelerate a second transition (the potential change in quantity, quality and timing of food availability, related mainly to climate change effects) due to the time reduction of biogeochemical cycles. The biogeochemical cycles will speed the change between “trophic cages”, and the lack of long-lived organisms will accelerate this rushed “loop”. These changes are having and will have dramatic influences on the distribution and composition of the communities populating the seafloor and thus should be considered in the conservation decision-making processes. In fact, the criteria to protect specific areas has to consider all the above mentioned factors shaping the future seascape. Minimizing the anthropogenic pressure on biodiversity (Coll *et al.,.* 2012) and considering the functional ecology of the MAF species (Rossi et al.,. 2017a) will be the key to preserve the ecosystem services of such complex habitat-forming organisms.

Changes in the MAFs will alter the capability to store carbon (sequestration), which has already diminished (Arias-Ortiz *et al.,* 2018; Steffen *et al.,* 2018). The acceleration of biogeochemical cycles will act as a positive feedback and increase to a certain point in which the dominant species will reach a new equilibrium. Thus, the approximately 30% of greenhouse atmospheric carbon removed by the oceans (Le Quere *et al.,* 2013) would partly remain, as previously explained, in fast cycling ecosystem functioning. Looking at this panorama, it seems urgent to identify which ecosystem services are directly affected by the climate change impacts on MAFs. So far, only new technology (especially ROVs, AUVs and landers) will help to better understand such processes, providing quantitative data from shallow to deep waters. This technology is now cheaper and easier to handle and facilitate the essential map the oceanic floor~~s~~ that are so far, only projected in general models that lack actual quantitative data (Halpern *et al.,*. 2015).

Many questions are still open and need to be addressed in the near future: Which organisms will be more affected, passive or active suspension feeders? Will the autotrophic component increase or decrease? Will climate change favour species that are less capable to store carbon in their structures? And more intriguing: how long will this transition phase take?

In general, all these questions and the above-mentioned thoughts are essential to push administrations towards a stronger commitment to the protection and restoration of the oceans' marine benthos. It is not only a biodiversity and fisheries issue. The marine animal forest conservation is a key point for ocean health, as it may be part of the solution to mitigate the greenhouse gas problems of the planet because represents a carbon sink complex structure.

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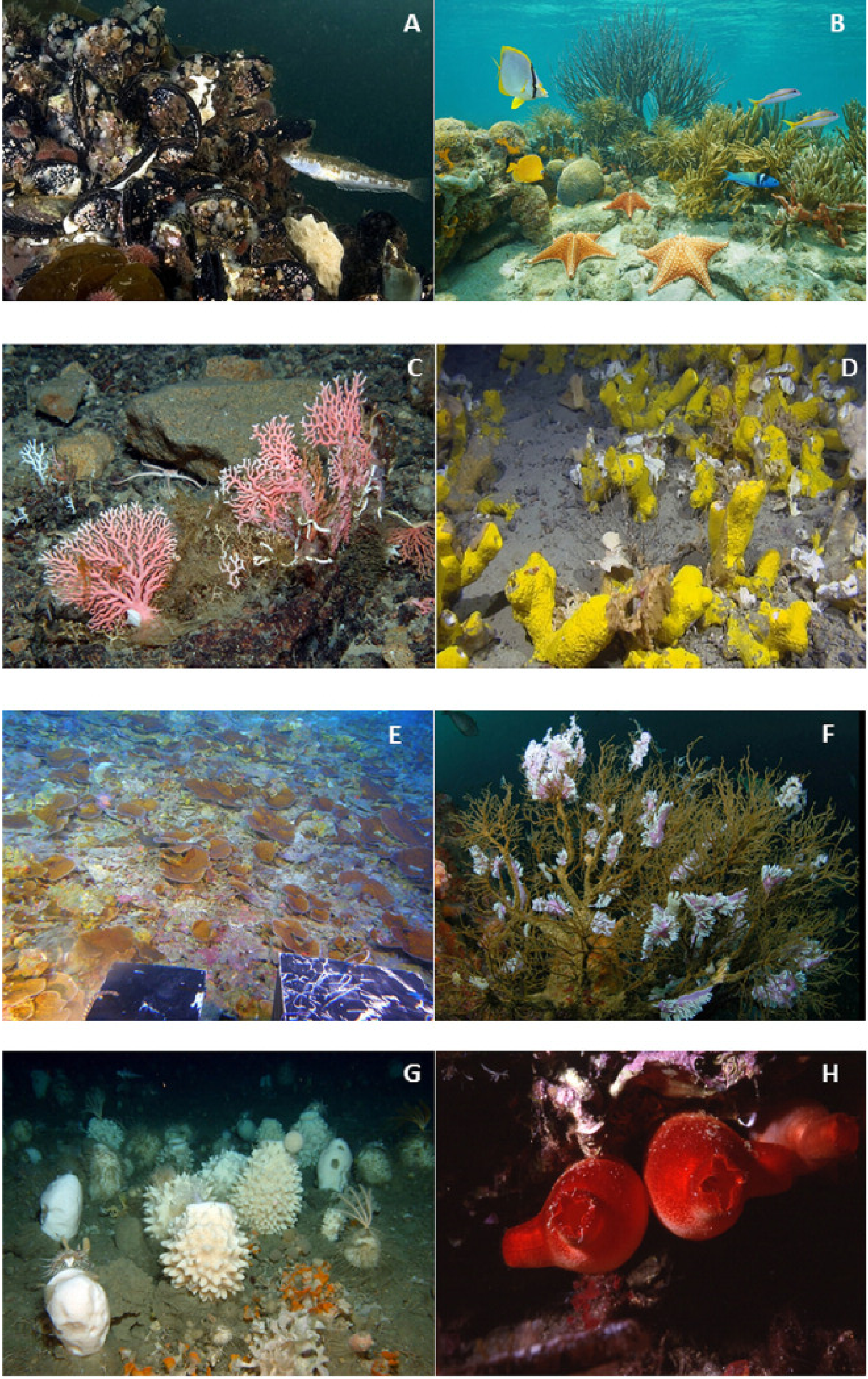
FIGURES

Figure 1. Different marine animal forests of the world, at different depths and latitudes. A) Mussel bed in Patagonia (Chile); B) Caribbean coral reef; C) Hydrocoral *Errina* ssp. in the Antarctic Peninsula; D) Sponge ground in deep Atlantic waters; E) Mesophotic corals in Hawaii; F) Hydrozoan *Solanderia ericopsis* with *Jason mirabilis* nudibranchs; G) Antarctic continental platform sponge ground; H) Mediterranean ascidian *Halocyntia papillosa*. [Photos from (A) Cárdenas and Montiel, 2017 (© Americo Montiel and César Cárdenas); (B) ADOBE STOCK; (C) Gutt et al., 2017 (© Julian Gutt-Alfred Wegener Institute); (D) Orejas and Jiménez, 2017 (© Pal Buhl-Mortensen, IMR, Norway); (E) Kahng *et al.*, 2017 (© Sam Kahng); (F) Di Camillo *et al.*, 2017 (© Ian Skipworth); (G) Gutt *et al.*, 2017 (© Julian Gutt-Alfred Wegener Institute); (H) Rossi *et al.* 2017a (© Sergio Rossi)].

Figure 2. Different drivers affecting MAFs of the world. Climate change is already changing the biophysical features of the water column, which have a direct effect on MAFs. Not only sea warming, also ocean acidification, sea level rise and change in circulation patters will surely change the planet seascapes. Repercussions will be different depending on the region and on the dominance of certain benthic organisms, the species interactions, the metabolic constraints, the capability of dispersion and the presence of alien species that may take advantage on the new physical, chemical and biological conditions in the future oceans (artwork by Alberto Gennari).

Figure 3. Schematic overview of the abiotic and biotic factors that have a direct (filled and black arrows) or indirect impact (stripped and broken line arrows) on the autotrophic and/or heterotrophic energy input of MAF-forming organisms.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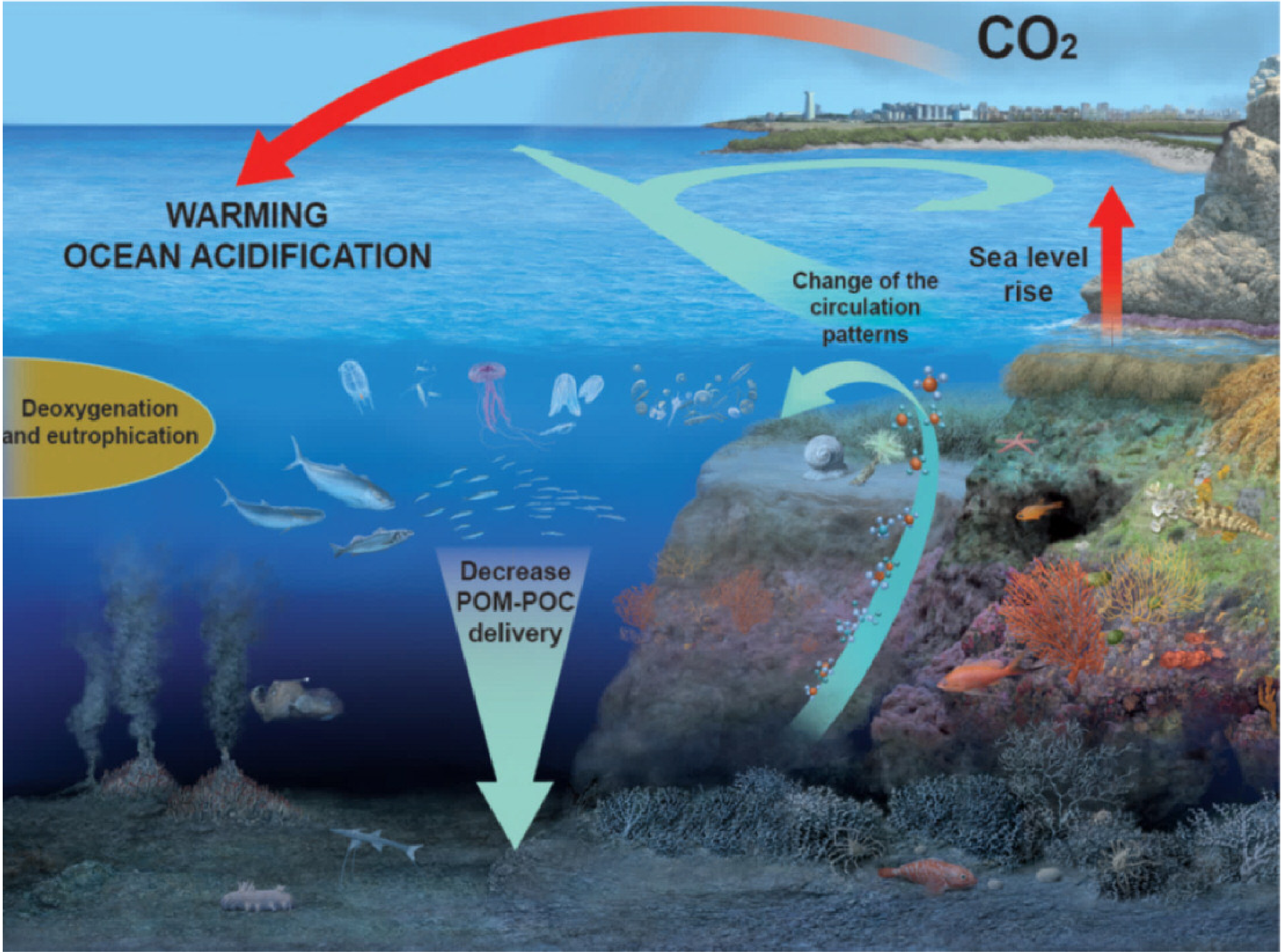
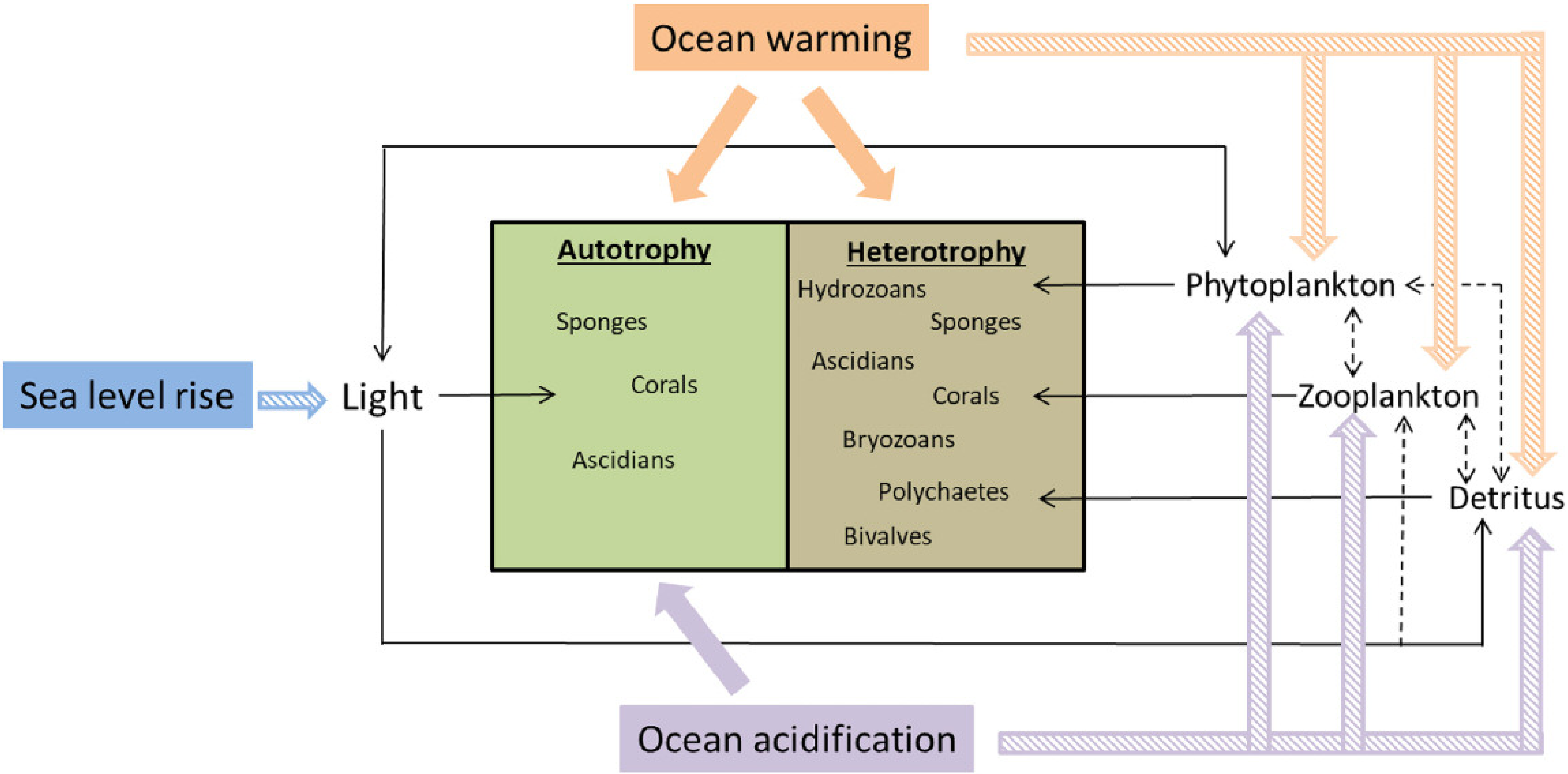


CO_2
WARMING
OCEAN ACIDIFICATION
Sea level
rise
Change of the
circulation
patterns
Deoxygenation
and eutrophication
Decrease
POM-POC
delivery


Ocean warming
Autotrophy
Sponges
Corals
Ascidians
Heterotrophy
Hydrozoans
Sponges
Ascidians
Corals
Bryozoans
Polychaetes
Bivalves
Phytoplankton
Zooplankton
Detritus
Sea level rise
Light
Ocean acidification