Quo Vadimus

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

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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, this 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.

Keywords: benthic–pelagic coupling, benthic suspension feeders, climate change, energy fluxes, heterotrophy, ocean warming, primary productivity, secondary productivity, seston availability, water stratification

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 on both large spatial and temperature scales [e.g. rising temperature, acidification, sea level rise (SLR)], 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 chronic 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 and 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 (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 and 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, replacing long-lived complex structures. In other words, long-lived structures are substituted by fast-growing ones (gorgonians, polychaetes, etc., Rossi, 2013), which may be better adapted to frequent disturbance (Ladd *et al.*, 2019). As a result, having transformed the 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, 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.*, 2016). 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
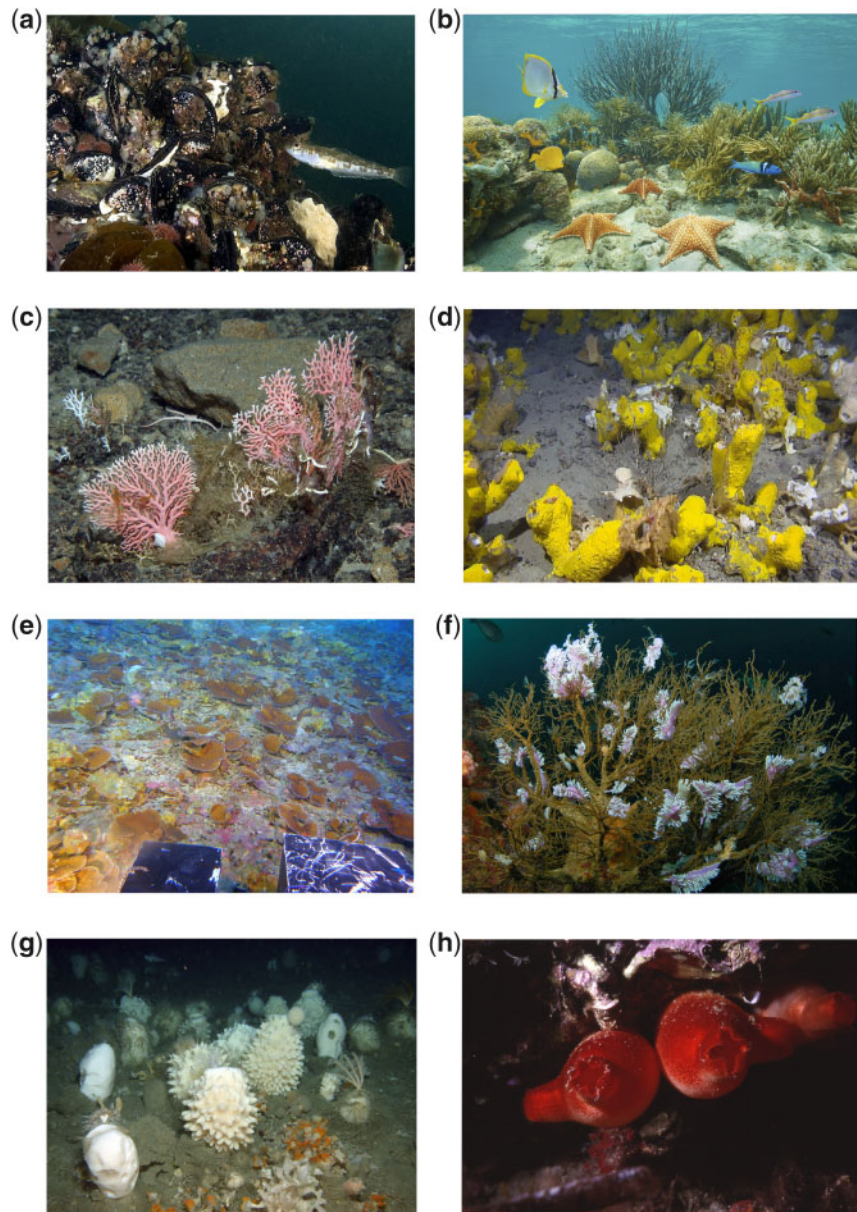
Figure 1. Different MAFs of the world, at different depths, and latitudes. (a) Mussel bed in Patagonia (Chile); (b) Caribbean coral reef; (c) Hydrocoral *Errina* ssp. in the Antarctic Peninsula; (d) Sponge ground in deep Atlantic waters; (e) Mesophotic corals in Hawaii; (f) Hydrozoan *Solanderia ericopsis* with *Jason mirabilis* nudibranchs; (g) Antarctic continental platform sponge ground; (h) Mediterranean ascidian *Halocynthia 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)].

strategies (switching from autotrophy to heterotrophy, depending on the environmental conditions, Fabricius and Klumpp, 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 suboptimal, 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.*, 2017). It is unlikely that these habitats will recover their past biodiversity and structure

should conditions stabilize. The problems related to 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 (Chust *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
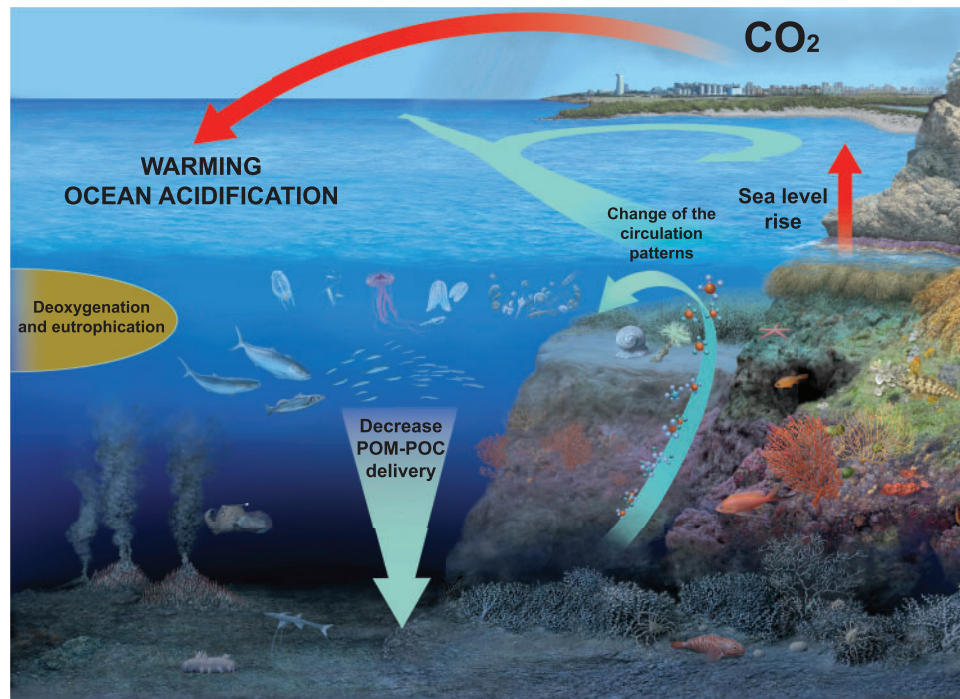
Figure 2. Different drivers affecting MAFs of the world. Climate change is already changing the biophysical features of the water column, which have a direct effect on MAFs. Not only sea warming, also ocean acidification, SLR and change in circulation patterns will surely change the planet seascapes. 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).

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: there will be a 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 (Steinacher *et al.*, 2010; Bopp *et al.*, 2013), accompanied by a reduced export flux of particulate organic carbon (POC) 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., 2015), 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. (2018) 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 towards shallower depths (Brewer and Peltzer, 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 and 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 towards dominance by smaller-sized individuals (microzooplankton) and to alter dominance patterns in favour 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).

Furthermore, climate change impacts work synergistically with other disturbances reducing the availability of food for suspension feeders (Kuhnz 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
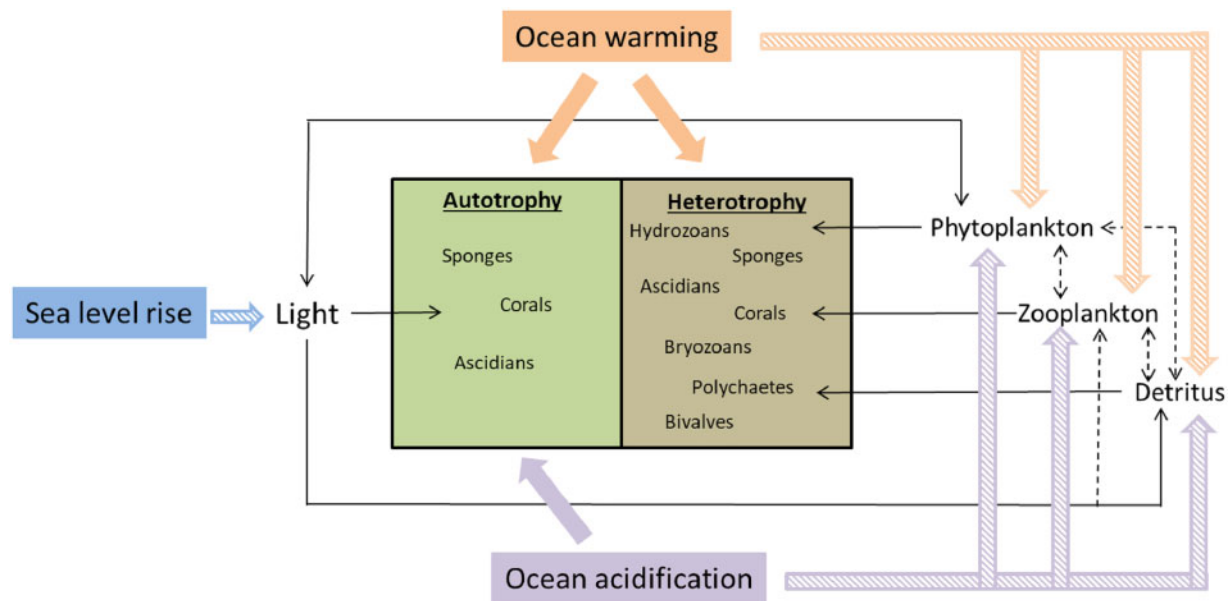
Figure 3. Schematic overview of the abiotic and biotic factors that have a direct (filled and black arrows) or indirect impact (stripped and broken line arrows) on the autotrophic and/or heterotrophic energy input of MAF-forming organisms.

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, and also their role as an essential part of the biogeochemical cycles. In general, the future soft bottoms are expected to favour 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 in pH, increase in turbidity and sedimentation in coastal waters, increase in seawater temperature) favours 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 vs. heterotrophic contributions to the host's energy budget may be a key to understand why they are becoming dominant under certain circumstances (Fabricius and Klumpp, 1995; Ramsby *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 harbour 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 (Kahng *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 (Kahng *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 mixo-trophic scleractinian corals (Sinniger et al., 2013) that may be less resilient than shallow reefs, considering the increase in 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, octo-corals, sponges, and black corals) are more common in the deeper zone (70–150 m depth) (Semmler et al., 2017). The benthic spe-cies 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 strat-egies 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 and Roberts, 2017), the particulate flux could decrease in some areas by up to 55% (Sweetman et al., 2017), probably altering 80% of the communi-ties. In the deep sea floor, were the POC flux may be limited (1–2 g C m^{-2} year^{-1}; Watling et al., 2013), a reduction of available or-ganic 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 produc-tivity, 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 have also 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, and 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 en-ergy 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, oc-curred due to anomalous high sea surface temperatures, and wa-ter 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, and 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 spe-cies 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 tro-phic 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 stor-age, 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 with faster metabolic activity (Munday et al., 2009), which depends on the amount of energy stored in the offspring. The source of this en-ergy is the mother colony or individual that will invest such mac-romolecules 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, >60% of studied species in aquatic systems have responded to ocean warming by advancing their reproductive phenology (Greve et al., 2005; Poloczanska et al., 2016). Since re-productive 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 phe-nological shifts can reduce reproductive success of species and af-fect 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 con-centration 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 favourable 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 in temperature (Rossi et al., 2019). Despite the potential severe consequences of the undermining of repro-ductive success for the long-term persistence of species popula-tions, 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.*, 2016).

Larval nutritional condition and species phenology will affect the potential seascape composition in a near future, (e.g. decades), but population connectivity has also to be 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. This is important because it implies a higher concentration of larvae in smaller areas and a significant decrease in connectivity in certain zones 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 have to consider all the aforementioned 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 ~30% of greenhouse atmospheric carbon removed by the oceans (Le Quéré *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 floors 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 aforementioned 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 MAF 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.

References
Adjeroud, M., Kayal, M., and Penin, L. 2017. Importance of recruitment processes in the dynamics and resilience of coral reef assemblages. *In* Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 549–570. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Adloff, F., Somot, S., Sevault, F., Jordà, G., Aznar, R., Déqué, M., and Herrmann, M. 2015. Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. Climate Dynamics, 45: 2775–2802.

Airoldi, L., and Beck, M. W. 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanography and Marine Biology, 45: 345–405.

Andrello, M., Mouillot, D., Somot, S., Thuiller, W., and Manel, S. 2015. Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. Diversity and Distributions, 21: 139–150.

Arias-Ortiz, A., Serrano, O., Masqué, P., Lavery, P. S., Mueller, U., Kendrick, G. A., and Rozaimi, M. 2018. A marine heatwave drives massive losses from the world's largest seagrass carbon stocks. Nature Climate Change, 8: 338.

Bar-On, Y. M., Phillips, R., and Milo, R. 2018. The biomass distribution on Earth. Proceedings of the National Academy of Sciences of the United States of America, 115: 6506–6511.

Bell, J. J., Davy, S. K., Jones, T., Taylor, M. W., and Webster, N. S. 2013. Could some coral reefs become sponges reefs as our climate changes? Global Change Biology, 19: 2613–2624.

Berggren, A.-M., Beer, J., Possnert, G., Aldahan, A., Kubik, P., Christl, M., Johnsen, S. J. et al. 2009. A 600-year annual 10Be record from the NGRIP ice core, Greenland. Geophysical Research Letters, 36: 1–5.

Bianchi, C. N. 2007. Biodiversity issues for the forthcoming tropical Mediterranean Sea. Hydrobiologia, 580: 7.

Bianchi, C. N., Morri, C., Lasagna, R., Montefalcone, M., Gatti, G., Parravicini, V., and Rovere, A. 2017. Resilience of the marine animal forest: lessons from Maldivian coral reefs after the mass mortality of 1998. In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 1241–1269. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., and Halloran, P. 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. Biogeosciences, 10: 6225–6245.

Borghini, M., Bryden, H., Schroeder, K., Sparnocchia, S., and Vetrano, A. 2014. The Mediterranean is becoming saltier. Ocean Science, 10: 693–700.

Breitburg, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., and Garçon, V. 2018. Declining oxygen in the global ocean and coastal waters. Science, 359: eaam7240.

Brewer, P. G., and Peltzer, E. T. 2017. Depth perception: the need to report ocean biogeochemical rates as functions of temperature, not depth. Philosophical Transactions of the Royal Society A, 375: 20160319.

Brochier, T., Echevin, V., Tam, J., Chaigneau, A., Goubanova, K., and Bertrand, A. 2013. Climate change scenarios experiments predict a future reduction in small pelagic fish recruitment in the Humboldt Current system. Global Change Biology, 19: 1841–1853.

Brümmer, F., Pfannkuchen, M., Baltz, A., Hauser, T., and Thiel, V. 2008. Light inside sponges. Journal of Experimental Marine Biology and Ecology, 367: 61–64.

Büscher, J. V., Form, A. U., and Riebesell, U. 2017. Interactive effects of ocean acidification and warming on growth, fitness and survival of the cold-water coral Lophelia pertusa under different food availabilities. Frontiers in Marine Science, 4: 101.

Caesar, L., Rahmstorf, S., Robinson, A., Feulner, G., and Saba, V. 2018. Observed fingerprint of a weakening Atlantic Ocean overturning circulation. Nature, 556: 191.

Cárdenas, C. A., and Montiel, A. 2017. Coexistence in cold waters: animal forests in seaweed-dominated habitats in Southern high-latitudes. In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 257–276. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Caron, D. A. 2016. Mixotrophy stirs up our understanding of marine food webs. Proceedings of the National Academy of Sciences of the United States of America, 113: 2806–2808.

Castillo, K. D., Ries, J. B., Bruno, J. F., and Westfield, I. T. 2014. The reef building coral Siderastrea siderea exhibits parabolic responses to ocean acidification and warming. Proceedings of the Royal Society of London. Series B, Biological Science, 281: 20141856.

Chust, G., Allen, J. I., Bopp, L., Schrum, C., Holt, J., Tsiaras, K., Zavatarelli, M. et al. 2014. Biomass changes and trophic amplification of plankton in a warmer ocean. Global Change Biology, 20: 2124–2139.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series, 210: 223–253.

Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W. W. L., Christensen, V., Karpouzi, V. S. et al. 2012. The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. Global Ecology and Biogeography, 21: 465–480.

Comeau, S., and Cornwall, C. E. 2017. Contrasting effects of ocean acidification on coral reef "animal forests" versus seaweed "kelp forests". In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 1083–1108. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Cornwall, C. E., Comeau, S., and McCulloch, M. T. 2017. Coralline algae elevate pH at the site of calcification under ocean acidification. Global Change Biology, 23: 4245–4256.

Cruz, I. C. S., Meira, V. H., de Kikuchi, R. K. P., and Creed, J. C. 2016. The role of competition in the phase shift to dominance of the zoanthid Palythoa cf. variabilis on coral reefs. Marine Environmental Research, 115: 28–35.

Curry, R., Dickson, B., and Yashayaev, I. 2003. A change in the freshwater balance of the Atlantic Ocean over the past four decades. Nature, 426: 826–829.

D'Alelio, D., Libralato, S., Wyatt, T., and Ribera d'Alcalà, M. 2016. Ecological-network models link diversity, structure and function in the plankton food-web. Scientific Reports, 6: 21806.

Danovaro, R., Dell'Anno, A., Corinaldesi, C., Magagnini, M., Noble, R., Tamburini, C., and Weinbauer, M. 2008. Major viral impact on the functioning of benthic deep-sea ecosystems. Nature, 454: 1084–1088.

Daufresne, M., Lengfellner, K., and Sommer, U. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences of the United States of America, 106: 12788–12793.

De Clippele, L. H., Huvenne, V. A. I., Orejas, C., Lundälv, T., Fox, A., Hennige, S. J., and Roberts, J. M. 2018. The effect of local hydrodynamics on the spatial extent and morphology of cold-water coral habitats at Tisler Reef, Norway. Coral Reefs, 37: 253–266.

DeVries, T., Le Quéré, C., Andrews, O., Berthet, S., Hauck, J., Ilyina, T., Landschützer, P. et al. 2019. Decadal trends in the ocean carbon sink. Proceedings of the National Academy of Science, 116: 11646–11651.

Di Camillo, C. G., Bavestrello, G., Cerrano, C., Gravili, C., Piraino, S., Puce, S., and Boero, F. 2017. Hydroids (Cnidaria, Hydrozoa): a neglected component of animal forests. In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 397–428. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Doney, S. C. 2006. Oceanography: plankton in a warmer world. Nature, 444: 695.

Duarte, B., Martins, I., Rosa, R., Matos, A. R., Roleda, M. Y., Reusch, T. B. H., Engelen, A. H. et al. 2018. Climate change impacts on seagrass meadows and macroalgal forests: an integrative perspective on acclimation and adaptation potential. Frontiers in Marine Science, 5: 190.

Edmunds, P. J. 2011. Zooplanktivory ameliorates the effects of ocean acidification on the reef coral Porites spp. Limnology and Oceanography, 56: 2402–2410.

Edwards, M., and Richardson, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature, 430: 881.

Enríquez, S., Méndez, E. R., and Iglesias-Prieto, R. 2005. Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnology and Oceanography, 50: 1025–1032.

Fabricius, K. E., and Klumpp, D. W. 1995. Widespread mixotrophy in reef-inhabiting soft corals: the influence of depth, and colony expansion and contraction on photosynthesis. Marine Ecology Progress Series, 125: 195–204.

Fanelli, E., Cartes, J. E., Papiol, V., and López-Pérez, C. 2013. Environmental drivers of megafaunal assemblage composition and biomass distribution over mainland and insular slopes of the Balearic Basin (Western Mediterranean). Deep-Sea Research Part I: Oceanographic Research Papers, 78: 79–94.

Forrest, J., and Miller-Rushing, A. J. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365: 3101–3112.

Galli, G., Bramanti, L., Priori, C., Rossi, S., Santangelo, G., Tsounis, G., and Solidoro, C. 2016. Modelling red coral (*Corallium rubrum*) growth in response to temperature and nutrition. Ecological Modeling, 337: 137–148.

Galli, G., Solidoro, C., and Lovato, T. 2017. Marine heat waves hazard 3D maps and the risk for low motility organisms in a warming Mediterranean Sea. Frontiers in Marine Science, 4: 136.

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D. et al. 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Global Change Biology, 15: 1090–1103.

Gili, J. M., and Coma, R. 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends in Ecology & Evolution, 13: 316–321.

Gooday, A. J., Bett, B. J., Escobar, E., Ingole, B., Levin, L. A., Neira, C., Raman, A. V. et al. 2010. Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. Marine Ecology, 31: 125–147.

Gori, A., Linares, C., Viladrich, N., Clavero, A., Orejas, C., Fiorillo, I., Ambroso, S. et al. 2013. Effects of food availability on the sexual reproduction and biochemical composition of the Mediterranean gorgonian *Paramuricea clavata*. Journal of Experimental Marine Biology and Ecology, 444: 38–45.

Greve, M., Gremmen, N. J., Gaston, K. J., and Chown, S. L. 2005. Nestedness of Southern Ocean island biotas: ecological perspectives on a biogeographical conundrum. Journal of Biogeography, 32: 155–168.

Griffiths, J. R., Kadin, M., Nascimento, F. J. A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E. et al. 2017. The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. Global Change Biology, 23: 2179–2196.

Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Darzi, Y. et al. 2016. Plankton networks driving carbon export in the oligotrophic ocean. Nature, 532: 465.

Gutt, J., Cummings, V., Dayton, P., Isla, E., Jentsch, A., and Schiapparelle, S. 2017. Antarctic marine animal forests: three-dimensional communities in Southern Ocean ecosystems. *In* Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 315–344. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., Lowndes, J. S. et al. 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications, 6: 7615.

Harasti, D. 2016. Declining seahorse populations linked to loss of essential marine habitats. Marine Ecology Progress Series, 546: 173–181.

Harvey, L. D. 2004. Declining temporal effectiveness of carbon sequestration: implications for compliance with the United National Framework Convention on Climate Change. Climatic Change, 63: 259–290.

Henry, L. A., and Roberts, J. M. 2017. Global biodiversity in cold-water coral reefs ecosystems. *In* Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 235–256. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Henson, S., Cole, H., Beaulieu, C., and Yool, A. 2013. The impact of global warming on seasonality of ocean primary production. Biogeosciences, 10: 4357–4369.

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A. et al. 2018. Chapter 3: impacts of 1.5°C global warming on natural and human systems. *In* Global Warming of 1.5°C an IPCC Special Report on the Impacts of Global Warming of 1.5°C Above Pre-industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change. Intergovernmental Panel on Climate Change. 243 pp.

Houlbrèque, F., and Ferrier-Pagès, C. 2009. Heterotrophy in tropical scleractinian corals. Biological Reviews, 84: 1–17.

Howes, E. L., Joos, F., Eakin, M., and Gattuso, J. P. 2015. An updated synthesis of the observed and projected impacts of climate change on the chemical, physical and biological processes in the oceans. Frontiers in Marine Science, 2: 36.

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., Baird, A. H. et al. 2018a. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science, 359: 80–83.

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J. et al. 2017. Coral reefs in the Anthropocene. Nature, 546: 82.

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., Heron, S. F. et al. 2018b. Global warming transforms coral reef assemblages. Nature, 556: 492–496.

IPCC. 2018. Summary for Policymakers. *In*: Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global Warming of 1.5°C Above Pre-industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty, Ed. by Masson-Delmotte V., Zhai P., Pörtner H. O., Roberts D., Skea J., Shukla P. R., Pirani A. et al. World Meteorological Organization, Geneva, Switzerland. 32 pp.

Jackson, J. B. C. 2001. What was natural in the coastal oceans? Proceedings of the National Academy of Sciences of the United States of America, 98: 5411–5418.

Jones, D. O. B., Yool, A., Wei, C.-L., Henson, S. A., Ruhl, H. A., Watson, R. A., and Gehlen, M. 2014. Global reductions in seafloor biomass in response to climate change. Global Change Biology, 20: 1861–1872.

Kahng, S., Copus, J. M., and Wagner, D. 2017. Mesophotic coral ecosystems. *In* Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 855–886. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Keil, R. 2017. Anthropogenic forcing of carbonate and organic carbon preservation in marine sediments. Annual Review of Marine Science, 9: 151–172.

Keil, R. G., Neibauer, J. A., Biladeau, C., van der Elst, K., and Devol, A. H. 2016. A multiproxy approach to understanding the "enhanced" flux of organic matter through the oxygen-deficient waters of the Arabian Sea. Biogeosciences, 13: 2077–2092.

Kuhnz, L. A., Ruhl, H. A., Huffard, C. L., and Smith, K. L. Jr 2014. Rapid changes and long-term cycles in the benthic megafaunal community observed over 24 years in the abyssal northeast Pacific. Progress in Oceanography, 124: 1–11.

Ladd, M. C., Shantz, A. A., and Burkepile, D. E. 2019. Newly dominant benthic invertebrates reshape competitive networks on contemporary Caribbean reefs. Coral Reefs, doi:10.1007/s00338-019-01832-6.

Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., Buitenhuis, E. et al. 2015. Drivers and uncertainties of future global marine primary production in marine ecosystem models. Biogeosciences, 12: 6955–6984.

Lazzari, P., Mattia, G., Solidoro, C., Salon, S., Crise, A., Zavatarelli, M., Oddo, P. et al. 2014. The impacts of climate change and environmental management policies on the trophic regimes in the Mediterranean Sea: scenario analyses. Journal of Marine Systems, 135: 137–149.

Learmonth, J. A., MacLeod, C. D., Santos, M. B., Pierce, G. J., Crick, H. Q. P., and Robinson, R. A. 2006. Potential effects of climate

change on marine mammals. Oceanography and Marine Biology, 44: 431.

Lenz, E. A., Bramanti, L., Lasker, H. R., and Edmunds, P. J. 2015. Long-term variation of octocoral populations in St. John, US Virgin Islands. Coral Reefs, 34: 1099–1109.

Le Quéré, C., Andres, R. J., Boden, T., Conway, T., Houghton, R. A., House, J. I., Marland, G. et al. 2013. The global carbon budget 1959–2011. Earth System Science Data, 5: 165–185.

Libralato, S., Caccin, A., and Pranovi, F. 2015. Modeling species invasions using thermal and trophic niche dynamics under climate change. Frontiers in Marine Science, 2: 29.

Marbà, N., Jordà, G., Agustí, S., Girard, C., and Duarte, C. M. 2015. Footprints of climate change on Mediterranean Sea biota. Frontiers in Marine Science, 2: 56.

Maxwell, P. S., Eklöf, J. S., van Katwijk, M. M., O'brien, K. R., de la Torre-Castro, M., Boström, C., Bouma, T. J. et al. 2017. The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems—a review. Biological Reviews, 92: 1521–1538.

Milisenda, G., Vitale, S., Massi, D., Enea, M., Gancitano, V., Giusto, G. B., Badalucco, C. et al. 2017. Spatio-temporal composition of discard associated with the deep water rose shrimp fisheries (Parapenaeus longirostris, Lucas 1846) in the south-central Mediterranean Sea. Mediterranean Marine Science, 18: 53–63.

Morgan, K. M., Perry, C. T., Smithers, S. G., Johnson, J. A., and Daniell, J. J. 2016. Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings. Scientific Reports, 6: 29616.

Munday, P. L., Leis, J. M., Lough, J. M., Paris, C. B., Kingsford, M. J., Berumen, M. L., and Lambrechts, J. 2009. Climate change and coral reef connectivity. Coral Reefs, 28: 379–395.

Norström, A. V., Nyström, M., Lokrantz, J., and Folke, C. 2009. Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Marine Ecology Progress Series, 376: 295–306.

Orejas, C., and Jiménez, C. 2017. The builders of the oceans—Part I: coral architecture from the tropic to the poles, from shallow to deep. In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 627–656. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology, 13: 1860–1872.

Perry, C. T., Alvarez-Filip, L., Graham, N. A. J., Mumby, P. J., Wilson, S. K., Kench, P. S., Manzello, D. P. et al. 2018. Loss of coral reef growth capacity to track future increases in sea level. Nature, 558: 396.

Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V. et al. 2016. Responses of marine organisms to climate change across oceans. Frontiers in Marine Science, 3: 62.

Puig, P., Canals, M., Company, J. B., Martín, J., Amblas, D., Lastras, G., and Palanques, A. 2012. Ploughing the deep sea floor. Nature, 489: 286–289.

Puseddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., and Danovaro, R. 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proceedings of the National Academy of Sciences of the United States of America, 111: 8861–8866.

Ramsby, B. D., Shirur, K. P., Iglesias-Prieto, R., and Goulet, T. L. 2014. Symbiodinium photosynthesis in Caribbean octocorals. PLoS One, 9: e106419.

Reay, D. S., Dentener, F., Smith, P., Grace, J., and Feely, R. A. 2008. Global nitrogen deposition and carbon sinks. Nature Geoscience, 1: 430–431.

Richardson, A. J., and Schoeman, D. S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science, 305: 1609–1612.

Rixen, M., Beckers, J.-M., Levitus, S., Antonov, J., Boyer, T., Maillard, C., Fichaut, M. et al. 2005. The Western Mediterranean Deep Water: a proxy for climate change. Geophysical Research Letters, 32: 1–4.

Rizzo, L., Pusceddu, A., Stabili, L., Alifano, P., and Fraschetti, S. 2017. Potential effects of an invasive seaweed (Caulerpa cylindracea, Sonder) on sedimentary organic matter and microbial metabolic activities. Scientific Reports, 7: 12113.

Rocha, L. A., Pinheiro, H. T., Shepherd, B., Papastamatiou, Y. P., Luiz, O. J., Pyle, R. L., and Bongaerts, P. 2018. Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. Science, 361: 281–284.

Rossi, S. 2013. The destruction of the 'animal forests' in the oceans: towards an over-simplification of the benthic ecosystems. Ocean & Coastal Management, 84: 77–85.

Rossi, S., Bramanti, L., Gori, A., and Orejas, C. 2017a. An overview of the animal forests of the world. In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 1–28. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Rossi, S., Coppari, M., and Viladrich, N. 2017b. Benthic–pelagic coupling: new perspectives in the animal forests. In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 855–886. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Rossi, S., and Gili, J. M. 2009. Near bottom phytoplankton and seston: importance in the pelagic–benthic coupling processes. In Marine Phytoplankton, pp. 45–85. Ed. by W. T. Kersey and S. P. Munger Nova Science Publishers, Inc., New York.

Rossi, S., Gili, J. M., Coma, R., Linares, C., Gori, A., and Vert, N. 2006. Temporal variation in protein, carbohydrate, and lipid concentrations in Paramuricea clavata (Anthozoa, Octocorallia): evidence for summer–autumn feeding constraints. Marine Biology, 149: 643–651.

Rossi, S., Gravili, C., Milisenda, G., Bosch-Belmar, M., De Vito, D., and Piraino, S. 2019 Effects of global warming on reproduction and potential dispersal of Mediterranean cnidarians. The European Zoological Journal, 86: 255–271.

Rossi, S., Schubert, N., Brown, D., Soares, M., Grosso, V., Rangel-Huerta, E., and Maldonado, E. 2018. Linking host morphology and symbiont performance in octocorals. Scientific Reports, 8: 12823.

Roth, M. S. 2014. The engine of the reef: photobiology of the coral–algal symbiosis. Frontiers in Microbiology, 5, 422.

Roughgarden, J., Gilbert, S. F., Rosenberg, E., Zilber-Rosenberg, I., and Lloyd, E. A. 2018. Holobionts as units of selection and a model of their population dynamics and evolution. Biological Theory, 13: 44–65.

Roxy, M. K., Modi, A., Murtugudde, R., Valsala, V., Panickal, S., Prasanna Kumar, S., Ravichandran, M. et al. 2016. A reduction in marine primary productivity driven by ràpid warming over the tropical Indian Ocean. Geophysical Research Letters, 43: 826–833.

Ruzicka, R. R., Colella, M. A., Porter, J. W., Morrison, J. M., Kidney, J. A., Brinkhuis, V., Lunz, K. S. et al. 2013. Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. Marine Ecology Progress Series, 489: 125–141.

Sanders, D., and Baron-Szabo, R. C. 2005. Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. Palaeo3, 216: 139–181.

Schaper, S. V., Dawson, A., Sharp, P. J., Caro, S. P., and Visser, M. E. 2012. Individual variation in avian reproductive physiology does not reliably predict variation in laying date. General and Comparative Endocrinology, 179: 53–62.

Schubert, N., Brown, D., and Rossi, S. 2017. Symbiotic versus asymbiotic octocorals: physiological and ecological implications.

In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 887–918. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Semmler, R. F., Hoot, W. C., and Reaka, M. L. 2017. Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs? Coral Reefs, 36: 433–444.

Shlesinger, T., Grinblat, M., Rapuano, H., Amit, T., and Loya, Y. 2018. Can mesophotic reefs replenish shallow reefs? Reduced coral reproductive performance casts a doubt. Ecology, 99: 421–437.

Sinniger, F., Morita, M., and Harii, S. 2013. "Locally extinct" coral species *Seriatopora hystrix* found at upper mesophotic depths in Okinawa. Coral Reefs, 32: 153.

Smetacek, V., and Cloern, J. E. 2008. On phytoplankton trends. Science, 319: 1346–1348.

Soares, M. O., Tavares, T. L., and Carneiro, P. B. M. 2019. Mesophotic ecosystems: distribution, impacts, and conservation in the South Atlantic. Diversity and Distributions, 25: 255–268.

Steffen, W., Rockström, J., Richardson, K., Lenton, T. M., Folke, C., Liverman, D., Summerhayes, C. P. *et al.* 2018. Trajectories of the Earth System in the Anthropocene. Proceedings of the National Academy of Sciences of the United States of America, 115: 8252–8259.

Steinacher, M., Joos, F., Frölicher, T. L., Bopp, L., Cadule, P., Cocco, V., Doney, S. C. *et al.* 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. Biogeosciences, 7: 979–1005.

Storlazzi, C. D., Elias, E., Field, M. E., and Presto, M. K. 2011. Numerical modeling of the impact of sea-level rise on fringing coral reef hydrodynamics and sediment transport. Coral Reefs, 30: 83–96.

Sweetman, A. K., Thurber, A. R., Smith, C. R., Levin, L. A., Mora, C., Wei, C.-L., Gooday, A. J. *et al.* 2017. Major impacts of climate change on deep-sea benthic ecosystems. Elementa: Science of the Anthropocene, 5: 4.

Taviani, M., Angeletti, L., Beuck, L., Campiani, E., Canese, S., Foglini, F., Freiwald, A. *et al.* 2016. Reprint of 'On and off the beaten track: megafaunal sessile life and Adriatic cascading processes'. Marine Geology, 375: 146–160.

Thrush, S. F., and Dayton, P. K. 2002. Disturbance to marine habitats by trawling and dredging: implications for marine biodiversity. Annual Review of Ecology, Evolution, and Systematics, 33: 449–473.

Thurstan, R. H., Pandolfi, J. M., and zu Ermgassen, P. S. 2017. Animal forests through time: historical data to understand present changes in marine ecosystems. *In* Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 947–964. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer, Germany.

Towle, E. K., Enochs, I. C., and Langdon, C. 2015. Threatened Caribbean coral is able to mitigate the adverse effects of ocean acidification on calcification by increasing feeding rate. PLoS One, 10: e0123394.

Turner, S. J., Thrush, S. F., Hewitt, J. E., Cummings, V. J., and Funnell, G. 1999. Fishing impacts and the degradation or loss of habitat structure. Fisheries Management and Ecology, 6: 401–420.

Unsworth, R. K. F., Ambo-Rappe, R., Jones, B. L., La Nafie, Y. A., Irawan, A., Hernawan, U. E., Moore, A. M. *et al.* 2018. Indonesia's globally significant seagrass meadows are under widespread threat. Science of the Total Environment, 634: 279–286.

Vargas-Yáñez, M., García-Martínez, M. C., Moya, F., Balbín, R., López-Jurado, J. L., Serra, M., Zunino, P. *et al.* 2017. Updating temperature and salinity mean values and trends in the Western Mediterranean: the RADMED project. Progress in Oceanography, 157: 27–46.

Vargas-Yáñez, M., Moya, F., García-Martínez, M. C., Tel, E., Zunino, P., Plaza, F., Salat, J. *et al.* 2010. Climate change in the Western Mediterranean Sea 1900–2008. Journal of Marine Systems, 82: 171–176.

Vargas-Yáñez, M., and Sabatés, A. 2007. Mesoscale high-frequency variability in the Alboran Sea and its influence on fish larvae distributions. Journal of Marine Systems, 68: 421–438.

Veron, J. E. N., Hoegh-Guldberg, O., Lenton, T. M., Lough, J. M., Obura, D. O., Pearce-Kelly, P., Sheppard, C. R. C. *et al.* 2009. The coral reef crisis: the critical importance of <350 ppm CO_2. Marine Pollution Bulletin, 58: 1428–1436.

Viola, F., Francipane, A., Caracciolo, D., Pumo, D., La Loggia, G., and Noto, L. V. 2016. Co-evolution of hydrological components under climate change scenarios in the Mediterranean area. Science of the Total Environment, 544: 515–524.

Watling, L., Guinotte, J., Clark, M. R., and Smith, C. R. 2013. A proposed biogeography of the deep ocean floor. Progress in Oceanography, 111: 91–112.

Watling, L., and Norse, E. A. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conservation Biology, 12: 1180–1197.

Watson, J. R., Siegel, D. A., Kendall, B. E., Mitarai, S., Rassweiller, A., and Gaines, S. D. 2011. Identifying critical regions in small-world marine metapopulations. Proceedings of the National Academy of Sciences of the United States of America, 108: E907–913.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C. *et al.* 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314: 787–790.

Yesson, C., Fisher, J., Gorham, T., Turner, C. J., Hammeken Arboe, N., Blicher, M. E., and Kemp, K. M. 2017. The impact of trawling on the epi-benthic megafauna of the west Greenland shelf. ICES Journal of Marine Science, 74: 866–876.

Handling editor: Marta Coll