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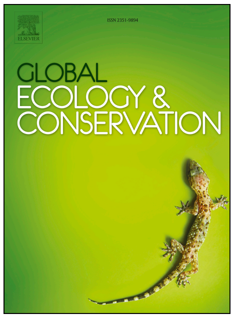

Ecological connectivity across ocean depths: Implications for protected area design

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Ecological connectivity across ocean depths: implications for protected area design

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Abstract

Coastal nations have embarked on a rapid program of marine protected area (MPA) establishment, incentivised by the approaching 2020 deadline of United Nations global marine protection targets. Alongside, efforts are underway to extend protection into areas beyond national jurisdiction through a new international legally binding instrument. These developments are welcome but there are risks that in meeting them, nations will still fail to supply adequate protection to marine life. An increasing number of MPAs protect the seabed while the water column remains open to fishing. This is because vulnerable habitats in need of protection are disproportionately perceived to be those on the seabed, while the water column is viewed as much less at risk. The seabed and water column are, however, inextricably linked. Transitions between human-defined vertical ocean zones are blurred, with animals and oceanographic features moving across depths. Here, we explore a rapidly growing literature on ecological and environmental connections through the water column, and between the water column and the seabed, to consider whether vertically stratified management is justified from an ecological standpoint. We find that emerging research increasingly links upper-ocean communities and processes to seabed ecology and biogeochemistry suggesting that exploitation of the water column is likely to have a significant and widely distributed footprint in the deep-sea. We conclude that there is a strong a priori case for surface to seabed protection within MPAs, and that this should be the default, precautionary approach to safeguard intact ecosystems with as near to natural function as possible.

Highlights

- Despite rapid expansion of MPAs nations may still fail to adequately protect oceans
- Seabed habitats are frequently protected without overlying waters
- Evidence increasingly links upper-ocean life to seabed ecology and biogeochemistry
- Pelagic exploitation likely has a widely distributed footprint in the deep-sea
- Open ocean MPAs should, by default, incorporate surface to seabed protection

Keywords

Areas beyond national jurisdiction; Convention on Biological Diversity; High seas; Marine protected areas; Pelagic-benthic coupling; Sustainable Development Goal 14

1 Introduction

Two major developments are underway in the world of marine conservation. First, following adoption into Sustainable Development Goal 14 (United Nations 2015) of the Convention on Biological Diversity's target for ≥10% ocean protection by 2020 (Convention on Biological Diversity 2010), there is renewed impetus to meet this target. Coastal nations of the world are embarked on a rapid program of marine protected area (MPA) establishment that at last looks set to achieve this coverage target (Convention on Biological Diversity 2017), following nearly two decades of slow progress (O'Leary et al. 2018). The second, is that a process has been underway at the United Nations for more than two years to negotiate a mechanism to create MPAs in areas beyond national jurisdiction, amongst other conservation measures (UNGA 2015). This shared ocean space constitutes approximately 61% of the oceans, 44% of the surface of the Earth and 65% of the volume of the biosphere but remains the least protected space on the planet (Gjerde et al. 2016). After a promising start, the process looks set to produce a legal instrument within the next two years, following a conference of the UN General Assembly.

These developments are welcome but there are real risks that in meeting them, nations will still fail to offer adequate protection to the sea. Ecological science is clear that the most effective protected areas are those fully protected from exploitation and other mitigable sources of human harm (e.g. Edgar et al. 2014; Giakoumi et al. 2017; Gill et al. 2017). But from a socio-political perspective, the easiest protected areas to establish are those where protection is weak and impose few alterations to existing patterns of use. Many MPAs offer little, to no, real protection (Costello and Ballantine 2015). This is a particular risk when it comes to protection of the open sea, which constitutes much of areas beyond national jurisdiction.

In the open ocean, vulnerable habitats in need of protection are disproportionately perceived to be those on the seabed, especially the deep-sea because of the visibility of direct impacts from fishing and awareness of lengthy recovery times (Clark et al. 2016; Jones et al. 2017). The water column is seen to be much less at risk, a judgement based on the absence of fixed habitat structures that fishing gears might damage (Fitzsimons and Wescott 2008; Grober-Dunsmore et al. 2008). Indeed, arguments are often made that there is little point in water column protection due to the mobility of the organisms that inhabit it (Game et al. 2009).

The net outcome of these viewpoints, is that an increasing number of protected areas, including many of a recent wave of large-scale MPAs (O'Leary et al. 2018), offer protection to the seabed while the water column remains open to fishing (Costello and Ballantine 2015). The Australian government has gone so far as to re-zone their national MPA system, previously held up as a global exemplar of best practice, opening a further 17% (≥350 000 km^2) to commercial fishing, removing much protection from the water column (Australian Government 2018).

Here we explore a rapidly growing literature on ecological and environmental connections through the water column, and between the water column and the seabed, to inform our perspective on whether vertically stratified management is justified from an ecological standpoint. We argue that while we have imperfect knowledge, we know enough to be sure that the greatest ecological benefits are achieved through full protection of MPAs and that fishing the water column will erode those benefits. Continued adoption of vertical zonation and partial protection will mean that MPAs fail to adequately conserve marine life or secure the goods and services provided by the oceans.

2 Ecological connectivity between surface and seabed ecosystems

Seabed and water column communities are often considered separately. Emphasising this distinction, scientists divide the open ocean into a series of realms based on depth: epipelagic (0-200 m), mesopelagic (200-1 000 m), bathypelagic (1 000-4 000 m), abyssopelagic (4 000 m to directly above the ocean floor) and hadopelagic (ocean water in submarine trenches). However, this vertical classification is a convenience and an oversimplification. Different depths are linked through a wide variety of mechanisms including energy production and transfer in food webs, cycling of nutrients and raw materials, shifts in habitat use as creatures develop and grow, and daily and seasonal vertical migrations (Arellano et al. 2014; Davison et al. 2013; Howey et al. 2016; Nakamura and Sato 2014). The transitions between these human-conceived vertical layers are gradients, not sharp boundaries, and ecological distinctions are blurred with ocean currents and animals connecting the various depths.

2.1 Food-web interactions and surface to seabed relationships

There are many well-known examples of linkages between seabed and water column ecosystems, particularly in coastal regions, that illustrate how disruptions affect ecosystem structure, function and provision of services. For example, sea otter loss led to the decline of kelp-forest plants due to reduced predation by otters on herbivores (Estes et al. 2011). Loss of grazing parrotfish can reduce the resilience of coral reefs to bleaching events and storms through seaweed overgrowth of dead coral (Mumby 2009). Overfishing of apex predators has led to increased abundance of mid-trophic level fishes (Ferretti et al. 2010; Polovina et al. 2009) and changes to entire fish communities (Daskalov et al. 2007; Ellingsen et al. 2015). Less evidence of such connections exists for open water ecosystems, although control of surface productivity by predators has been demonstrated which, by inference, will affect ecosystems from the surface to the seabed (Box 1).

Deep-sea fauna ultimately rely for food on primary productivity in the epipelagic realm sinking to the seafloor, or being shuttled by animal movements, with the exception of some chemosynthetic communities on, for example, hydrothermal vents (Drazen and Sutton 2017; Smith et al. 2008; Stasko et al. 2016; Trueman et al. 2014). With increasing depth there is an associated decrease in food supply (Buesseler et al. 2007). Open water ecosystems therefore subsidise deep-sea and seabed habitats with detritus, nutrients and prey, increasing the productivity of the latter (Mauchline and Gordon 1991; Trueman et al. 2014) (Box 1). Energy transfer between seabed ecosystems and water column habitats may also be driven from seabed habitats such as hydrothermal vents, cold-water coral reefs, and seamounts. Hydrothermal vents – deep water hot springs – eject chemical rich plumes that alter the microbial community in the water column, dispersing vertically up to *c*.500 m above and across the seabed, increasing plankton biomass and abundance, thereby enhancing local productivity (Levin et al. 2016). Deep cold-water coral reefs form large mounds (*c*.600 m) in the North Atlantic that have been shown to induce downwelling of surface waters, dragging down organic matter essential for the functioning of these ecosystems (Soetaert et al. 2016). Seamounts can also enhance local productivity through the creation of oceanographic features such as upwellings, eddies, and spiralling water masses called 'Taylor columns'. They drive higher surface productivity and support diverse seabed ecosystems and a wide range of pelagic species including sharks, tunas and billfish (Morato et al. 2010; Watling and Auster 2017).

Taken together, these lines of evidence suggest that recent changes in pelagic systems due to human exploitation and greenhouse gas emissions are likely to have a significant and widely distributed footprint in the deep-sea, based on alterations to levels of productivity, abundance of open water marine life and oceanography (Box 1).

Box 1: Evidence for the relationship between open water habitats and deep-sea species richness and functioning.

The influence on seabed ecosystems of food-web cascades in open water ecosystems have not yet been well studied. However, strong positive relationships have been detected between surface primary productivity and species richness and functioning of deep-sea fish communities in the Mediterranean Sea, off New Zealand, along the west Antarctic Peninsula, and in the east equatorial Pacific (Leathwick et al. 2006; Loubere 1991; Louzao et al. 2017; McClatchie et al. 1997; Smith et al. 2006; Tecchio et al. 2013). Likewise, under the centre of the Ross Ice Shelf where phytoplankton production is prevented by lack of light, there is reduced abundance, diversity, and activity of seabed fauna relative to similar depths in the open Ross Sea (Brunchhausen et al. 1979). The equatorial Pacific and the Southern Ocean abyssal regions (bottom depths of $\geq$3 000 m) are considered hotspots for abyssal biodiversity because they receive relatively high food input from the overlying waters due to elevated surface ocean productivity (Smith et al. 2008). In other places, such as the southwest Ross Sea, only weak associations between seabed fauna and surface primary productivity have been found (Barry et al. 2013), perhaps because ocean currents move organic material laterally to other parts of the seafloor. In the Pacific, for example, by one estimate lateral advection and active flux of particulate organic matter by animals may account for up to 53% of the total flux of carbon at the seafloor (Jahnke et al. 1990). Species richness of deep-sea organisms is greatest at higher latitudes (30-50°) and concentrated in areas of high seasonal surface productivity and high export of particulate organic materials (Weber et al. 2016; Woolley et al. 2016).

The biomass of fish that feed both on organisms that live on the seabed and in the water column increases below 1 000 m and peaks at around 1 500 m depth (Mauchline and Gordon 1991; Sutton et al. 2008; Trueman et al. 2014). Pelagic subsidies, additional resources in the form of nutrients, detritus or prey passed from open water habitat to deep-sea and seabed habitats, are considered key in supporting bottom-associated fish populations, which then transfer nutrients from the water column to the seabed community (Mauchline and Gordon 1991; Trueman et al. 2014). In the North Atlantic, pelagic subsidies transported by vertically migrating animals support up to 50% more biomass of seafloor dwelling fishes than would be predicted based on food web models (Trueman et al. 2014). Depletion of mesopelagic fish by fishing has been predicted to decrease the abundance of deep-sea bottom-living fish through reduced downward transfer of food and increased predation on juvenile demersal fish by piscivorous fish as a consequence of reduced mesopelagic prey (Johnson 2011). Similarly, reduction of mesopelagic fish biomass is predicted to result in population declines across ecosystems (Smith et al. 2011), affecting species including small pelagics, tuna, sharks and marine mammals (Johnson 2011).

While few documented impacts on deep-sea and seabed habitats arising from pelagic fishing in an open ocean environment exist, evidence suggests that depletion of whales by commercial whaling resulted in decreased habitat and nutrient availability in the deep-sea due to fewer dead whale 'falls', as well as changes in food-web structure (O'Leary and Roberts 2017 and references therein). Similarly, reductions by commercial fisheries in the biomass of fish and other marine life that act as conduits for transfer of nutrients and organic matter through the water column would likely have impacts that reverberate through ecosystems (see Box 2).

2.2 Biogeochemical cycling mediated by marine organisms

The ocean acts as a major carbon sink, absorbing atmospheric carbon and trapping it in sediments (Le Quéré et al. 2015). Ocean carbon sequestration is driven by 'pumps' that are physical, i.e. ocean circulation, and biological, i.e. organisms. The biological carbon pump is driven mainly by planktonic photosynthetic organisms (Guidi et al. 2016). Each day, around 100 million tonnes of carbon dioxide are estimated to be fixed into organic material by phytoplankton (Behrenfield et al. 2006). This equates to *c*.50 billion tonnes each year (Westberry et al. 2008), roughly equivalent to annual anthropogenic carbon dioxide emissions in 2010[1]. One-fifth of this is exported to the deep-sea by

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[1] Greenhouse gas emissions were equivalent to *c*.49 gigatonnes of carbon dioxide per year in 2010. IPCC (2014) Summary for Policymakers [online] www.ipcc.ch/pdf/assessment-report/ar5/wg3/ipcc_wg3_ar5_summary-for-policymakers.pdf [accessed August 9th 2017].

the sinking of particles from the surface ocean, although only a fraction of that is buried in deep-sea sediments (Dunne et al. 2007).

Animals can be important mediators of biogeochemical cycles (Box 2). Species which undertake regular movements between upper and deeper waters, such as zooplankton (Turner 2015), mesopelagic fish (Robinson et al. 2010) or deep-diving predators like tuna and sharks (Fuller et al. 2015; Howey et al. 2016) link different depth zones and/or seabed environments. These movements facilitate biogeochemical connections across the water column that promote carbon uptake and storage and thereby affect climate regulation (Giering et al. 2014; Robinson et al. 2010), modify fluxes of nutrients and oxygen in the water column (Bianchi et al. 2013; Hernández-León et al. 2008; Roman et al. 2014; Turner 2015), and help sustain the metabolic requirements of midwater (Bianchi et al. 2013; Burd et al. 2010) and seabed ecosystems (Drazen and Sutton 2017; Trueman et al. 2014).

Long-term data from the Northeast Pacific and the Northeast Atlantic illustrate how variations in climate and upper ocean conditions are linked to variations in deep-sea communities and biogeochemical processes at the sea floor (Smith Jr et al. 2009). For example, the Northern Oscillation Index and the Bakun Upwelling Index in the Pacific were significantly correlated with the flux of particulate organic carbon at 3 500 m depth when lagged by 6 and 2-3 months respectively (Smith Jr et al. 2009). Changes in deep-sea fauna have also been significantly correlated to climatic events in the Pacific when lagged by several months, with smaller animals displaying shorter response times than larger ones (Ruhl and Smith Jr 2004; Smith Jr et al. 2009). Similarly, positive variations in the monthly North Atlantic Oscillation index were linked to increases in the amount of particulate organic carbon reaching 3 000 m, with a lag of 0-3 months, and changes in deep-sea fauna were linked to climate-driven variations in the quantity and composition of sinking organic matter (Smith Jr et al. 2009). These relationships demonstrate strong connections between the intensity of surface primary productivity and carbon flux to the deep-sea. It can therefore be expected that activities that affect open water habitats and the organisms that mediate transfer of production such as fishing (Bailey et al. 2009) and deep-sea mining (Miller et al. 2018), as well as impacts like climate change (Sweetman et al. 2017), will affect deep-sea ecosystems.

Box 2: Role of animals in open ocean biogeochemical cycles

Zooplankton influence carbon flux from the surface to deep-sea through production of fast-sinking fecal pellets and large vertical migrations (Turner 2015) as well as through respiration (Hernández-León and Ikeda 2005). Estimates of the contribution of zooplankton fecal pellets to total particulate carbon export from surface waters to deep waters range from <1% to 100%, although most studies estimate the contribution to be <40%, depending on seasonality, depth, and community composition amongst other factors (Turner 2015). Through vertical migrations, zooplankton also transfer food ingested near the surface to deeper waters in the mesopelagic zone where it becomes available to deep-sea organisms through excretion, respiration or predation (Jónasdóttir et al. 2015; Sutton et al. 2017; Turner 2015). This active flux has been shown to be equivalent to up to 70% of the sinking particulate organic carbon, although typically is reported as being 10-50% of the total vertical flux of carbon downward from surface waters (Turner 2015). Global annual respiration of mesozooplankton (planktonic animals sized 0.2-20 mm such as copepods) across all depth zones of the ocean has been estimated to be between 8.8 and 17.2 billion tonnes of carbon, equivalent to 17-32% of global open ocean primary productivity, although uncertainty in estimates remain (Hernández-León and Ikeda 2005).

The magnitude of nutrient flows through the water column are potentially very large, although they are difficult to measure. For example, excretion by mesozooplankton in the upper 200 m of the oceans has been estimated to account for *c*.1.8±0.6 x 10^{12} kg of nitrogen per year globally – approximately 12-23% of the total global oceanic requirements for phytoplankton and bacterial production (Hernández-León et al. 2008). Conservative estimates suggest the high magnesium calcite crystals that form in the guts of teleost fish and are excreted by them, account for 3-15% of total oceanic carbonate production (Wilson et al. 2009). Less conservative estimates, based on realistic physiological assumptions, place this estimate as high as 45% (Wilson et al. 2009), and recent upward re-evaluation of mesopelagic fish biomass would push this figure even higher (Wilson 2014). In the Northeast Pacific Ocean, export of carbon from the surface 200 m into deeper water, mediated by the vertical migrations of mesopelagic fish, has been estimated as being responsible for 15-17% of total carbon exported to greater depths (Davison et al. 2013). An upward transfer of nutrients is conducted through shallow-water defecation by Southern Ocean sperm whales which transfer *c*.50 tonnes of iron from depth toward the surface annually (Lavery et al. 2010). There the iron supplies a key nutrient for phytoplankton growth, enhancing new primary production and stimulating the net export of 200 000 tonnes of carbon per year to the deep-sea (Lavery et al. 2010). In the Gulf of Maine, 23 000 tonnes of nitrogen are estimated to be replenished into surface waters by whales and seals annually, equating to more than the input of all the region’s rivers combined (Roman and McCarthy 2010). Other large megafauna, such as marine mammals, sharks and tunas feed deep and defecate in shallow waters, also contribute to this upward nutrient pump (e.g. Kiszka et al. 2015; Williams et al. 2018).

Habitats in the open ocean are structured by the animals that live there (O'Leary and Roberts 2017). While we do not know the full extent of interactions between marine life and biogeochemical cycling, the large biomass of life contained in the oceanic mid-waters means their role is likely to be highly significant. Certainly, emerging evidence suggests this is the case. Removing biomass of open water animals through fishing will therefore inevitably have consequences for ecosystem functioning and provision of services, although the full scale of these consequences cannot currently be quantified.

3 Pelagic fishing and its broader ecosystem impacts

The assumption is often made that protection of the seabed can be achieved without protection of overlying waters. Currently, fishing remains the largest direct anthropogenic threat to marine life in open ocean habitats, particularly those in areas beyond national jurisdiction, although other activities such as deep-sea mining are increasingly becoming relevant to this conversation (Kroodsma et al. 2018; Lascelles et al. 2014; Merrie et al. 2014; Miller et al. 2018). Many fishery management closures offer protection to seabed habitats from destructive fishing practices but allow continued fishing within the water column above (e.g. Helson et al. 2010).

In areas beyond national jurisdiction, the UN General Assembly requires closures to bottom fishing of areas containing vulnerable marine ecosystems where significant adverse impacts are likely (Resolution 61/105, 2006). Such closures are often temporary, permit fishing in the water column above, and fail to restrict ongoing fishing activity (Wright et al. 2015). The direct effects of deep-sea bottom trawling on benthic habitats are well known (Clark et al. 2016; Pusceddu et al. 2014), and closures that protect sensitive seabed habitats from damage are essential. However, the influence of pelagic fisheries on seabed communities and habitats is poorly understood.

The above distinctions between protection measures given to the seabed and water column rest on two assumptions: (1) fishing the water column does not adversely affect seabed habitat, and (2) fishing will not disrupt important linkages between ecological processes in the water column and on the seabed. Neither of these assumptions can be strongly justified. Fishing the water column has significant impacts on water column habitat, because the habitat structure is vested in the organisms that live there, which fishing removes (O'Leary and Roberts 2017). The ecological processes and linkages across depth zones and between the water column and seabed that are outlined above, also make it highly likely that fishing the water column will have significant effects on seabed life. Pelagic fisheries typically target large apex predators (e.g. tuna, billfish, sharks) and dramatically reduce their abundance (Ortuño Crespo and Dunn 2017). Pelagic fisheries also adversely impact non-target species caught or killed incidentally (bycatch/bykill), including charismatic species of conservation concern such as sea turtles (Lewison et al. 2014), marine mammals (Read et al. 2006), and sharks (Queiroz et al. 2016), many of which traverse ocean depth zones. Such large reductions will have big effects on species' ecological roles and food web structure, significantly altering the natural functioning and linkages of open ocean ecosystems, including those between the water column and seabed.

Measuring the impacts of pelagic fisheries on open ocean ecosystems is challenging because of their dynamism, heterogeneity, distance from land, and scale (Ortuño Crespo and Dunn 2017). Determining the effect of pelagic fisheries on seabed habitats is therefore difficult, particularly given the lack of research on the impact of fishing below 1 000 m (Ortuño Crespo and Dunn 2017). One of the only studies we know of that has attempted to quantify the effect of deep-sea bottom trawl fisheries, found that changes in overall fish abundance in the northeast Atlantic fell significantly at all depths from 800 m to 2 500 m depth, despite the maximum depth of commercial fisheries being only *c*.1 500 m, and most trawling taking place in <1 000 m depth (Bailey et al. 2009). The deeper reach of fishing impacts was hypothesised to be due to fish moving between different depths across the continental slope during normal activity, and migrations to deeper depths as they age. Given the current sparse state of knowledge regarding the strength and nature of these linkages, it is hard to predict the severity of impacts for any particular location. The default, precautionary position should therefore be to protect the whole of the water column and seabed if the desired conservation goal is to protect entire, intact ecosystems.

Shallow-water and topographically complex habitats, and areas characterised by predictable oceanographic conditions such as upwellings, are often considered to have stronger links between the seabed and water column than surface vs. deeper waters (Grober-Dunsmore et al. 2008). However, this perspective is likely to have developed not because of real biological differences in structure and function, but rather due to a variety of other factors. For example, characterising coupling for deep-sea habitats is challenging because interactions are likely to be indirect, passing through multiple communities at various ocean depths before reaching the deep-sea. Effects to deep-sea ecosystems arising from changes in the pelagic realm are therefore likely to only become evident after a time lag (Smith Jr et al. 2009). Moreover, these patterns may be complicated as changes in the epipelagic realm may not influence the seabed directly below, but further away through the transport of primary production via ocean currents (Thresher et al. 2011). Additionally, organic matter can accumulate in ocean sediments over time which means that deep-sea ecosystems may be buffered from variable food inputs from the water column by the presence of a persistent sediment food bank (Smith et al. 2006) hindering our ability to detect linkages.

Furthermore, deep-sea ecosystems are often considered within research as broad habitat types which likely masks water-column signals in the deep-sea (Smith et al. 2006). A lack of long-term monitoring programmes (Henson 2014), particularly in these data-poor environments, hinder our ability to accurately describe and measure connections between pelagic and seabed communities, and there is a need for more interdisciplinary research considering the interactions between biological and physical components of habitats from the seabed to sea-surface.

4 Implications for protected area design

While so far less affected by human influences than coastal regions, waters of the open ocean are under increasing human influence and threat (Halpern et al. 2015; Kroodsma et al. 2018). Open ocean megafauna, such as sea turtles and sharks (Lascelles et al. 2014) are in steep decline and protection is urgent and must proceed without full knowledge of how MPAs will perform, how best to locate them and how sensitive outcomes will be to the level of protection given. For pragmatic reasons, decision-makers often prioritise multiple-use areas in MPAs, thereby maximising the volume of ocean that remains open to fishing (Costello and Ballantine 2015). Many argue that while pelagic fisheries may result in some indirect effects to seabed communities, these are not comparable to impacts from bottom fisheries and therefore demand fewer restrictions (Grober-Dunsmore et al. 2008). While the prevention of physical destruction of seabed habitat should be of high conservation priority given its irreversibility on meaningful timescales (Clark et al. 2016; Jones et al. 2017), so too should be protection of the water column above these habitats to safeguard linkages that are likely to be essential for full seabed functioning. We sorely need greater research on pelagic fishing effects in offshore environments, the deep-sea and on the seabed. However, the rapid expansion of human activities and influences argues for application of the precautionary approach and use of best available scientific evidence.

We know that marine life responds most to full protection that extends across ocean depths, that these benefits take time to accrue and that conservation outcomes can be eroded by edge effects (e.g. Edgar et al. 2014; Giakoumi et al. 2017; Gill et al. 2017). Vertical zoning of protection in MPAs will lead to significant within-MPA edge effects that will undermine whole ecosystem conservation goals. Based on our review of the evidence, the best advice for effective marine conservation, we argue, is to protect the whole volume of MPAs. Furthermore, ensuring continuity of management from seabed to sea surface will help to preserve vertical and horizontal connectivity in the absence of extensive knowledge of connectivity patterns and without complex and costly conservation planning, monitoring and enforcement. Maintaining ecological connectivity will also provide benefits to marine life and people beyond ameliorating the impacts of fishing enhancing ecosystem resilience and protecting their capacity to deliver ecosystem services in the face of climate change (Roberts et al. 2017).

The challenges of identifying linkages between ocean depths have implications for MPAs and other spatially defined conservation tools, particularly in terms of monitoring and evaluation. For example, fully protecting the water column in one place may confer benefits to the seabed elsewhere due to the transport of primary production or other nutrients through ocean currents (Thresher et al. 2011), that we may not be aware of. Ecosystem linkages and connections in the fluid open sea environment imply that particular attention be given to managing MPAs as networks to deliver collective benefits, supported by strong management of human activities in the waters surrounding MPAs. To ensure successful ocean conservation and sustainable use, management needs to be developed strategically with spatial and non-spatial management measures designed to work in concert with each other to deliver benefits.

High levels of open ocean connectivity also suggest that there will be greater difficulties in assigning benefits to particular MPAs in this environment. Decision-makers may therefore need to accept that the whole network of MPAs, together with management outside them, will need to work in concert to deliver benefits. In short, networks of open ocean MPAs will be giant experiments, but the potential rewards are great.

Global goals for ocean conservation (the Convention on Biological Diversity and the Sustainable Development Goals) were established to address causes of biodiversity loss and promote its recovery. The current preference for multiple-use areas that restrict as few activities as possible will fail to achieve this ambition, intentions which are often reflected in national and international policy. These are not altruistic goals. Biodiversity underpins human health and wellbeing (Diaz et al. 2006) being critical for ecosystem function and service provision (Gamfeldt et al. 2015; Oliver et al. 2015; Reich et al. 2012; Soliveres et al. 2016). Short-changing biodiversity protection will therefore short-change humanity.

5 Conclusions

Globally, countries now appear likely to meet the ‘quantity’ aspect of global goals for marine protected areas, currently set at 10% ocean coverage (Convention on Biological Diversity 2017). But it is almost certain that the world will fail to meet the ‘quality’ aspects (e.g. equitably and effectively managed, well-connected, and ecologically representative networks of MPAs). Adopting the approach of allowing water column fishing in present and future MPAs in open ocean areas, including beyond national jurisdiction, will on the balance of evidence examined, fail to deliver sufficient protection.

Our findings support the view of the International Union for the Conservation of Nature (IUCN) standards for MPAs which strongly advise against vertical zoning, arguing that “It often does not make ecological sense, as vertical ecological connections exist in marine ecosystems that we are just only beginning to understand, and because it is near impossible to enforce in any legally effective manner”(Day et al. 2011). Where vertical zoning is applied, the IUCN states that the protected area should be assigned to the weakest management category for reporting purposes (Day et al. 2011). This view is maintained in their latest review of MPA standards (IUCN WCPA 2018). Evidence of ecological linkages between seabed and open water habitats reviewed here, particularly those facilitated by ocean megafauna and mesopelagic fish that are, or could be, seriously impacted by exploitation, highlights the need for integrated three-dimensional protection. While we recognise that implementing full protection within MPAs will be challenging given pressure from industrial interests, recent rapid progress in establishing very large and highly protected MPAs shows that it is feasible to do so when political will is present (O'Leary et al. 2018).

Substantial uncertainties remain in our understanding of ocean ecology. However, we can be certain that protecting the seabed while fishing the water column will not produce the same conservation outcome as surface to seabed protection would. Moreover, we argue that vertical zonation of MPAs will not only reduce the efficacy of management and present further challenges to enforcement, but will also make accurate reporting on conservation targets difficult, and further blur the lines as to what constitutes a protected area (Costello and Ballantine 2015; Spalding et al. 2016). To safeguard biodiversity and ecosystem function, and fully represent habitats in the open ocean, precautionary management indicates surface to seabed protection is warranted.

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