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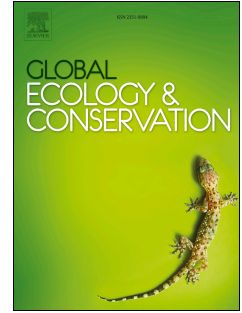
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Ecological connectivity across ocean depths: Implications for protected area design

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1 **Ecological connectivity across ocean depths: implications for protected area design**

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5

6 **Abstract**

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

25

26 **Highlights**

- 27
- 28 • Despite rapid expansion of MPAs nations may still fail to adequately protect oceans
 - 29 • Seabed habitats are frequently protected without overlying waters
 - 30 • Evidence increasingly links upper-ocean life to seabed ecology and biogeochemistry
 - 31 • Pelagic exploitation likely has a widely distributed footprint in the deep-sea
 - 32 • Open ocean MPAs should, by default, incorporate surface to seabed protection

32 **Keywords**

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

35 1 Introduction

36 Two major developments are underway in the world of marine conservation. First, following
37 adoption into Sustainable Development Goal 14 (United Nations 2015) of the Convention on
38 Biological Diversity's target for $\geq 10\%$ ocean protection by 2020 (Convention on Biological Diversity
39 2010), there is renewed impetus to meet this target. Coastal nations of the world are embarked on a
40 rapid program of marine protected area (MPA) establishment that at last looks set to achieve this
41 coverage target (Convention on Biological Diversity 2017), following nearly two decades of slow
42 progress (O'Leary et al. 2018). The second, is that a process has been underway at the United
43 Nations for more than two years to negotiate a mechanism to create MPAs in areas beyond national
44 jurisdiction, amongst other conservation measures (UNGA 2015). This shared ocean space
45 constitutes approximately 61% of the oceans, 44% of the surface of the Earth and 65% of the volume
46 of the biosphere but remains the least protected space on the planet (Gjerde et al. 2016). After a
47 promising start, the process looks set to produce a legal instrument within the next two years,
48 following a conference of the UN General Assembly.

49 These developments are welcome but there are real risks that in meeting them, nations will still fail
50 to offer adequate protection to the sea. Ecological science is clear that the most effective protected
51 areas are those fully protected from exploitation and other mitigable sources of human harm (e.g.
52 Edgar et al. 2014; Giakoumi et al. 2017; Gill et al. 2017). But from a socio-political perspective, the
53 easiest protected areas to establish are those where protection is weak and impose few alterations
54 to existing patterns of use. Many MPAs offer little, to no, real protection (Costello and Ballantine
55 2015). This is a particular risk when it comes to protection of the open sea, which constitutes much
56 of areas beyond national jurisdiction.

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

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

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

77 2 Ecological connectivity between surface and seabed ecosystems

78 Seabed and water column communities are often considered separately. Emphasising this
79 distinction, scientists divide the open ocean into a series of realms based on depth: epipelagic (0-
80 200 m), mesopelagic (200-1 000 m), bathypelagic (1 000-4 000 m), abyssopelagic (4 000 m to directly
81 above the ocean floor) and hadopelagic (ocean water in submarine trenches). However, this vertical
82 classification is a convenience and an oversimplification. Different depths are linked through a wide
83 variety of mechanisms including energy production and transfer in food webs, cycling of nutrients
84 and raw materials, shifts in habitat use as creatures develop and grow, and daily and seasonal
85 vertical migrations (Arellano et al. 2014; Davison et al. 2013; Howey et al. 2016; Nakamura and Sato
86 2014). The transitions between these human-conceived vertical layers are gradients, not sharp
87 boundaries, and ecological distinctions are blurred with ocean currents and animals connecting the
88 various depths.

89 2.1 Food-web interactions and surface to seabed relationships

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

100 Deep-sea fauna ultimately rely for food on primary productivity in the epipelagic realm sinking to the
101 seafloor, or being shuttled by animal movements, with the exception of some chemosynthetic
102 communities on, for example, hydrothermal vents (Drazen and Sutton 2017; Smith et al. 2008;
103 Stasko et al. 2016; Trueman et al. 2014). With increasing depth there is an associated decrease in
104 food supply (Buesseler et al. 2007). Open water ecosystems therefore subsidise deep-sea and
105 seabed habitats with detritus, nutrients and prey, increasing the productivity of the latter
106 (Mauchline and Gordon 1991; Trueman et al. 2014) (Box 1). Energy transfer between seabed
107 ecosystems and water column habitats may also be driven from seabed habitats such as
108 hydrothermal vents, cold-water coral reefs, and seamounts. Hydrothermal vents – deep water hot
109 springs – eject chemical rich plumes that alter the microbial community in the water column,
110 dispersing vertically up to c.500 m above and across the seabed, increasing plankton biomass and
111 abundance, thereby enhancing local productivity (Levin et al. 2016). Deep cold-water coral reefs
112 form large mounds (c.600 m) in the North Atlantic that have been shown to induce downwelling of
113 surface waters, dragging down organic matter essential for the functioning of these ecosystems
114 (Soetaert et al. 2016). Seamounts can also enhance local productivity through the creation of
115 oceanographic features such as upwellings, eddies, and spiralling water masses called ‘Taylor
116 columns’. They drive higher surface productivity and support diverse seabed ecosystems and a wide
117 range of pelagic species including sharks, tunas and billfish (Morato et al. 2010; Watling and Auster
118 2017).

119 Taken together, these lines of evidence suggest that recent changes in pelagic systems due to
120 human exploitation and greenhouse gas emissions are likely to have a significant and widely

121 distributed footprint in the deep-sea, based on alterations to levels of productivity, abundance of
 122 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).

123

124 **2.2 Biogeochemical cycling mediated by marine organisms**

125 The ocean acts as a major carbon sink, absorbing atmospheric carbon and trapping it in sediments
 126 (Le Quéré et al. 2015). Ocean carbon sequestration is driven by 'pumps' that are physical, i.e. ocean
 127 circulation, and biological, i.e. organisms. The biological carbon pump is driven mainly by planktonic
 128 photosynthetic organisms (Guidi et al. 2016). Each day, around 100 million tonnes of carbon dioxide
 129 are estimated to be fixed into organic material by phytoplankton (Behrenfield et al. 2006). This
 130 equates to c.50 billion tonnes each year (Westberry et al. 2008), roughly equivalent to annual
 131 anthropogenic carbon dioxide emissions in 2010¹. One-fifth of this is exported to the deep-sea by

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].

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

134 Animals can be important mediators of biogeochemical cycles (Box 2). Species which undertake
135 regular movements between upper and deeper waters, such as zooplankton (Turner 2015),
136 mesopelagic fish (Robinson et al. 2010) or deep-diving predators like tuna and sharks (Fuller et al.
137 2015; Howey et al. 2016) link different depth zones and/or seabed environments. These movements
138 facilitate biogeochemical connections across the water column that promote carbon uptake and
139 storage and thereby affect climate regulation (Giering et al. 2014; Robinson et al. 2010), modify
140 fluxes of nutrients and oxygen in the water column (Bianchi et al. 2013; Hernández-León et al. 2008;
141 Roman et al. 2014; Turner 2015), and help sustain the metabolic requirements of midwater (Bianchi
142 et al. 2013; Burd et al. 2010) and seabed ecosystems (Drazen and Sutton 2017; Trueman et al. 2014).

143 Long-term data from the Northeast Pacific and the Northeast Atlantic illustrate how variations in
144 climate and upper ocean conditions are linked to variations in deep-sea communities and
145 biogeochemical processes at the sea floor (Smith Jr et al. 2009). For example, the Northern
146 Oscillation Index and the Bakun Upwelling Index in the Pacific were significantly correlated with the
147 flux of particulate organic carbon at 3 500 m depth when lagged by 6 and 2-3 months respectively
148 (Smith Jr et al. 2009). Changes in deep-sea fauna have also been significantly correlated to climatic
149 events in the Pacific when lagged by several months, with smaller animals displaying shorter
150 response times than larger ones (Ruhl and Smith Jr 2004; Smith Jr et al. 2009). Similarly, positive
151 variations in the monthly North Atlantic Oscillation index were linked to increases in the amount of
152 particulate organic carbon reaching 3 000 m, with a lag of 0-3 months, and changes in deep-sea
153 fauna were linked to climate-driven variations in the quantity and composition of sinking organic
154 matter (Smith Jr et al. 2009). These relationships demonstrate strong connections between the
155 intensity of surface primary productivity and carbon flux to the deep-sea. It can therefore be
156 expected that activities that affect open water habitats and the organisms that mediate transfer of
157 production such as fishing (Bailey et al. 2009) and deep-sea mining (Miller et al. 2018), as well as
158 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 $c.1.8 \pm 0.6 \times 10^{12}$ 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.

159 **3 Pelagic fishing and its broader ecosystem impacts**

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

167 In areas beyond national jurisdiction, the UN General Assembly requires closures to bottom fishing
 168 of areas containing vulnerable marine ecosystems where significant adverse impacts are likely
 169 (Resolution 61/105, 2006). Such closures are often temporary, permit fishing in the water column
 170 above, and fail to restrict ongoing fishing activity (Wright et al. 2015). The direct effects of deep-sea
 171 bottom trawling on benthic habitats are well known (Clark et al. 2016; Pusceddu et al. 2014), and

172 closures that protect sensitive seabed habitats from damage are essential. However, the influence of
173 pelagic fisheries on seabed communities and habitats is poorly understood.

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

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

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

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

224 **4 Implications for protected area design**

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

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

253 The challenges of identifying linkages between ocean depths have implications for MPAs and other
254 spatially defined conservation tools, particularly in terms of monitoring and evaluation. For example,
255 fully protecting the water column in one place may confer benefits to the seabed elsewhere due to
256 the transport of primary production or other nutrients through ocean currents (Thresher et al.
257 2011), that we may not be aware of. Ecosystem linkages and connections in the fluid open sea
258 environment imply that particular attention be given to managing MPAs as networks to deliver
259 collective benefits, supported by strong management of human activities in the waters surrounding
260 MPAs. To ensure successful ocean conservation and sustainable use, management needs to be
261 developed strategically with spatial and non-spatial management measures designed to work in
262 concert with each other to deliver benefits.

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

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

276 **5 Conclusions**

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

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

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

305

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