

This is a repository copy of *Ecological connectivity across ocean depths : implications for protected area design*.

White Rose Research Online URL for this paper:  
<http://eprints.whiterose.ac.uk/134977/>

Version: Accepted Version

---

**Article:**

O'Leary, Bethan Christine [orcid.org/0000-0001-6595-6634](https://orcid.org/0000-0001-6595-6634) and Roberts, Callum Michael [orcid.org/0000-0003-2276-4258](https://orcid.org/0000-0003-2276-4258) (2018) *Ecological connectivity across ocean depths : implications for protected area design*. *Global Ecology and Conservation*. ISSN 2351-9894

<https://doi.org/10.1016/j.gecco.2018.e00431>

---

**Reuse**

This article is distributed under the terms of the Creative Commons Attribution (CC BY) licence. This licence allows you to distribute, remix, tweak, and build upon the work, even commercially, as long as you credit the authors for the original work. More information and the full terms of the licence here:  
<https://creativecommons.org/licenses/>

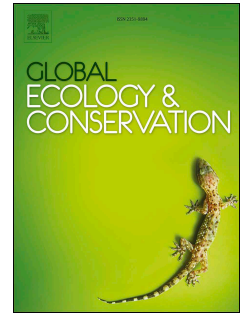
**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.

# Accepted Manuscript

Ecological connectivity across ocean depths: Implications for protected area design

Bethan C. O'Leary, Callum M. Roberts



PII: S2351-9894(18)30102-1

DOI: [10.1016/j.gecco.2018.e00431](https://doi.org/10.1016/j.gecco.2018.e00431)

Article Number: e00431

Reference: GECCO 431

To appear in: *Global Ecology and Conservation*

Received Date: 13 November 2017

Revised Date: 20 August 2018

Accepted Date: 20 August 2018

Please cite this article as: O'Leary, B.C., Roberts, C.M., Ecological connectivity across ocean depths: Implications for protected area design, *Global Ecology and Conservation* (2018), doi: 10.1016/j.gecco.2018.e00431.

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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

2 Bethan C. O'Leary<sup>a\*</sup>, Callum M. Roberts<sup>a</sup>

3 <sup>a</sup>Department of Environment and Geography, University of York, York, YO10 5NG, United Kingdom

4 \*Corresponding author: [bethan.oleary@york.ac.uk](mailto:bethan.oleary@york.ac.uk), +44 (0)1904 322999

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
  - 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 2010<sup>1</sup>. One-fifth of this is exported to the deep-sea by

<sup>1</sup> 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](http://www.ipcc.ch/pdf/assessment-report/ar5/wg3/ipcc_wg3_ar5_summary-for-policymakers.pdf) [accessed August 9<sup>th</sup> 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; Kroodsmas 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

## 306 6 Acknowledgements

307 BO'L is supported by The Pew Charitable Trusts. The views expressed herein are those of the authors  
308 and do not necessarily reflect the views of The Pew Charitable Trusts.

## 309 7 Funding

310 This work was supported by The Pew Charitable Trusts.

## 311 8 Role of the funding sources

312 The authors declare that the research was conducted in the absence of any commercial or financial  
313 relationships that could be construed as a potential conflict of interest. The funders had no input  
314 into the study design; collection, analysis, and interpretation of data; in the writing of the report; or  
315 in the decision to submit the paper for publication.

## 316 9 References

- 317 Arellano, S.M., Van Caest, A.L., Johnson, S.B., Vrijenhoek, R.C., Young, C.M., 2014. Larvae from deep-  
318 sea methane seeps disperse in surface waters. *Proceedings of the Royal Society B: Biological*  
319 *Sciences* 281, 20133276. doi:10.1098/rspb.2013.3276
- 320 Australian Government, 2018. Management plans for marine parks.  
321 <https://parksaustralia.gov.au/marine/management/plans/> (accessed 12 April 2018).
- 322 Bailey, D.M., Collins, M.A., Gordon, J.D.M., Zuur, A.F., Priede, I.G., 2009. Long-term changes in deep-  
323 water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? *Proceedings of*  
324 *the Royal Society B: Biological Sciences* 276, 1965-1969. doi:10.1098/rspb.2009.0098
- 325 Barry, J.P., Grebmeier, J.M., Smith, J.E., Dunbar, R.B., 2013. Oceanographic Versus Seafloor-Habitat  
326 Control of Benthic Megafaunal Communities in the S.W. Ross Sea, Antarctica, In *Biogeochemistry of*  
327 *the Ross Sea*. eds G.R. Ditullio, R.B. Dunbar, pp. 327-353. American Geophysical Union.
- 328 Behrenfield, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan,  
329 A.J., Falkowski, P.G., Letelier, R.M., Boss, E.S., 2006. Climate-driven trends in contemporary ocean  
330 productivity. *Nature* 444, 752-755. doi:10.1038/nature05317
- 331 Bianchi, D., Stock, C., Galbraith, E.D., Sarmiento, J.L., 2013. Diel vertical migration: Ecological controls  
332 and impacts on the biological pump in a one-dimensional ocean model. *Global Biogeochemical*  
333 *Cycles* 27, 478-491. doi:10.1002/gbc.20031
- 334 Brunchhausen, P.M., Raymond, J.A., Jacobs, S.S., DeVries, A.L., Thorndike, E.M., DeWitt, H.H., 1979.  
335 Fish, crustaceans, and the sea floor under the Ross Ice Shelf. *Science* 203, 449-451.
- 336 Buesseler, K.O., Lamborg, C.H., Boyd, P.W., Lam, P.J., Trull, T.W., Bidigare, R.R., Bishop, J.K.B.,  
337 Casciotti, K.L., Dehairs, F., Elskens, M., Honda, M., Karl, D.M., Siegel, D.A., Silver, M.W., Steinberg,  
338 D.K., Valdes, J., Van Mooy, B., Wilson, S., 2007. Revisiting Carbon Flux Through the Ocean's Twilight  
339 Zone. *Science* 316, 567-570. doi:10.1126/science.1137959
- 340 Burd, A.B., Hansell, D.A., Steinberg, D.K., Anderson, T.R., Aristegui, J., Baltar, F., Beupre, S.R.,  
341 Buesseler, K.O., Dehairs, F., Jackson, G.A., Kadko, D.C., Koppelman, R., Lampitt, R.S., Nagata, T.,  
342 Reinthaler, T., Robinson, C., Robison, B.H., Tamburini, C., Tanaka, T., 2010. Assessing the apparent  
343 imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological  
344 activity: What the @#! is wrong with present calculations of carbon budgets? *Deep-Sea Research*  
345 *Part II: Topical Studies in Oceanography* 57, 1557-1571. doi:10.1016/j.dsr2.2010.02.022

- 346 Clark, M.R., Althaus, F., Schlacher, T.A., Williams, A., Bowden, D.A., Rowden, A.A., 2016. The impacts  
347 of deep-sea fisheries on benthic communities: a review. *ICES Journal of Marine Science* 73, i51-i69.  
348 doi:10.1093/icesjms/fsv123
- 349 Convention on Biological Diversity, 2010. COP Decision X/2. Strategic plan for biodiversity 2011–  
350 2020. <https://www.cbd.int/decision/cop/?id=12268> (accessed 29 October 2017).
- 351 Convention on Biological Diversity, 2017. Global marine protected area target of 10% to be achieved  
352 by 2020. <https://www.cbd.int/doc/press/2017/pr-2017-06-05-mpa-pub-en.pdf> (accessed 6  
353 September 2017).
- 354 Costello, M.J., Ballantine, B., 2015. Biodiversity conservation should focus on no-take Marine  
355 Reserves: 94% of Marine Protected Areas allow fishing. *Trends in Ecology & Evolution* 30, 507-509.  
356 doi:10.1016/j.tree.2015.06.011
- 357 Daskalov, G.M., Grishin, A.N., Rodionov, S., Mihneva, V., 2007. Trophic cascades triggered by  
358 overfishing reveal possible mechanisms of ecosystem regime shifts. *PNAS* 104, 10518-10523.  
359 doi:10.1073/pnas.0701100104
- 360 Davison, P.C., Checkley, D.M., Koslow, J.A., Barlow, J., 2013. Carbon export mediated by mesopelagic  
361 fishes in the northeast Pacific Ocean. *Progress in Oceanography* 116, 14-30.  
362 doi:10.1016/j.pocean.2013.05.013
- 363 Day, J., Dudley, N., Hockings, M., Holmes, G., Laffoley, D., Stolton, S., 2011. Guidelines for applying  
364 the IUCN Protected Area Management Categories to Marine Protected Areas, IUCN, Gland,  
365 Switzerland.
- 366 Diaz, S., Fargione, J., Chapin, F.S.I., Tilman, D., 2006. Biodiversity Loss Threatens Human Well-Being.  
367 *PloS Biology* 4, e277. doi:10.1371/journal.pbio.0040277
- 368 Drazen, J.C., Sutton, T.T., 2017. Dining in the Deep: The Feeding Ecology of Deep-Sea Fishes. *Annual*  
369 *Review of Marine Science* 9, 337-366. doi:10.1146/annurev-marine-010816-060543
- 370 Dunne, J.P., Sarmiento, J.L., Gnanadesikan, A., 2007. A Synthesis of Global Particle Export from the  
371 Surface Ocean and Cycling through the Ocean Interior and on the Seafloor. *Global Biogeochemical*  
372 *Cycles* 21. doi:10.1029/2006GB002907
- 373 Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S.,  
374 Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M.,  
375 Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears,  
376 N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine  
377 protected areas with five key features. *Nature* 506, 216-220. doi:10.1038/nature13022
- 378 Ellingsen, K.E., Anderson, M.J., Shackell, N.L., Tveraa, T., Yoccoz, N.G., Frank, K.T., 2015. The role of a  
379 dominant predator in shaping biodiversity over space and time in a marine ecosystem. *Journal of*  
380 *Animal Ecology* 84, 1242-1252. doi:10.1111/1365-2656.12396
- 381 Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R.,  
382 Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett,  
383 E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E.,  
384 Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. *Science* 333, 301-306.  
385 doi:10.1126/science.1205106
- 386 Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K., 2010. Patterns and ecosystem  
387 consequences of shark declines in the ocean. *Ecology Letters* 13, 1055-1071. doi:10.1111/j.1461-  
388 0248.2010.01489.x

- 389 Fitzsimons, J.A., Wescott, G., 2008. Getting the measure of Marine Protected Areas: surface area or  
390 volume as measures for reserve system auditing? *Aquatic Conservation: Marine and Freshwater*  
391 *Ecosystems* 18, 518-526. doi:10.1002/aqc.867
- 392 Fuller, D.W., Schaefer, K.M., Hampton, J., Caillot, S., Leroy, B.M., Itano, D.G., 2015. Vertical  
393 movements, behavior, and habitat of bigeye tuna (*Thunnus obesus*) in the equatorial central Pacific  
394 Ocean. *Fisheries Research* 172, 57-70. doi:10.1016/j.fishres.2015.06.024
- 395 Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K.,  
396 Bustamante, R., Possingham, H.P., Richardson, A.J., 2009. Pelagic protected areas: the missing  
397 dimension in ocean conservation. *Trends in Ecology & Evolution* 24, 360-369.  
398 doi:10.1016/j.tree.2009.01.011
- 399 Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E., Griffin, J.N., 2015. Marine  
400 biodiversity and ecosystem functioning: what's known and what's next? *Oikos* 124, 252-265.  
401 doi:10.1111/oik.01549
- 402 Giakoumi, S., Scianna, C., Plass-Johnson, J., Micheli, F., Grorud-Colvert, K., Thiriet, P., Claudet, J., Di  
403 Carlo, G., Di Franco, A., Gaines, S.D., García-Charton, J.A., Lubchenco, J., Reimer, J., Sala, E., Guidetti,  
404 P., 2017. Ecological effects of full and partial protection in the crowded Mediterranean Sea: a  
405 regional meta-analysis. *Scientific Reports* 7, 8940. doi:10.1038/s41598-017-08850-w
- 406 Giering, S.L.C., Sanders, R., Lampitt, R.S., Anderson, T.R., Tamburini, C., Boutrif, M., Zubkov, M.V.,  
407 Marsay, C.M., Henson, S.A., Saw, K., Cook, K., Mayor, D.J., 2014. Reconciliation of the carbon budget  
408 in the ocean's twilight zone. *Nature* 507, 480-483. doi:10.1038/nature13123
- 409 Gill, D.A., Mascia, M.B., Ahmadi, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S.,  
410 Free, C.M., Geldmann, J., Holst, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D.,  
411 Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., 2017. Capacity shortfalls hinder the  
412 performance of marine protected areas globally. *Nature* 543, 665-669. doi:10.1038/nature21708
- 413 Gjerde, K., Nordtvedt Reeve, L.L., Harden-Davis, H., Ardron, J., Dolan, R., Durussel, C., Earle, S.,  
414 Jimenez, J.A., Kalas, P., Laffoley, D., Oral, N., Page, R., Ribeiro, M.C., Rochette, J., Spadone, A., Thiele,  
415 T., Thomas, H.L., Wagner, D., Warner, R., Wilhelm, A., Wright, G., 2016. Protecting Earth's last  
416 conservation frontier: scientific, management and legal priorities for MPAs beyond national  
417 boundaries. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26, 45-60.  
418 doi:10.1002/aqc.2646
- 419 Grober-Dunsmore, R., Wooninck, L., Field, J., Ainsworth, C., Beets, J., Berkeley, S., Bohnsack, J.,  
420 Boulon, R., Brodeur, R., Brodziak, J., Crowder, L., Gleason, D., Hixon, M., Kaufman, L., Lindberg, B.,  
421 Miller, M., Morgan, L., Wahle, C., 2008. Vertical Zoning in Marine Protected Areas: Ecological  
422 Considerations for Balancing Pelagic Fishing with Conservation of Benthic Communities. *Fisheries* 33,  
423 598-610. doi:10.1577/1548-8446-33.12.598
- 424 Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Darzi, Y., Audic, S., Berline, L.,  
425 Brum, J.R., Coelho, L.P., Espinoza, J.C.I., Malviya, S., Sunagawa, S., Dimier, C., Kandels-Lewis, S.,  
426 Picheral, M., Poulain, J., Searson, S., Tara Oceans Consortium Coordinators, Stemmann, L., Not, F.,  
427 Hingamp, P., Speich, S., Follows, M., Karp-Boss, L., Boss, E., Ogata, H., Pesant, S., Weissenbach, J.,  
428 Wincker, P., Acinas, S.G., Bork, P., de Vargas, C., Iudicone, D., Sullivan, M.B., Raes, J., Karsenti, E.,  
429 Bowler, C., Gorsky, G., 2016. Plankton Networks Driving Carbon Export in the Oligotrophic Ocean.  
430 *Nature* 532, 465-470. doi:10.1038/nature16942
- 431 Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J.S., Tockwood,  
432 R.C., Selig, E.R., Selkoe, K.A., Walbridge, S., 2015. Spatial and temporal changes in cumulative human  
433 impacts on the world's oceans. *Nature Communications* 6, 7615. doi:10.1038/ncomms8615

- 434 Helson, J., Leslie, S., Clement, G., Wells, R., Wood, R., 2010. Private rights, public benefits: Industry-  
435 driven seabed protection. *Marine Policy* 34, 557-566. doi:10.1016/j.marpol.2009.11.002
- 436 Henson, S.A., 2014. Slow science: the value of long ocean biogeochemistry records. *Philosophical*  
437 *Transactions of the Royal Society A* 372, 20130334. doi:10.1098/rsta.2013.0334
- 438 Hernández-León, S., Fraga, C., Ikeda, T., 2008. A global estimation of mesozooplankton ammonium  
439 excretion in the open ocean. *Journal of Plankton Research* 30, 577-585. doi:10.1093/plankt/fbn021
- 440 Hernández-León, S., Ikeda, T., 2005. A global assessment of mesozooplankton respiration in the  
441 ocean. *Journal of Plankton Research* 27, 153-158. doi:10.1093/plankt/fbh166
- 442 Howey, L.A., Tolentino, E.R., Papastamatiou, Y.P., Brooks, E.J., Abercrombie, D.L., Watanabe, Y.Y.,  
443 Williams, S., Brooks, A., Chapman, D.D., Jordan, L.K.B., 2016. Into the deep: the functionality of  
444 mesopelagic excursions by an oceanic apex predator. *Ecology and Evolution* 6, 5290-5304.  
445 doi:10.1002/ece3.2260
- 446 IUCN WCPA, 2018. Applying IUCN's Global Conservation Standards to Marine Protected Areas  
447 (MPA). Delivering effective conservation action through MPAs, to secure ocean health & sustainable  
448 development, Version 1.0. Gland, Switzerland. 4pp.
- 449 Jahnke, R.A., Reimers, C.E., Craven, D.B., 1990. Intensification of recycling of organic matter at the  
450 sea floor near ocean margins. *Nature* 348, 50-54. doi:10.1038/348050a0
- 451 Johnson, P.M., 2011. Trade-offs between biodiversity conservation and maintaining fisheries yield  
452 from Australian marine environments; approaches using the Atlantis ecosystem modelling  
453 framework. University of Tasmania, Hobart.
- 454 Jónasdóttir, S.H., Visser, A.W., Richardson, K., Heath, M.R., 2015. Seasonal copepod lipid pump  
455 promotes carbon sequestration in the deep North Atlantic. *PNAS* 112, 12122-12126.  
456 doi:10.1073/pnas.1512110112
- 457 Jones, D.O.B., Kaiser, S., Sweetman, A.K., Smith, C.R., Menot, L., Vink, A., Trueblood, D., Greinert, J.,  
458 Billett, D.S.M., Martinez Arbizu, P., Radziejewska, T., Singh, R., Ingole, B., Stratmann, T., Simon-Lledó,  
459 E., Durden, J.M., Clark, M.R., 2017. Biological responses to disturbance from simulated deep-sea  
460 polymetallic nodule mining. *PLoS ONE* 12, e0171750. doi:10.1371/journal.pone.0171750
- 461 Kiszka, J.J., Heithaus, M.R., Wirsing, A.J., 2015. Behavioural drivers of the ecological roles and  
462 importance of marine mammals. *Marine Ecology Progress Series* 523, 267-281.  
463 doi:10.3354/meps11180
- 464 Kroodsma, D.A., Mayorga, J., Hochberg, T., Miller, N.A., Boerder, K., Ferretti, F., Wilson, A., Bergman,  
465 B., White, T.D., Block, B.A., Woods, P., Sullivan, B., Costello, C., Worm, B., 2018. Tracking the global  
466 footprint of fisheries. *Science* 359, 904-908. doi:10.1126/science.aao5646
- 467 Lascelles, B., Notarbartolo di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E.,  
468 Llewellyn, F., Louzao, M., Ridoux, V., Tetley, M.J., 2014. Migratory marine species: their status,  
469 threats and conservation management needs. *Aquatic Conservation: Marine and Freshwater*  
470 *Ecosystems* 24, 111-127. doi:10.1002/aqc.2512
- 471 Lavery, T.J., Roudnew, B., Gill, P., Seymour, J., Seuront, L., Johnson, G.C., Mitchell, J.G., Smetacek, V.,  
472 2010. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proceedings*  
473 *of the Royal Society B: Biological Sciences* 277, 3527-3531. doi:10.1098/rspb.2010.0863
- 474 Le Quéré, C., Moriarty, R., Andrew, R.M., Peters, G.P., Ciais, P., Friedlingstein, P., Jones, S.D., Sitch, S.,  
475 Tans, P., Arneeth, A., Boden, T.A., Bopp, L., Bozec, Y., Canadell, J.G., Chini, L.P., Chevallier, F., Cosca,  
476 C.E., Harris, I., Hoppema, M., Houghton, R.A., House, J.I., Jain, A.K., Johannessen, T., Kato, E., Keeling,

- 477 R.F., Kitidis, V., Klein Goldewijk, K., Koven, C., Landa, C.S., Landschützer, P., Lenton, A., Lima, I.D.,  
478 Marland, G., Mathis, J.T., Metzl, N., Nojiri, Y., Olsen, A., Ono, T., Peng, S., Peters, W., Pfiel, B.,  
479 Poulter, B., Raupach, M.R., Regnier, P., Rödenbeck, C., Saito, S., Salisbury, J.E., Schuster, U.,  
480 Schwinger, J., Séférian, R., Segschneider, J., Steinhoff, T., Stocker, B.D., Sutton, A.J., Takahashi, T.,  
481 Tilbrook, B., van der Werf, G.R., Viovy, N., Wang, Y.-P., Wanninkhof, R., Wiltshire, A., Zeng, N., 2015.  
482 Global carbon budget 2014. *Earth System Science Data* 7, 47-85. doi:10.5194/essd-7-47-2015
- 483 Leathwick, J.R., Elith, J., Francis, M.P., Hastie, T., Taylor, P., 2006. Variation in demersal fish species  
484 richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Marine*  
485 *Ecology Progress Series* 321, 267-281. doi:10.3354/meps321267
- 486 Levin, L.A., Baco, A.R., Bowden, D.A., Colaco, A., Cordes, E.E., Cunha, M.R., Demopoulos, A.W.J.,  
487 Gobin, J., Grupe, B.M., Le, J., Metaxas, A., Netburn, A.N., Rouse, G.W., Thurber, A.R., Tunnicliffe, V.,  
488 Van Dover, C.L., Vanreusel, A., Watling, L., 2016. Hydrothermal Vents and Methane Seeps:  
489 Rethinking the Sphere of Influence. *Frontiers in Marine Science* 3, 72. doi:10.3389/fmars.2016.00072
- 490 Lewison, R.L., Crowder, L.B., Wallace, B.P., Moore, J.E., Cox, T., Zydalis, R., McDonald, S., DiMatteo,  
491 A., Dunn, D.C., Koti, C.Y., Bjorkland, R., Kelez, S., Soykan, C., Stewart, K.R., Sims, M., Boustany, A.,  
492 Read, A.J., Halpin, P., Nichols, W.J., Safina, C., 2014. Global patterns of marine mammal, seabird, and  
493 sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *PNAS* 111, 5271-5276.  
494 doi:10.1073/pnas.1318960111
- 495 Loubere, P., 1991. Deep-Sea Benthic Foraminiferal Assemblage Response to a Surface Ocean  
496 Productivity Gradient: A Test. *Paleoceanography* 6, 193-204. doi:10.1029/90PA02612
- 497 Louzao, M., Navarro, J., Delgado-Huertas, A., Gil de Sola, L., Forero, M.G., 2017. Surface  
498 oceanographic fronts influencing deep-sea biological activity: Using fish stable isotopes as ecological  
499 tracers. *Deep-Sea Research Part II: Topical Studies in Oceanography* 140, 117-126.  
500 doi:10.1016/j.dsr2.2016.10.012
- 501 Mauchline, J., Gordon, J.D.M., 1991. Oceanic pelagic prey of benthopelagic fish in the benthic  
502 boundary layer of a marginal oceanic region. *Marine Ecology Progress Series* 74, 109-115.  
503 doi:10.3354/meps074109
- 504 McClatchie, S., Millar, R.B., Webster, F., Lester, P.J., Hurst, R., Bagley, N., 1997. Demersal fish  
505 community diversity off New Zealand: Is it related to depth, latitude and regional surface  
506 phytoplankton? *Deep-Sea Research Part I: Oceanographic Research Papers* 44, 647-667.  
507 doi:10.1016/S0967-0637(96)00096-9
- 508 Merrie, A., Dunn, D.C., Metian, M., Boustany, A.M., Takei, Y., Elferink, A.O., Ota, Y., Christensen, V.,  
509 Halpin, P.N., Österblom, H., 2014. An ocean of surprises – Trends in human use, unexpected  
510 dynamics and governance challenges in areas beyond national jurisdiction. *Global Environmental*  
511 *Change* 27, 19-31. doi:10.1016/j.gloenvcha.2014.04.012
- 512 Miller, K.A., Thompson, K.F., Johnston, P., Santillo, D., 2018. An Overview of Seabed Mining Including  
513 the Current State of Development, Environmental Impacts, and Knowledge Gaps. *Frontiers in Marine*  
514 *Science* 4, 418. doi:10.3389/fmars.2017.00418
- 515 Morato, T., Hoyle, S.D., Allain, V., Nicol, S.J., 2010. Seamounts are hotspots of pelagic biodiversity in  
516 the open ocean. *PNAS* 107, 9707-9711. doi:10.1073/pnas.0910290107
- 517 Mumby, P.J., 2009. Herbivory versus corallivory: are parrotfish good or bad for Caribbean coral  
518 reefs? *Coral Reefs* 28, 683-690. doi:10.1007/s00338-009-0501-0
- 519 Nakamura, I., Sato, K., 2014. Ontogenetic shift in foraging habit of ocean sunfish *Mola mola* from  
520 dietary and behavioral studies. *Marine Biology* 161, 1263-1273. doi:10.1007/s00227-014-2416-8



- 521 O'Leary, B.C., Ban, N.C., Fernandez, M., Friedlander, A.M., García-Borboroglu, P., Golbuu, Y.,  
522 Guidetti, P., Harris, J.M., Hawkins, J.P., Langlois, T., McCauley, D.J., Pikitch, E.K., Richmond, R.H.,  
523 Roberts, C.M., 2018. Addressing criticisms of large-scale marine protected areas, In *BioScience*.
- 524 O'Leary, B.C., Roberts, C.M., 2017. The Structuring Role of Marine Life in Open Ocean Habitat:  
525 Importance to International Policy. *Frontiers in Marine Science* 4, 268.  
526 doi:10.3389/fmars.2017.00268
- 527 Oliver, T.H., Isaac, N.J.B., August, T.A., Woodcock, B.A., Roy, D.B., Bullock, J.M., 2015. Declining  
528 resilience of ecosystem functions under biodiversity loss. *Nature Communications* 8, 10122.  
529 doi:10.1038/ncomms10122
- 530 Ortuño Crespo, G., Dunn, D.C., 2017. A review of the impacts of fisheries on open-ocean ecosystems.  
531 *ICES Journal of Marine Science*. doi:10.1093/icesjms/fsx084
- 532 Polovina, J.J., Abecassis, M., Howell, E.A., Woodworth, P., 2009. Increases in the relative abundance  
533 of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North  
534 Pacific, 1996–2006. *Fisheries Bulletin* 107, 523-531.
- 535 Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., Danovaro, R., 2014.  
536 Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning.  
537 *PNAS* 111, 8861-8866. doi:10.1073/pnas.1405454111
- 538 Queiroz, N., Humphries, N.E., Mucientes, G., Hammerschlag, N., Lima, F.P., Scales, K.L., Miller, P.I.,  
539 Sousa, L.L., Seabra, R., Sims, D.W., 2016. Ocean-wide tracking of pelagic sharks reveals extent of  
540 overlap with longline fishing hotspots. *PNAS* 113, 1582-1587. doi:10.1073/pnas.1510090113
- 541 Read, A.J., Drinker, P., Northridge, S., 2006. Bycatch of Marine Mammals in U.S. and Global Fisheries.  
542 *Conservation Biology* 20, 163-169. doi:10.1111/j.1523-1739.2006.00338.x
- 543 Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B., Eisenhauer, N., 2012. Impacts  
544 of Biodiversity Loss Escalate Through Time as Redundancy Fades. *Science* 336, 589-592.  
545 doi:10.1126/science.1217909
- 546 Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P., Duarte, C.M., Lubchenco, J., Pauly, D., Sáenz-  
547 Arroyo, A., Sumaila, U.R., Wilson, R.W., Worm, B., Castilla, J.C., 2017. Marine reserves can mitigate  
548 and promote adaptation to climate change. *PNAS* 114, 6167-6175. doi:10.1073/pnas.1701262114
- 549 Robinson, C., Steinberg, D.K., Anderson, T.R., Arístegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.-F.,  
550 Hernández-León, S., Jackson, G.A., Koppelman, R., Quéguiner, B., Ragueneau, O., Rassoulzadegan,  
551 F., Robison, B.H., Tamburini, C., Tanaka, T., Wishnern, K.F., Zhang, J., 2010. Mesopelagic zone  
552 ecology and biogeochemistry – a synthesis. *Deep-Sea Research Part II: Topical Studies in*  
553 *Oceanography* 57, 1504-1518. doi:10.1016/j.dsr2.2010.02.018
- 554 Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D.P., McCarthy, J., Nation, J.B., Nicol, S.,  
555 Pershing, A., Smetacek, V., 2014. Whales as marine ecosystem engineers. *Frontiers in Ecology and*  
556 *the Environment* 12, 377-385. doi:10.1890/130220
- 557 Roman, J., McCarthy, J.J., 2010. The Whale Pump: Marine Mammals Enhance Primary Productivity in  
558 a Coastal Basin. *PLoS ONE* 5, e13255. doi:10.1371/journal.pone.0013255
- 559 Ruhl, H.A., Smith Jr, K.L., 2004. Shifts in Deep-Sea Community Structure Linked to Climate and Food  
560 Supply. *Science* 305, 513-515. doi:10.1126/science.1099759
- 561 Smith, A.D.M., Brown, C.J., Bulman, C.M., Fulton, E.A., Johnson, P., Kaplan, I.C., Lozano-Montes, H.,  
562 Mackinson, S., Marzloff, M., Shannon, L.J., Shin, Y.-J., Tam, J., 2011. Impacts of Fishing Low-Trophic  
563 Level Species on Marine Ecosystems. *Science* 333, 1147-1150. doi:10.1126/science.1209395

- 564 Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M., 2008. Abyssal food  
565 limitation, ecosystem structure and climate change. *Trends in Ecology & Evolution* 23, 518-528.  
566 doi:10.1016/j.tree.2008.05.002
- 567 Smith, C.R., Mincks, S., DeMaster, D.J., 2006. A synthesis of benthic-pelagic coupling on the Antarctic  
568 shelf: Food banks, ecosystem inertia and global climate change. *Deep-Sea Research Part II: Topical  
569 Studies in Oceanography* 53, 875-894. doi:10.1016/j.dsr2.2006.02.001
- 570 Smith Jr, K.L., Ruhl, H.A., Bett, B.J., Billett, D.S.M., Lampit, R.S., Kaufmann, R.S., 2009. Climate, carbon  
571 cycling, and deep-ocean ecosystems. *PNAS* 106, 19211-19218. doi:10.1073/pnas.0908322106
- 572 Soetaert, K., Mohn, C., Rengstorf, A., Grehan, A., van Oevelen, D., 2016. Ecosystem engineering  
573 creates a direct nutritional link between 600-m deep cold-water coral mounds and surface  
574 productivity. *Scientific Reports* 6, 35057. doi:10.1038/srep35057
- 575 Soliveres, S., Van Der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., Alt, F., Arndt, H.,  
576 Baumgartner, V., Binkenstein, J., Birkhofer, K.L.U., Blaser, S., Blüthgen, N., Boch, S., Böhm, S.,  
577 Börschig, C., Buscot, F., Diekötter, T., Heinze, J., Hölzel, N., Jung, K., Klaus, V.H., Kleinebecker, T.,  
578 Klemmer, S., Krauss, J., Lange, M., Morris, E.K., Müller, J., Oelmann, Y., Overmann, J., Pašalić, E.,  
579 Rillig, M.C.S., H.M., Schloter, M., Schmitt, B., Schöning, I., Schrupf, M., Sikorski, J., Socher, S.A.,  
580 Solly, E.F., Sonnemann, I., Sorkau, E., Steckel, J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M.,  
581 Türke, M., Venter, P.C., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., Wolters,  
582 V., Wubet, T., Wurst, S., Fischer, M., Allan, E., 2016. Biodiversity at multiple trophic levels is needed  
583 for ecosystem multifunctionality. *Nature* 536. doi:10.1038/nature19092
- 584 Spalding, M.D., Meliane, I., Bennett, N.J., Dearden, P., Patil, P.G., Brumbaugh, R.D., 2016. Building  
585 towards the marine conservation end-game: consolidating the role of MPAs in a future ocean.  
586 *Aquatic Conservation: Marine and Freshwater Ecosystems* 26, 185-199. doi:10.1002/aqc.2686
- 587 Stasko, A.D., Swanson, H., Majewski, A., Atchison, S., Resist, J., Power, M., 2016. Influences of depth  
588 and pelagic subsidies on the size-based trophic structure of Beaufort Sea fish communities. *Marine  
589 Ecology Progress Series* 549, 153-166. doi:10.3354/meps11709
- 590 Sutton, T.T., Clark, M.R., Dunn, D.C., Halpin, P.N., Rogers, A.D., Guinotte, J., Bograd, S.J., Angel, M.V.,  
591 Perez, J.A.A., Wishner, K., Haedrich, R.L., J. Lindsay, D.J., Drazen, J.C., Vereshchaka, A., Piatkowski, U.,  
592 Morato, T., Błachowiak-Samołyk, K., Robison, B.H., Gjerde, K.M., Pierrot-Bults, A., Bernal, P.,  
593 Reygondeau, G., Heino, M., 2017. A global biogeographic classification of the mesopelagic zone.  
594 *Deep-Sea Research Part I: Oceanographic Research Papers* 126, 85-102.  
595 doi:10.1016/j.dsr.2017.05.006
- 596 Sutton, T.T., Porteiro, F.M., Heino, M., Bryrkjedal, I., Langhelle, G., Anderson, C.I.H., Home, J.,  
597 Sjøiland, H., Falkenbaugh, T., Godøc, O.R., Bergstad, O.A., 2008. Vertical structure, biomass and  
598 topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. *Deep-Sea  
599 Research Part II: Topical Studies in Oceanography* 55, 161-184. doi:10.1016/j.dsr2.2007.09.013
- 600 Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.-L., Gooday, A.J., Jones,  
601 D.O.B., Rex, M., Yasuhara, M., Ingels, J., Ruhl, H.A., Frieder, C.A., Danovaro, R., Würzberg, L., Baco,  
602 A., Grupe, B.M., Pasulka, A., Meyer, K.S., Dunlop, K.M., Henry, L.-A., Roberts, J.M., 2017. Major  
603 impacts of climate change on deep-sea benthic ecosystems. *Elementa: Science of the Anthropocene*  
604 5, 4. doi:10.1525/elementa.203
- 605 Tecchio, S., van Oevelen, D., Soetaert, K., Navarro, J., Ramírez-Llodra, E., 2013. Trophic Dynamics of  
606 Deep-Sea Megabenthos Are Mediated by Surface Productivity. *PLoS ONE* 8, e63796.  
607 doi:10.1371/journal.pone.0063796

- 608 Thresher, R.E., Adkins, J., Fallon, S.J., Gowlett-Holmes, K., 2011. Extraordinarily high biomass benthic  
609 community on Southern Ocean seamounts. *Scientific Reports* 1, 119. doi:10.1038/srep00119
- 610 Trueman, C.N., Johnston, G., O'Hea, B., MacKenzie, K.M., 2014. Trophic interactions of fish  
611 communities at midwater depths enhance long-term carbon storage and benthic production on  
612 continental slopes. *Proceedings of the Royal Society B: Biological Sciences* 281.  
613 doi:10.1098/rspb.2014.0669
- 614 Turner, J.T., 2015. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological  
615 pump. *Progress in Oceanography* 130, 205–248. doi:10.1016/j.pocean.2014.08.005
- 616 UNGA, 2015. Resolution 69/292. Development of an international legally binding instrument under  
617 the United Nations Convention on the Law of the Sea on the conservation and sustainable use of  
618 marine biological diversity of areas beyond national jurisdiction.
- 619 United Nations, 2015. Sustainable Development Goal 14: conserve and sustainable use the oceans,  
620 seas, and marine resources for sustainable development.  
621 <https://sustainabledevelopment.un.org/sdg14> (accessed 2 March 2017).
- 622 Watling, L., Auster, P.J., 2017. Seamounts on the High Seas Should Be Managed as Vulnerable  
623 Marine ecosystems. *Frontiers in Marine Science* 4, 14. doi:10.3389/fmars.2017.00014
- 624 Weber, T., Cram, J.A., Leung, S.W., DeVries, T., Deutsch, C., 2016. Deep ocean nutrients imply large  
625 latitudinal variation in particle transfer efficiency. *PNAS* 113, 8506-8611.  
626 doi:10.1073/pnas.1604414113
- 627 Westberry, T., Behrenfield, M.J., Siegel, D.A., Boss, E., 2008. Carbon-Based Primary Productivity  
628 Modeling with Vertically Resolved Photoacclimation. *Global Biogeochemical Cycles* 22, GB2024.  
629 doi:10.1029/2007GB003078
- 630 Williams, J.J., Papastamatiou, Y.P., Caselle, J.E., Bradley, D., Jacoby, D.M.P., 2018. Mobile marine  
631 predators: an understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the*  
632 *Royal Society B: Biological Sciences* 285, 20172456. doi:10.1098/rspb.2017.2456
- 633 Wilson, R.W., 2014. Fish, In The Significance and Management of Natural Carbon Stores in the Open  
634 Ocean. Full report. eds D. Laffoley, J. Baxter, F. Thevenon, J. Oliver, pp. 79-92. IUCN, Gland,  
635 Switzerland.
- 636 Wilson, R.W., Millero, F.J., Taylor, J.R., Walsh, P.J., Christensen, V., Jennings, S., Grosell, M., 2009.  
637 Contribution of fish to the marine inorganic carbon cycle. *Science* 323, 359-362.  
638 doi:10.1126/science.1157972
- 639 Woolley, S.N.C., Tittensor, D.P., Dunstan, P.K., Guillera-Aroita, G., Lahoz-Monfort, J.J., Wintle, B.A.,  
640 Worm, B., O'Hara, T.D., 2016. Deep-sea diversity patterns are shaped by energy availability. *Nature*  
641 533, 393-396. doi:10.1038/nature17937
- 642 Wright, G., Ardron, J., Gjerde, K., Currie, D., Rochette, J., 2015. Advancing marine biodiversity  
643 protection through regional fisheries management: A review of bottom fisheries closures in areas  
644 beyond national jurisdiction. *Marine Policy* 61, 134-148. doi:10.1016/j.marpol.2015.06.030