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Review Paper

Ecological connectivity across ocean depths: Implications for protected area design

Bethan C. O'Leary*, Callum M. Roberts

Department of Environment and Geography, University of York, York, YO10 5NG, United Kingdom

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ABSTRACT

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

1. Introduction

Two major developments are underway in the world of marine conservation. First, following adoption into Sustainable Development Goal 14 (United Nations, 2015) of the Convention on Biological Diversity's target for ≥10% ocean protection by 2020 (Convention on Biological Diversity, 2010), there is renewed impetus to meet this target. Coastal nations of the world are embarked on a rapid program of marine protected area (MPA) establishment that at last looks set to achieve this coverage target (Convention on Biological Diversity, 2017), following nearly two decades of slow progress (O'Leary et al., 2018). The second, is that a process has been underway at the United Nations for more than two years to negotiate a mechanism to create MPAs in areas beyond national jurisdiction, amongst other conservation measures (UNGA, 2015). This shared ocean space

* Corresponding author.
E-mail address: bethan.oleary@york.ac.uk (B.C. O'Leary).

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constitutes approximately 61% of the oceans, 44% of the surface of the Earth and 65% of the volume of the biosphere but remains the least protected space on the planet (Gjerde et al., 2016). After a promising start, the process looks set to produce a legal instrument within the next two years, following a conference of the UN General Assembly.

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

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

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

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

2. Ecological connectivity between surface and seabed ecosystems

Seabed and water column communities are often considered separately. Emphasising this distinction, scientists divide the open ocean into a series of realms based on depth: epipelagic (0–200 m), mesopelagic (200–1000 m), bathypelagic (1000–4000 m), abyssopelagic (4000 m to directly above the ocean floor) and hadopelagic (ocean water in submarine trenches). However, this vertical classification is a convenience and an oversimplification. Different depths are linked through a wide variety of mechanisms including energy production and transfer in food webs, cycling of nutrients and raw materials, shifts in habitat use as creatures develop and grow, and daily and seasonal vertical migrations (Arellano et al., 2014; Davison et al., 2013; Howey et al., 2016; Nakamura and Sato, 2014). The transitions between these human-conceived vertical layers are gradients, not sharp boundaries, and ecological distinctions are blurred with ocean currents and animals connecting the various depths.

2.1. Food-web interactions and surface to seabed relationships

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

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