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Entering the Twilight Zone: The ecological role and importance of mesopelagic fishes

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Ocean waters between 200 and 1000m deep – the Twilight Zone – sustain immense quantities of fish, believed to be greater than the combined mass of all fish living closer to the surface, that the fishing industry is keen to exploit. But their value to the planet's life support system and in climate mitigation is likely far greater than their value as food.

We must urgently protect them from fishing while we undertake research to determine their importance in global ocean processes.

1. EXECUTIVE SUMMARY

"Not everything that meets the eye is as it appears"

- Rod Serling, The Twilight Zone: Complete Stories

The above sentiment is certainly true of the ocean. Powerful and complex, the ocean dominates the Earth's global processes and supports life from the majestic to the bizarre. Most people, however, from their land-bound perspective, see the sea only as a playground backed by a vast expanse of featureless water. But the ocean has three-dimensions and holds 97% of the liveable space on the planet. What lies beneath deserves greater recognition and respect.

The ocean's three dimensions are structured. While some creatures criss-cross different depth zones, particularly deep-diving predators like whales and tuna, most life is specialised to live in particular layers. The twilight zone, between 200 m and 1,000 m, is a place where little sunlight penetrates. It is one of the least understood places on the planet because it is so vast and difficult to study. The creatures glimpsed there stretch the bounds between reality and fantasy. Nonetheless, it could be one of the most important parts of the global ocean for life on Earth and human wellbeing.

1.1 WHY THE TWILIGHT ZONE MATTERS

The twilight zone, referred to by scientists as the mesopelagic, constitutes about 20% of the global ocean volume and contains an extraordinary biomass of invertebrates and fish, such as squid and lanternfishes. Scientists have found tantalising evidence that by weight, mesopelagic fishes could make up more than 90% of all fish in the sea. Mesopelagic fishes are small, quirky looking and live throughout the world ocean. Areas of particularly high biomass include the north Atlantic, Arabian Sea and Mediterranean Sea, while the polar seas and south Atlantic generally appear to contain low mesopelagic biomass and diversity compared with other ocean basins (Figure 1).

Many mesopelagic fishes undertake a daily commute, migrating vertically at night to feed in shallow waters above 200 m in the safety of darkness and then retreating to the depths by day. This unseen mass movement is thought to be the largest daily migration on Earth. By eating, being eaten, breathing and defecating across ocean depths, they present a key mechanism for ocean uptake and sequestration of carbon, thereby helping to slow the rate of global warming, and are an important driver for other biogeochemical cycles. They are also a crucial food source for predators, particularly ocean-going megafauna like tuna and dolphins. Given their vast abundance, wide distribution and vertical migration, the collective influence of mesopelagic fishes on the structure and function of ocean ecosystems is likely to be great, but details of their ecological role are still to be fully established.

1.2 THREATS TO MESOPELAGIC FISHES

The vast abundance of mesopelagic fishes is attracting growing interest from the fishing industry, particularly to plug the expected deficit in feed for farm animals and aquaculture as the human population grows. Some nations, like Norway and members of the EU, are funding substantial research and trial commercial fisheries. Others are worried about the consequences of large-scale exploitation. The United States, for example, has proactively prohibited directed commercial fisheries for mesopelagic fishes in its Pacific waters for the time being due to concerns over potential adverse ecosystem consequences.

Much of the mesopelagic is at great risk today. Beyond the limits of national jurisdiction, there is a vast pool of water where no regulations exist to protect twilight zone fish. The high seas, as these international waters are colloquially known, constitute 61% of the world's ocean and 43% of the Earth's surface (Figure 1). They are owned by everyone and no-one, being collectively governed under the United Nations Law of the Sea. In recognition of growing human impact on high seas marine life, the UN is currently negotiating a new international agreement to improve management and conservation, however mesopelagic fishes have been largely ignored in these negotiations to date. That omission needs urgent rectification.

1.3 THE STUDY

To inform negotiations at the UN to protect biodiversity in international waters, to better manage emerging fishing activities and to better assess the wisdom of exploitation, this report considers the global importance of mesopelagic fishes in ocean ecosystems. We examine their roles as food for higher ocean predators and in the cycling of carbon and nutrients, and assemble information on fisheries activity to determine current exploitation threats. Finally, we identify key uncertainties in our understanding that it is essential that we fill to ensure effective conservation not just of the mesopelagic zone, but of its broader connections with the marine environment globally. Although many animal groups inhabit mesopelagic depths, we focus on mesopelagic fishes given their large biomass, daily vertical migrations, and rapidly increasing commercial interest.

1.3.1 Mesopelagic fishes are important as food for surface living predators

We analysed the importance of mesopelagic fish in the diets of tuna and sharks based on research published between 1996 and 2017. Mesopelagic fishes varied substantially in importance for different predator species, contributing the greatest proportion of prey, in terms of weight, for deeper diving (e.g. bigeye tuna, 26%) and deeper benthopelagic (e.g. longnose velvet dogfish, 83%) or pelagic-oceanic (e.g. bigeye thresher shark, 22%) species (Figure 2). There is circumstantial evidence for high importance of mesopelagic fish as food for large predators. For example, aggregations of yellowfin and bigeye tuna, overlap with, and appear to feed on, spawning aggregations of the lanternfish *Diaphus danae* in the Coral Sea. A seasonal tuna fishery in the equatorial Atlantic Ocean has been linked to the presence of large schools of the mesopelagic fish, *Vinciguerria nimbaria* (Photichtyidae). And off the coast of Costa Rica, vast 'superpods' of dolphins up to ten thousand strong have been filmed feeding on lanternfish they have trapped at the surface.

1.3.2 The role of mesopelagic fishes in carbon cycling

Determining the influence of marine life on environmental CO_2 levels has important consequences for understanding of global carbon cycling, particularly the uptake and storage of carbon from the atmosphere to the deep ocean. We identified three potential mechanisms by which mesopelagic fishes may contribute to carbon cycling (Box 1).

Estimates of the contribution of mesopelagic fishes to organic carbon export from the surface to the deep sea vary between more than 10% of the total carbon export from surface to deeper waters, to greater than 40%. It has been estimated that mesopelagic fishes play such an important role in carbon sequestration in the deep sea, that without them, atmospheric CO_2 levels would be 50% greater and global temperatures several degrees centigrade higher.

1.3.3 Fisheries interest and exploitation potetial

We searched peer-reviewed and grey literature for records of commercial or exploratory fisheries and levels of vulnerability of mesopelagic fishes. While there is considerable and relatively long-standing interest in industrial-scale exploitation of mesopelagic fish, we found few records of commercial and exploratory fisheries activity so far. Challenges faced in developing fisheries include patchy distribution of mesopelagic fish concentrations, trawl avoidance behaviour, difficulties in processing catches and high operating costs. We found very limited evidence of the likely vulnerability of mesopelagic fishes to exploitation, which represents a fundamental gap in our understanding and ability to sustainably manage future fisheries for them. The prevalence of overexploitation in existing and past fisheries signal the need for great caution in developing new fisheries in what is evidently a highly sensitive environment. Catches to date have been highly variable with larger catches often followed by rapid declines (Figure 3), underlining the need for a highly precautionary approach.

Box 1: Mechanisms by which mesopelagic fishes contribute to carbon cycling

Mechanism 1: Mesopelagic fishes consume organic matter from surface waters which is then metabolised at c.500-700m deep, and faeces produced at this depth transfers carbon to deep water.

Mechanism 2: Mesopelagic fishes precipitate and excrete calcium carbonate within their intestine as a by-product of drinking seawater for osmoregulation. Dense inorganic carbonate precipitates within faecal pellets may then facilitate sequestration of surface CO_2 to ocean depths by speeding up the sinking of organic carbon once excreted.

Mechanism 3: Mesopelagic fishes' gut carbonates produced at depth but excreted near the surface would rapidly dissolve and contribute to the net transfer carbonate alkalinity from the deep, to the surface ocean which may help counteract surface ocean acidification from rising atmospheric CO_2.

1.4 CONCLUSION

Mesopelagic fishes have potentially enormous importance in the global ocean, as prey for other species, many of these predators themselves, targets for valuable fisheries, and for their role in sequestering carbon into the deep sea and mitigating climate change. But there is a threat on the horizon as companies and nations prospect for new fishing opportunities to fill rising global demand for fishmeal and oil. The mesopelagic of the open ocean is one of the last remaining frontiers for exploitation. So far, even where targeted, mesopelagic fishes have been protected to some degree by their ability to avoid trawling gear and the high operating costs of commercial fisheries. However, as innovation of new fishing methods is likely, these features are unlikely to protect them for long. Based on what we already know, large-scale commercial fishing of mesopelagic fishes could have catastrophic consequences for marine life and global climate. The ecological and environmental value of the twilight zone almost certainly far exceeds its extractive value.

In recognition of growing human impact on high seas marine life, the UN is currently negotiating a new international treaty to protect biodiversity beyond national jurisdiction. The negotiations offer a crucial opportunity to extend protection to mesopelagic fish. Given the value of mesopelagic fish and the great planetary risks from unbridled exploitation, negotiators should ensure they can be properly protected through mechanisms including marine protected areas which extend from surface to seabed. As ever, there is much more science to be done to understand the roles mesopelagics play in nutrient and carbon cycling, and on their importance to ocean and planetary processes. Some of it is underway, and there are great opportunities for more research allied with the International Decade of Ocean Science for Sustainable Development which begins in 2021. We urge that there is a global moratorium on development of new mesopelagic fisheries while this research is undertaken.

Tweetable abstract

Deep living mesopelagic fishes are abundant, poorly known, potentially critical food for large predators, and key to mitigating climate change. It is vital we protect them from fishing until we better understand these roles. They are likely worth far more alive than dead.

2. THE MESOPELAGIC REALM

The open ocean is the largest ecosystem on Earth but also one of the least studied, especially in mid-waters. Here, between depths of 200 to 1,000 m is the 'mesopelagic' or 'twilight' zone, where virtually no light penetrates, and below which none does (Figure 1). As the mesopelagic zone lacks sufficient light to support photosynthesis [5], many of its inhabitants rely on the passive transport of organic material from surface to deeper waters, which is called "marine snow", and its subsequent remixing [5, 38]. In addition, active transfer of nutrients occurs through the process of vertical feeding migrations.

By volume, about 20% of the sea is mesopelagic [2] and this volume contains a huge biomass of fish and invertebrates [3], many of which make daily vertical migrations from deeper to shallower depths [4-6]. Scientists estimate the mesopelagic may contain up to 10 billion tons of fish, or about 90% of all the fish in the sea [3, 7]. With the worldwide fish catch in decline [9], and continued demand for fish meal and oil for aquaculture and farming [10] [11-13], there is growing interest in the development of commercial mesopelagic fishing [4, 8] (Box 2). However, before any exploitation occurs, it is critical to better understand the biology and ecology of marine life of this zone, so as not to inflict the irreversible damage from overfishing and destructive fishing that has affected other parts of the sea.

Life in the mesopelagic zone was originally identified from early echo sound traces as a 'deep scattering layer' that was sometimes so dense it was mistaken for the seabed [2]. This scattering layer phenomenon has been noted worldwide (Figure 2) [2, 14] and is particularly prevalent in the north Atlantic, Arabian Sea and Mediterranean Sea. It was less strong in polar seas and the South Atlantic where we now know levels of life and biodiversity in the mesopelagic are lower than typical [2, 14]. The density of mesopelagic fish in deep scattering layers is influenced by surface levels of phytoplankton production, temperature, and wind stress [2] although how these influences are mediated is not currently clear. Another finding is that abundance of mesopelagic fish increases in areas with complex seabed topography and oceanography [6, 14].

To date, mesopelagic fish have received little commercial exploitation, although that may change rapidly (Box 2). This means that UN negotiations on Biodiversity Protection Beyond National Jurisdiction are a timely and important opportunity to introduce safeguards on fisheries that may develop in future [15].

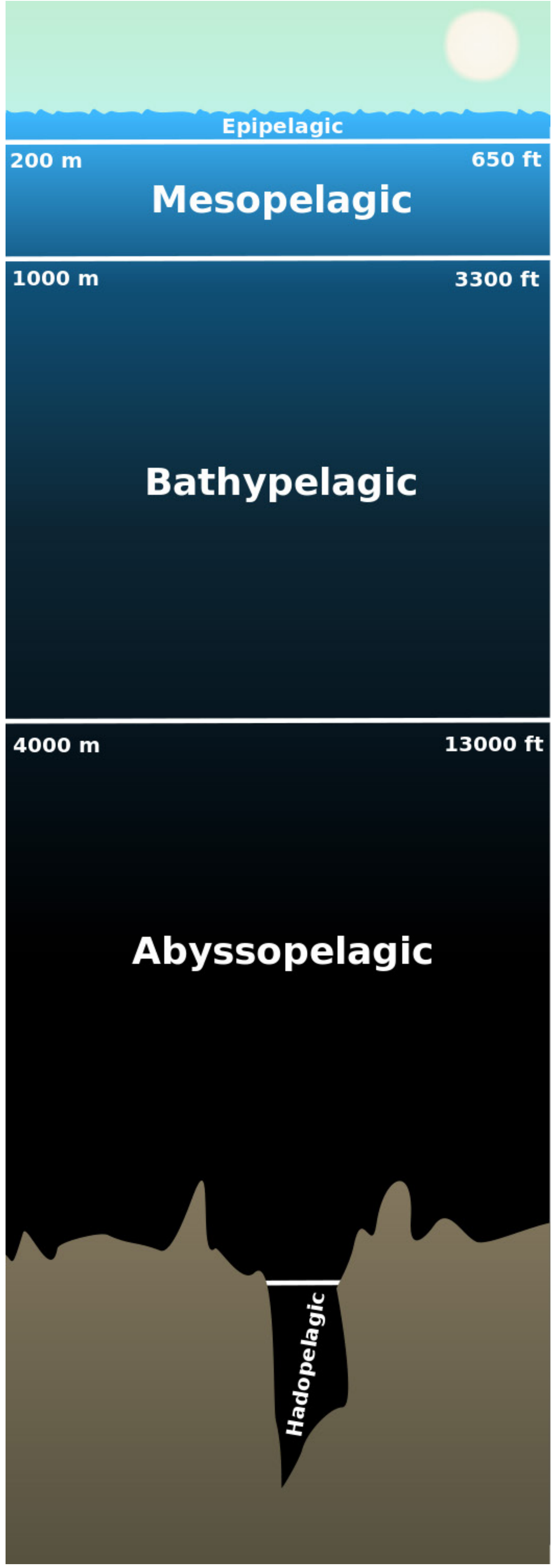

Figure 1: Depth zones of the world ocean (Wikimedia commons).

Box 2: Examples of recent initiatives to explore the potential for mesopelagic fisheries and the markets they would create.

MEESO, (Ecologically and Economically Sustainable Mesopelagic Fisheries, funded by EU Horizon 2020, 2019-2023, €6,396,633.75). This international collaboration between researchers from 10 EU member states is coordinated by the Institute of Marine Research Norway, to determine the development potential of sustainable mesopelagic fishing.

SUMMER, (Sustainable management of mesopelagic resources, funded by EU Horizon 2020, 2019-2023, €6,481,308.75). An international collaboration between researchers from EU member states, coordinated by Fundacion Azti, which for the mesopelagic aims to: i) estimate fish biomass, ii) quantify ecosystem services and iii) assess how fishing might affect ecosystem services. SUMMER will also consider the potential to incorporate mesopelagic fish into meal production, nutraceuticals (e.g. dietary or food supplements) and pharmaceuticals.

MESOPP, (Mesopelagic Southern Ocean Prey and Predators, funded by EU Horizon 2020, 2016-2019, €1,061,690). A collaborative network between European and Australian research teams interested in the Southern Ocean and Antarctica, to investigate how climate change will affect exploitation there.

PANDORA, (PAradigm for New Dynamic Ocean Resource Assessments and Exploitation, funded by EU Horizon 2020, 2018-2022, €5,598,388.75). A 25-partner consortium of researchers which aims to create long-term benefits for European fisheries through provision of better methods for stock assessment of mesopelagic fisheries.

Norwegian Mesopelagic Initiative, 2017. An international consortium of researchers aiming to develop sustainable mesopelagic fishing via improved gear and new technology, and to accredit mesopelagic catches from with sustainability labels.

Most species of mesopelagic fish undertake daily vertical migrations whereby they typically congregate in large numbers at around 500 m deep with less dense concentrations sometimes also present at about 800 m [2, 4]. At night these groupings disperse when fish move upward to feed in shallower waters, thereafter re-aggregating at depth after sunrise [4, 16]. Of the species which don't vertically migrate, most typically remain at 700 m or deeper [6, 16, 18]. Although brief in its duration and short in distance, the vertical movement of mesopelagic fish is remarkable for its vast geographic extent and the enormous number of species and individuals involved [17]. Collectively, it represents the greatest migration on Earth.

Within the mesopelagic as a whole, species' depth distributions and daily migration patterns show substantial geographic variation [18]. The exact mechanisms driving differences are unclear, but levels of oxygen, light, turbidity, and sea surface temperature all likely contribute [18]. Mesopelagic fish behaviour also changes at different times in species' life cycles. Initially larvae tend to occupy warmer, surface waters before moving deeper after some development;

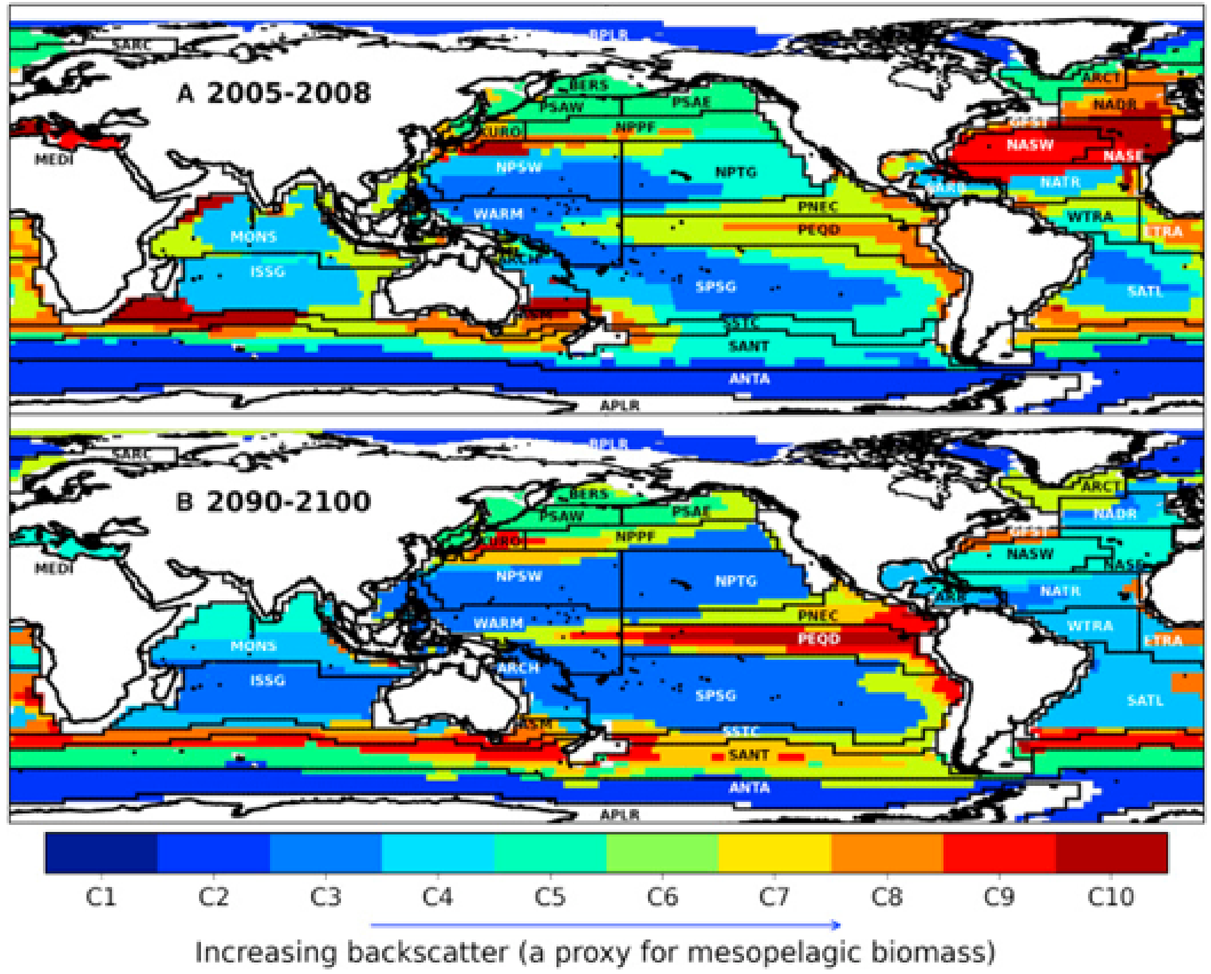

Figure 2: Present day distribution of mesopelagic biomass throughout the world ocean (reproduced from Proud et al. 2017).

there they subsequently remain, grow and begin to undertake vertical migrations [19, 20]. However much remains unknown about the periodicity of mesopelagic migrations, what proportion of a population moves, and how these factors vary geographically.

Mesopelagic fish groups include the characteristic and dominant lanternfish (Myctophidae), plus bristlemouths (Gonostomatidae), barbeled dragonfish (Stomiidae), hatchetfish (Sternoptychidae), lightfish (Phosichthyidae), barracudina (Paralepididae) and snake mackerels (Gempylidae), amongst others (Figure 3) [19]. Conditions for these fish include near darkness, cold water, low oxygen, high pressure and episodic and/or remote food supply [5]. To help cope with the dark, many species have large, highly light sensitive eyes, binocular vision and use bioluminescence to find food, mates or to confuse predators [21]. Mesopelagic fish are typically small (<10 cm), dark, thin, have short lifespans (<5 years), display early sexual maturity, and have low fecundity [16, 19]. However, a lot of basic biology about most species remains unknown.

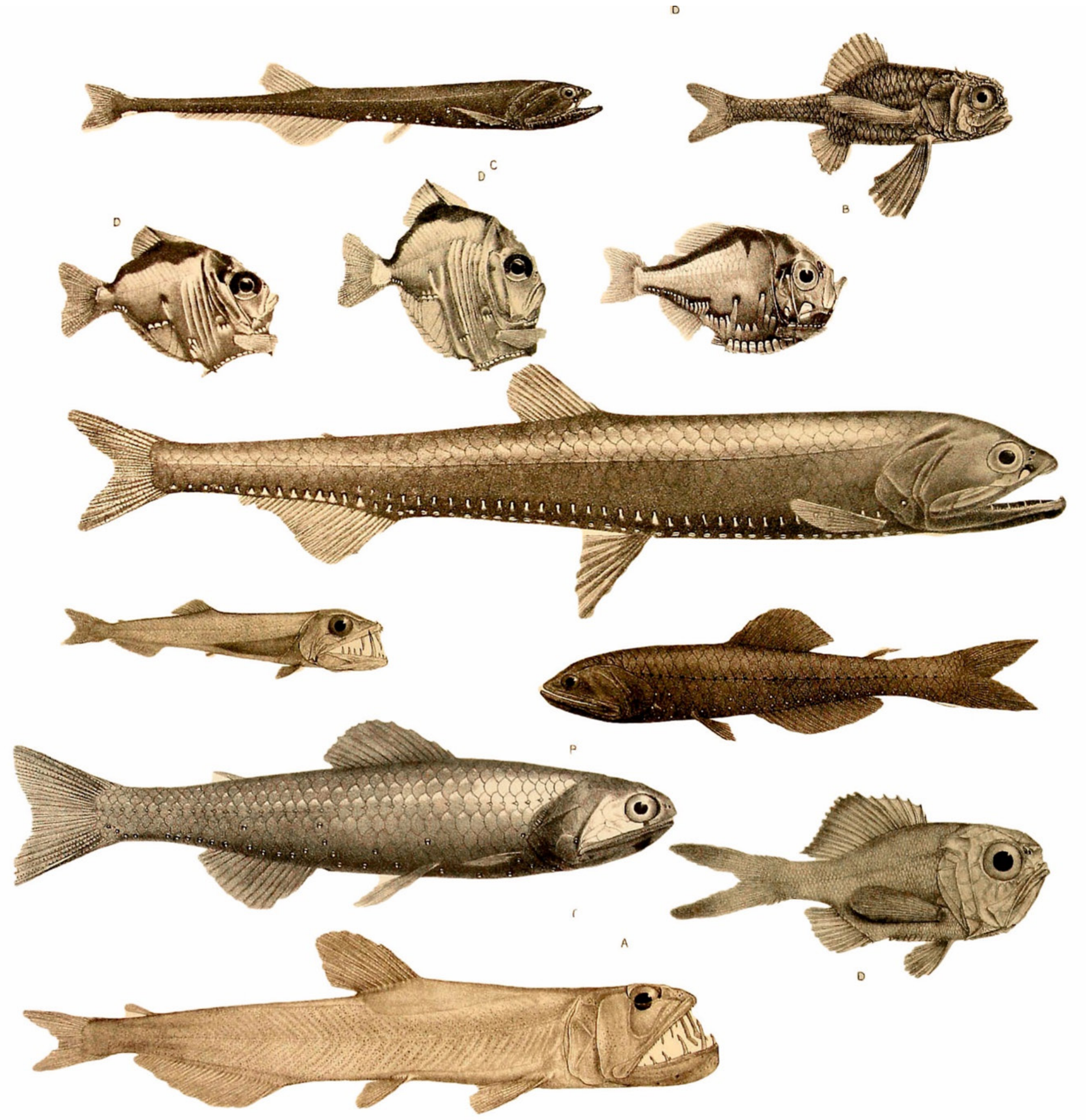

Figure 3: Examples of mesopelagic fish (source: Günther, 1887 Report of the scientific results of the voyage of H.M.S. Challenger during the years 1873-6).

Top row left, Elongated bristlemouth (*Gonostoma elongatum*), top row right, Ridgehead (*Poromitra megalops*); second row left, two forms of Diaphanous hatchet fish (*Sternoptyx diaphana*), second row right, Spiny hatchetfish (*Polyipnus spinosus*); third row, Silver lightfish (*Phosichthys argenteus*); fourth row left, Hammerjaw (*Omosudis lowii*), fourth row right Black lantern fish (*Nannobrachium nigrum*); fifth row left, Blue lanternfish (*Diaphus coeruleus*), fifth row right, Mediterranean slimehead (*Hoplostethus mediterraneus*); bottom row, Balbo sabretooth (*Evermannella balbo*).

3. FOOD WEB LINKS BETWEEN SURFACE OCEAN PREDATORS AND MESOPELAGIC FISH

As major consumers of zooplankton, taken at depth, mesopelagic fish transfer energy up the food chain, and relocate nutrients from deeper waters [5]. In turn they are eaten by open ocean predators such as billfish, tuna, sharks, rays, and whales which dive deep to feed on them [e.g. 24, 25, 26]. Although comprehensive dietary analyses are not available for most open ocean apex predators [22, 23], data for sharks [e.g. 27], tuna [22], billfish [e.g. 28], and marine mammals [e.g. 29] suggests the relative contribution of mesopelagic fish in their diets varies by location, season, and opportunity. For example, yellowfin tuna in the eastern Pacific have been shown to shift from feeding on bigger, shallow water prey, to smaller, mesopelagic species following declines in shallow water prey from over-exploitation and environmental change [23]. By contrast in the North Pacific, decadal reductions in abundance of sharks, tuna and marlin have occurred alongside increased abundance of mesopelagic lancetfish (*Alepisaurus ferox*) and snake mackerel (*Gempylus serpens*) which are important prey for them [30]. Modelling studies predict that a reduction of mesopelagic fish biomass could cause population declines of small pelagic tuna, sharks, marine mammals and some deep-sea fish [31 32].

3.1 THE DIETARY IMPORTANCE OF MESOPELAGIC FISH FOR TUNA AND SHARKS

To assess the relative contribution of mesopelagic fish in the diets of opportunistic, generalist, high trophic level tuna and sharks, we conducted a scientific literature search of articles published between 1996 and 2017 which reported the stomach contents of adult and juvenile wild-caught animals (i.e. not: larval stages, caged, artificially fed or fattened, or fish caught underneath Fish Aggregating Devices) as percent weight (%W) or mean percent weight (%MW) (Box 3). We then calculated weighted means for each prey group to account for the number of stomachs a study had examined.

Our results suggest that mesopelagic fishes vary substantially in their importance as food for different species of sharks and tuna. For deep diving predators such as bigeye tuna, longnose velvet dogfish, and bigeye thresher shark, they were the most important prey in terms of weight, contributing 26%, 83% and 22% respectively (Figure 4). This concurs with results from a recent meta-analysis of the diets of yellowfin, bigeye and albacore tuna which found that bigeye tuna consume large quantities of mesopelagic prey [22]. That study also noted regional differences in dietary diversity of these three species, with greater prey diversity consumed in low productivity offshore regions where feeding opportunities are fewer [22]. For sharks, we couldn't find any other meta-analysis to compare with our own.

When interpreting studies of stomach content analyses, it must be remembered that numerous factors affect the reliability of findings and that very large sample sizes are required to draw strong conclusions [34]. Certainly, reliance of ocean predators on mesopelagic fish is variable across time, place, and species life stages. For example, in the Coral Sea, aggregations of yellowfin and bigeye tuna overlap with, and appear to feed on, spawning aggregations of the lanternfish Diaphus danae [35]. Similarly in the equatorial Atlantic, a seasonal tuna fishery has been linked to the presence of large schools of the mesopelagic fish, Vinciguerria nimbaria (Photichtyidae) [36]. As a general conclusion it is safe to say that better understanding of the links between mesopelagic fish and their higher trophic level predators is required prior to any expansion of mesopelagic fishing, consistent with the precautionary approach.

Box 3: Analyses of stomach content studies to estimate mesopelagic fish consumption by large open ocean tuna and sharks.

Percentage weight (%W) of each prey taxon is calculated by dividing the total weight of a given taxon by the total weight of prey in all stomachs pooled, i.e. the percentage the prey item contributes to total prey weight in all stomachs sampled:

$$\%W = \frac{\sum(prey_i)}{\sum(prey_{i-j})} x100$$

Average percent weight (%MW) is determined by calculating the %W of all prey taxa for each individual stomach by dividing the volume of each prey taxon by the total volume of prey in that stomach, and calculating the mean:

$$\%MW = \frac{\left(\frac{prey_a fish_i}{\sum prey_i}\right) + \left(\frac{prey_b fish_j}{\sum prey_j}\right)}{N_{fish}} x100$$

Percentage Weight (%W) has drawbacks as a measure of prey importance: it suffers from pseudoreplication because prey items in individual stomachs are not independent; it emphasises the relative contribution of larger prey that are more slowly digested and easier to identify, and it only provides a single measure with no confidence internals [1]. However, it was the most commonly used dietary measure in identified studies for most species.
Weighted means give greater emphasis to studies with larger sample sizes and were calculated by multiplying the %W or %MW of each prey group with the number of stomachs sampled, divided by the total number of that species stomachs sampled across all studies.

$$Weighted\ mean = \frac{\%W\ or\ \%MW\ x\ N^{i}_{fish}}{\sum N^{i,j\ldots n}_{fish}}$$

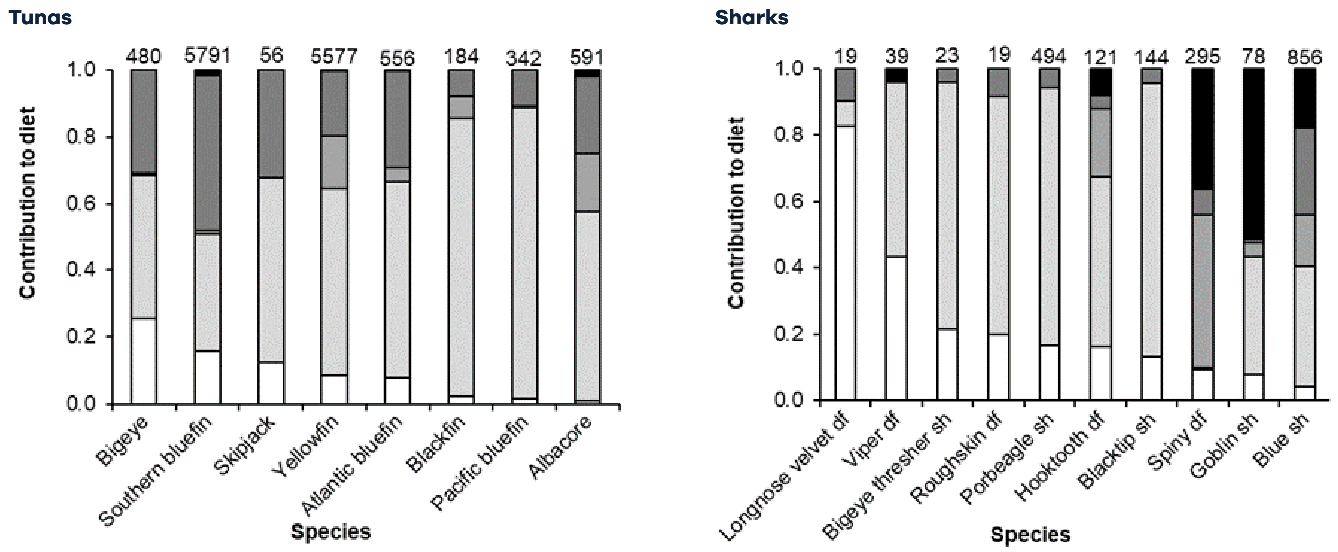

Figure 4: Average proportional contribution of mesopelagic fish (white), other fish (light grey), crustaceans (mid-grey), cephalopods (dark grey), and other organisms (black) to the diet of (a) tuna and (b) sharks (where the relative contribution of mesopelagic fish is ≥4%), ranked according to size of contribution from mesopelagic fish. Number of sampled stomachs included in analysis shown above each bar. Data cover the period 1996-2017 and represent the weighted mean from all included studies that reported %W. Abbreviations in (b): df = dogfish, sh = shark.

4. THE ROLE OF MESOPELAGIC FISH IN OCEAN CARBON CYCLING

The ocean is a major carbon sink, sequestering atmospheric carbon which becomes stored in bottom sediments. Biologically driven processes such as surface water productivity, and the transport of organic and inorganic carbon particles to depth with subsequent burial or breakdown, work with physical processes such as ocean circulation and gravity-driven sinking to allow the ocean to sequester greater quantities of carbon than it could without life. Phytoplankton are responsible for a large part of this ‘biological pump’, fixing around 50 billion tonnes of carbon dioxide into organic material each year via photosynthesis [37]. This organic material is then either consumed by organisms from higher trophic levels, respired, or is broken down by decomposers and recycled into further primary production, or sinks to become buried in deep-sea sediments.

As organic matter is transferred through the water column it is consumed by open water organisms ranging from microbes to fish, and then respired, used for growth and reproduction, egested or moved through food webs via predation [5, 38]. By consuming organic matter from surface waters then metabolising it at c.500-700m deep, faeces produced by mesopelagic fish transfers carbon to deep water [39]. The estimated extent of this contribution differs geographically. For example, figures for carbon that mesopelagic fish transport to depth are: 15-17% in the Northeast Pacific [40], in excess of 40% for the North Pacific Subtropical Gyre, less than 10% in the California Current [40], 28-55% in the western equatorial North Pacific [41], 8% on the Mid-Atlantic Ridge [42], and 12-32% in the Canary Islands [43]. Despite such variations, mesopelagic fish are clearly important to the organic and inorganic carbon cycles and a strong influence on zooplankton-mediated carbon export through predation.

Mesopelagic teleost fish also provide a second significant influence on ocean chemistry and biogeochemical cycles. They are able use internally generated bicarbonate to precipitate a calcium carbonate mineral from calcium ions present in ingested seawater and digested food within their intestine, and excrete this mineral within their faeces [44]. However, unlike most marine teleosts, the daily vertical migration of mesopelagics may provide a unique ecosystem service in the form an 'upward alkalinity pump'. Their gut carbonates are likely to be primarily produced when mesopelagic teleost fish carry out digestion in deeper water. The net effect of this calcification reaction in the intestine can be summarised as:

$$Ca^{2+} + 2HCO_3^- \leftrightarrow CaCO_3 + CO_2 + H_2O$$

However, it is likely these gut carbonate minerals are predominantly excreted near the surface due to a) the reduced ambient hydrostatic pressure there and b) an increased likelihood of the faeces being "pushed out" once they begin feeding activity near the surface. Because the excreted fish gut carbonates dissolve quickly in these shallow waters (Woosley et al., 2012), reversing the calcification reaction:

$$CaCO_3 + CO_2 + H_2O \leftrightarrow 2HCO_3^- + Ca^{2+}$$

this would result in the net transfer of dissolved alkalinity (bicarbonate) to the surface ocean, whilst the CO_2 generated by gut calcification would be excreted via the gills in the deeper ocean.

This 'upward alkalinity pump' would be environmentally highly beneficial because it helps counteract surface ocean acidification from rising atmospheric CO_2 [45]. However, conversely, animals in the mesopelagic may also fragment larger organic particles into smaller, slower-sinking ones [5, 46], thereby promoting release of CO_2. The balance of these processes and their influence on environmental CO_2 levels has important consequences for global carbon cycling but is currently difficult to quantify without more specific details of production and dissolution rates, and where these occur. As such it is a vital and increasingly active field of study [e.g. 47].

Finally, vertically migrating mesopelagic fish (and invertebrates) also contribute to a previously overlooked source of ammonium, excreted through their gills, and removal of fixed nitrogen in the deep ocean [48]. As ammonium is the most bioavailable form of nitrogen for anaerobic ammonium oxidation (termed "anammox"), mesopelagic animals play an important role in oxygen minimum zone biogeochemistry and nitrogen cycling in general.

5. FISHERIES POTENTIAL AND EXPLOITATION

Mesopelagic fish currently constitute unquantified bycatch in some trawl fisheries, particularly those for deep-sea shrimp [49-51]. However despite considerable and relatively long-standing interest in development of industrial-scale mesopelagic fisheries [Box 2, 8], very few commercial ones exist to date (Figure 5).

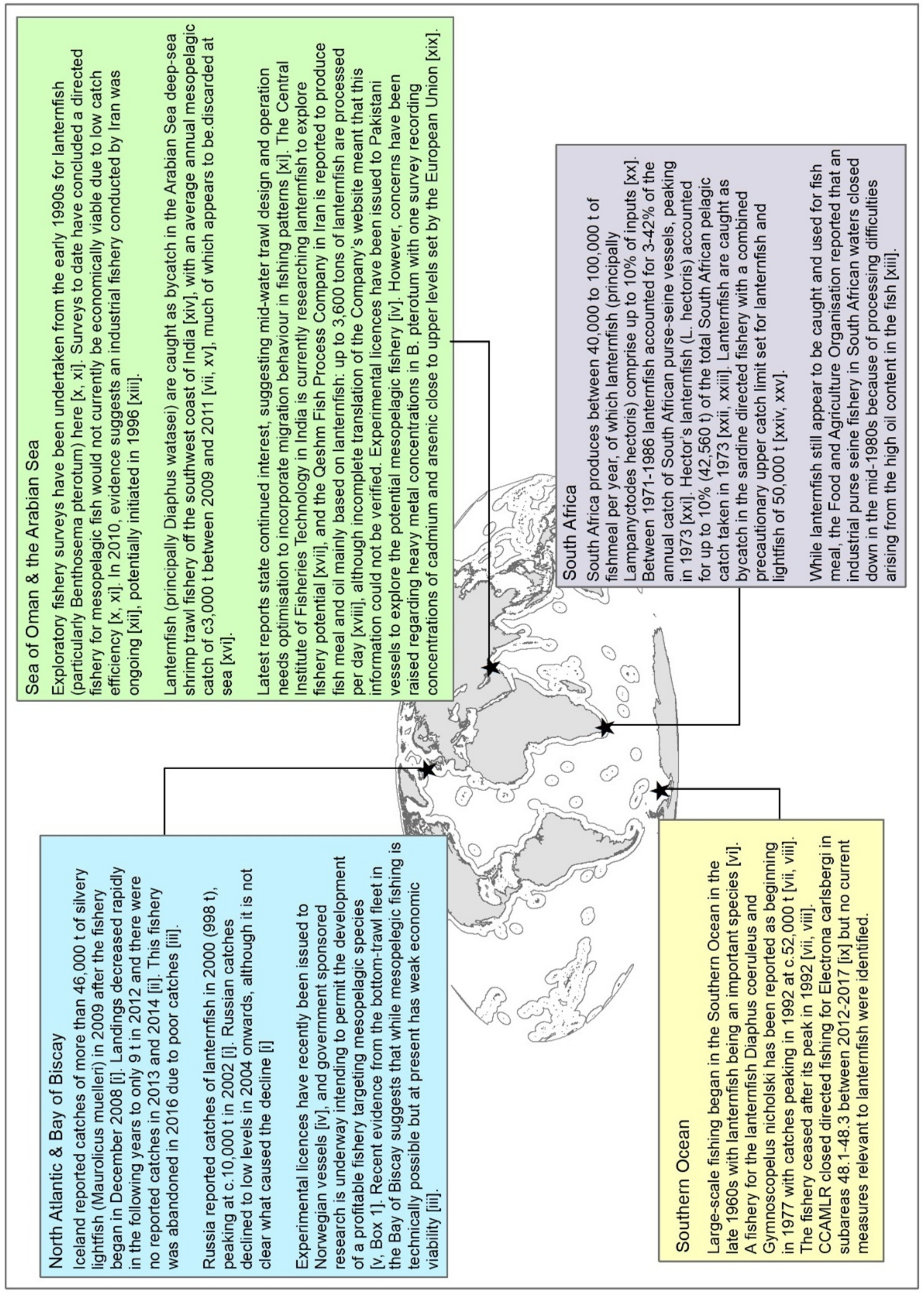

Figure 5: Evidence of existing fishery activity for lanternfish (Myctophidae) and identified constraints. Lanternfish were focussed on given their dominance in mesopelagic fish communities and commercial interest. References are indicated by Roman numerals and can be found at the end of the report.

The desire to target abundant Lanternfish has attracted particular interest [19], but these, like all mesopelagic fish groups, contain high content of fatty esters which cause diarrhoea, and a skin rash called seborrhoea which is potentially fatal (19, 52). As such mesopelagic fish are generally used to produce fish meal and oil rather than for direct human consumption [19, 53, 54, 55].

While not traditionally considered a mesopelagic species, blue whiting (*Micromesistius poutassou*) undertake vertical migrations between meso- and epipelagic realms [56] and have supported a large commercial fishery in the Northeast Atlantic since the 1980s [57]. However, abrupt changes in recruitment levels, likely driven by cyclical variations in oceanographic conditions, combined with high catches, have led to a boom-bust dynamic for the fishery [56, 58]. This example acts as a warning of potential problems from future mesopelagic fisheries, with ecological impacts arising when stocks are driven to low levels [56].

To date, evidence about vulnerability of mesopelagic fish to exploitation is mainly that catches have been highly variable with large initial catches rapidly followed by declines (Figure 5). Commercial fisheries have largely been inviable to date due to high operating costs, low catch rates due to patchy distribution of high fish concentrations, and animals able to modify their behaviour to avoid fishing gear [7, 59-62]. However with rising demand for fish and better capture methods being developed [62], it is inevitable that new mesopelagic fisheries will develop, with one currently under consideration in the Bay of Biscay for Mueller's bristle-mouth, *Maurolicus muelleri* [62], and Pakistan and Norway having also explored possibilities. By contrast the United States currently prohibits development of commercial mesopelagic fisheries in its Pacific waters due to concerns over potential adverse ecosystem consequences of fishing. This precautionary approach is very sensible given limited knowledge about the biology, ecology, and ecosystem roles of mesopelagic fish, and is one we advocate is taken up globally in the coming decade.

Finally, there is the question of equity to consider. Given that many concentrations of mesopelagic fish occur in international waters beyond national jurisdiction [2], the economic benefits of fishing them will likely accrue to just a few nations and large-scale corporations rather than supporting local livelihoods or contributing to worldwide food security [63]. Hence before any large-scale exploitation of mesopelagic fish begins, the likely social and economic impacts of creating them need careful prior investigation.

6. CONSERVATION IMPLICATIONS AND FUTURE PERSPECTIVES

By virtue of their extraordinary abundance, wide distribution and vertical migrations, mesopelagic fish and associated species are likely of great significance to the structure and function of ocean ecosystems. There are still many uncertainties to resolve about the quantity, composition and distribution of mesopelagic life in the sea, and global change is likely altering these characteristics fast. Warming seas, increased stratification, expansion of oxygen minimum zones, and changes in surface wind intensity and primary production under climate change are predicted to concentrate mesopelagic fish distribution into smaller areas (e.g. frontal regions) and shallower depths [2]. Shallowing depth profiles may reduce the capacity of mesopelagic fish to transport carbon to deeper waters, although in polar waters sea-ice reduction and increased primary production may counteract the issue there. Overall, it is hard to predict the likely effects of climate change on mesopelagic fish due to the complex additive, antagonistic, and synergistic effects involved.

As we have discussed, more scientific research is vital to better understand the roles that mesopelagic fish play in nutrient and carbon cycling, and for their importance to ocean and planetary processes as a whole. According to one estimate, without the carbon sequestration role played by mesopelagic fishes, atmospheric concentrations of CO_2 could be 50% greater, producing several degrees of global warming above pre-industrial conditions [82]. Opportunities for research could be allied with the International Decade of Ocean Science for Sustainable Development which begins in 2021. Greater scientific clarity needs to be acquired rapidly given fast-expanding global aquaculture with its huge demands for fishmeal and oil [10] and because fishing companies are investigating new capture methods for a resource that could replace the dwindling supplies from other fish stocks.

Throughout history, people have exploited first then asked questions later. In the ocean, we have sequentially overfished first coastal, then high seas, then deep sea waters [64]. The mesopelagic of the open ocean represents one of the last remaining frontiers for exploitation. We know enough already to appreciate how deeply unwise over-fishing the mesopelagic would be given the absolute necessity to protect the Earth's natural carbon stores and promote drawdown of carbon dioxide from the atmosphere. Given their role in carbon capture, mesopelagic fish are likely more valuable alive than dead due for their contribution to slowing the rate of climate change. Furthermore, exploiting mesopelagic fish may undermine existing commercial fisheries for higher trophic level species such as tuna and swordfish, as well as conservation efforts for marine mammals.

With the prospect of emerging mesopelagic exploitation, close regulatory oversight taking a highly precautionary approach is urgently required for both national and international waters. In recognition of the growing human impact on high seas marine life, the UN is currently negotiating a new agreement to improve the management and conservation of international waters. These negotiations offer a once-in-a-generation opportunity to empower nations to fulfil their duties to protect nature beyond national jurisdiction under the Convention on the Law of the Sea. To be effective, the new treaty will need to align agendas for conserving global biodiversity with those for climate change mitigation, and sustainable development. Given the value of mesopelagic fish and the great planetary risk from their unbridled exploitation, the treaty will need to include a mechanism for marine protected area creation with allows protection from the surface to the seabed [83,84].

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