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Contribution to the Themed Section: '*Mesopelagic resources*'

Developing the knowledge base needed to sustainably manage mesopelagic resources

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Recent estimates suggest that the mesopelagic zone could contain a total fish biomass of 2-19.5 gigatonnes, roughly equivalent to 100 times the annual catch of all existing fisheries. In addition to the possibility of direct consumption of mesopelagic species, there is interest in their use for fishmeal, as a source of dietary supplements for humans, and to bio-prospect pharmaceuticals. All of this, and the demands for a global food supply that can feed an ever-growing population, has driven interest in the mesopelagic. Thus, accurate quantification of the biomass of mesopelagic resources, their nutritional and genetic composition, their links to other components of the food web, to other oceanic realms and to biological and chemical oceanographic processes and cycles, are the focus of growing research activity. This information is needed to ensure the sustainable management of these resources. In this introduction, we summarize the contributions included in this theme set and provide some "food for thought" on the state-of-the-art in research on the mesopelagic, including identifying the knowledge that must be generated to support its sustainable management (e.g. the effect that extracting significant biomass might have on the pelagic ecosystem and the flow of material and energy through it).

Keywords: acoustic surveys, deep sea, energy transfer efficiency, food web, macroplankton, mesopelagic fish, microplankton, nutraceuticals, pharmaceuticals, transboundary resources, vertical migration.

Background and motivation for this article theme set

Until recently, there was comparatively little research activity on the mesopelagic zone (Figure 1a), and what there was focused on biological oceanographic processes such as carbon flux and on archaea and bacterioplankton (Table 1). Nonetheless, large mesopelagic organisms (mainly fish and squid) have long been proposed as potentially harvestable resources (e.g. FAO, 1997, 2001). Recent estimates suggest that the mesopelagic between 70°N and 70°S could contain a total fish biomass on the order of 9–19.5 gigatonnes (Gt; Irigoien *et al.*, 2014; Proud *et al.*, 2017, 2019), roughly equivalent to 100 times the annual catch of all existing fisheries. However, other estimates are considerably lower =2.4 to <1.4 Gt (Jennings and Collingridge, 2015; Anderson *et al.*, 2019). In addition to the possibility of direct consumption of mesopelagic species, there is interest in their use for fishmeal, as a source of "Omega-3" oils (as a dietary supplement for humans), and to bio-prospect for other nutraceuticals and pharmaceuticals. All of this, and the demands for a global food supply that can feed an ever-growing population (e.g. Springmann *et al.*, 2018), has driven a renewed interest in the mesopelagic (see IMR *et al.*, 2017; "Blue Growth Strategy," European Commission, Directorate-General for Maritime Affairs and Fisheries, Director-General, 2018; Figure 1a and b). Thus, accurate quantification of the biomass of mesopelagic resources, their nutritional and genetic composition, their diversity and their links to other components of the food web, to other oceanic realms and to biological and chemical oceanographic processes and cycles, are the focus of

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growing research activity (Figure 1a; and see Irigoien *et al.*, 2014; St. John *et al.*, 2016). This information is needed to ensure the sustainable management of these resources and the ecosystems to which they belong.

In order to ascertain the present state of knowledge about the mesopelagic, *ICES Journal of Marine Science* solicited contributions to the article theme set, "Mesopelagic resources—potential and risk." The intention was to motivate the submission of articles reporting novel advances to: estimate regional and global mesopelagic resources; more completely describe mesopelagic inhabitants, including basic knowledge of their biology and ecology; identify the trophic links between mesopelagic species (and those from other oceanic domains); characterize the functional roles of mesopelagic organisms in the ecosystem, including in the carbon cycle and sequestration of greenhouse gasses and other processes; explore the possible contribution of mesopelagic resources to global food security, human health, and marine bioprospecting; identify the economic and ecological risks of exploiting these resources and discuss the challenges facing the exploitation and sustainable management of mesopelagic resources, including legal responsibilities for regulating these transboundary resources. The contributions to this theme set provide new information on many of these topics.

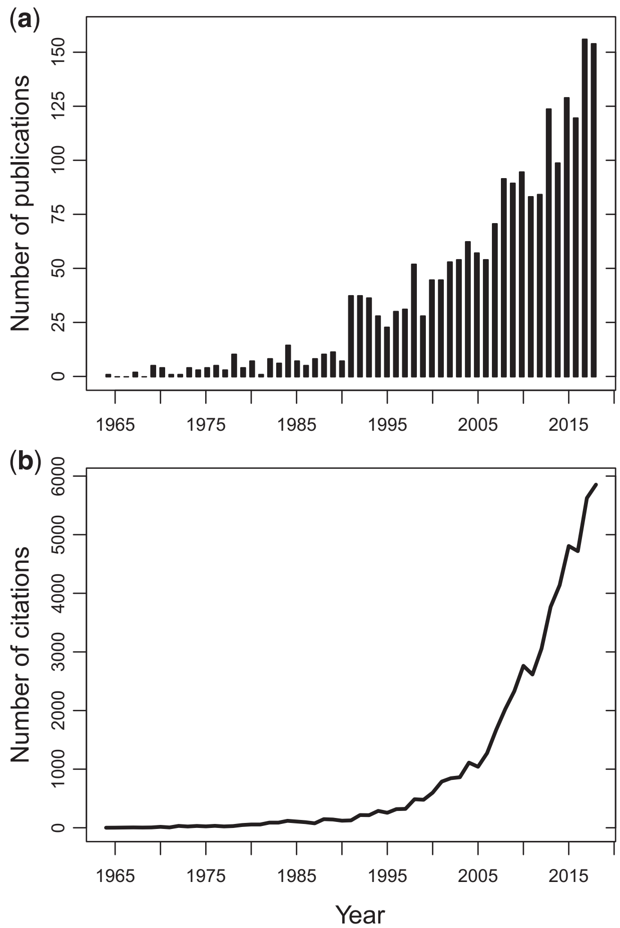

Figure 1. The number of publications (a) and citations (b) per year returned by a search of the Web of Science Core Collection for the term "mesopelagic" over the period 1945–2018, conducted on 25 February 2019. The total number of publications returned was 2025 and these were cited 54 703 times by 29 434 articles.

In this introduction, we summarize the contributions included in this theme set and provide some "Food for Thought" on the state-of-the-art in research on the mesopelagic, including identifying the knowledge that must be generated to support its sustainable management.

About the articles in this theme set, in the context of what is known/unknown

Habitat and distribution

Little is known about the composition, diversity, and distribution of mesopelagic communities, mostly owing to sparse data resulting from the challenges of sampling (St. John *et al.*, 2016). Thus, basic questions such as who is down there (biodiversity), what they are up to (trophic ecology), and what ecosystem processes (food web, material and energy fluxes) they support are still poorly known (Glover *et al.*, 2018). Dolan *et al.* (2019) describe the seasonal variation of heterotrophic protists (tintinnid ciliates, phaecodarian radiolarians, and amphisolenid dinoglagellates) in relation to water column structure. They report contrasting behaviour of the three protist groups compared with expectations, with distinct seasonal patterns among them. This study highlights that the most relevant ecological interactions in the mesopelagic ecosystem occur on fine temporal and spatial scales. Other recent research also supports the importance of looking at small scales to better understand the role of mesopelagic ecosystems in pelagic food webs (Proud *et al.*, 2018), and how regional and mesoscale ecosystems are structured (Proud *et al.*, 2017; Reygondeau *et al.*, 2018).

On the opposite extreme in terms of data availability are data-rich monitoring programs that collect larvae of all marine taxa. These monitoring programs are particularly relevant for mesopelagic species because sampling of early life stages provides a more accurate description of mesopelagic taxa compared with adults, which have comparatively lower catchability (Peña, 2019, and references therein). The CalCOFI ichthyoplankton monitoring program in the California upwelling is the longest ichthyoplankton community dataset in the world, with mesopelagic taxa representing the most specious groups. Thus, this dataset provides a unique opportunity to assess the impact of large-scale climate forcing on a mesopelagic community. This is particularly relevant in upwelling ecosystems such as the California current (CC) ecosystem, where mesopelagic and deep sea ecosystems are highly dependent on spatial and temporal variation of midwater oxygen concentration and the extension of the oxygen minimum zone (OMZ). Koslow *et al.* (2019) enlarge the study area of the CC compared with previous studies by combining information from central, south and Baja California to investigate the evolving response of mesopelagic fishes to declining midwater oxygen concentrations. The study shows a progressive latitudinal effect in the response of mesopelagic species across the three areas, with several warm-water mesopelagic species, apparently adapted to the shallower and intense OMZ off Baja California, increasing despite declining midwater oxygen concentrations. Warm water species are becoming increasingly dominant, initially off Baja California north of the CC. The authors suggest that this response is associated with the warming near-surface, owing to the increased flux of Pacific Equatorial Water into the southern CC during warm phases of the Pacific Decadal Oscillation and the El Niño-

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Table 1. The ten most cited articles returned by a search of the Web of Science Core Collection for the term "mesopelagic" over the period 1945–2018, conducted on 25 February 2019.

Publication	Year of publication	Number of citations
Karner, M. B., DeLong, E. F., and Karl, D. M. Archaeal dominance in the mesopelagic zone of the Pacific Ocean. Nature, 409: 507–520.	2001	870
DeLong, E. F., Preston, C. M., Mincer, T., Rich, V., Hallam, S. J., Frigaard, N. U., Martínez, A. *et al.* Community genomics among stratified microbial assemblages in the ocean's interior. Science, 311: 496–503.	2006	814
Morris, R. M., Rappé, M. S., Connon, S. A., Vergin, K. L., Siebold, W. A., Carlson, C. A. and Giovannoni, S. J. SAR11 clade dominates ocean surface bacterioplankton communities. Nature, 420: 806–810.	2002	627
Jiao, N., Herndl, G. J., Hansell, D. A., Benner, R., Kattner, G., Wilhelm, S. W., Kirchman, D.L *et al.* Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean. Nature Reviews Microbiology, 8: 593–599.	2010	444
Sunagawa, S., Coelho, L. P., Chaffron, S., Kultima, J. R., Labadie, K., Salazar, G., Djahanschiri, B. *et al.* Structure and function of the global ocean microbiome. Science, 348(6237), 1261359.	2015	380
Schwartzlose, R. A., and Alheit, J. Worldwide large-scale fluctuations of sardine and anchovy populations. African Journal of Marine Science, 21: 289–347.	1999	372
Herndl, G. J., Reinthaler, T., Teira, E., van Aken, H., Veth, C., Pernthaler, A., and Pernthaler, J. Contribution of Archaea to total prokaryotic production in the deep Atlantic Ocean. Applied and Environmental Microbiology, 71: 2303–2309.	2005	369
Furness, R. W., and Camphuysen, K. Seabirds as monitors of the marine environment. ICES Journal of Marine Science, 54: 726–737.	1997	343
Honjo, S. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. Journal of Marine Research, 38: 53–97.	1980	336
Pauly, D., Trites, A. W., Capuli, E., and Christensen, V. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science, 55: 467–481.	1998	329

The total number of publications returned was 2025.

Southern Oscillation. This study demonstrates the importance of accounting for synergistic effects between surface and deep water physical conditions to understand the temporal dynamics of mesopelagic species.

Trophic links and the vertical transfer of material and energy

While the regional and large-scale connections between mesopelagic species and higher trophic levels requires further quantification, their links to lower trophic levels are considerably better known. Six of the thirteen articles in this theme set are on the latter topic. Mei *et al.* (2019), Olivar *et al.* (2019), and Richards *et al.* (2019) use stable isotope ratios (SI; δ^{13}C and δ^{15}N) in muscle tissue, while Contreras *et al.* (2019) analyse the stomach content of the early life stages to characterize this link. For example, Mei *et al.* (2019) use SI values of larvae of six mesopelagic fish, and the diet of spawning females, to categorize the spawning strategies of these species as either capital or income breeders. The SI approach also allowed the authors to characterize the dietary niche of overlap of these mesopelagic larvae. Olivar *et al.* (2019) use transoceanic sampling across the equatorial and tropical Atlantic to assess the trophic position and diet of myctophid fish (the most important component of the mesopelagic fish community that undertakes diel vertical migrations, DVM) across contrasting ecosystems in terms of productivity and oxygen concentration. While species-specific differences were driven by their diets, myctophids inhabiting zones with low oxygen concentration held lower mean trophic level positions. Richards *et al.* (2019) contrast the diet of mesopelagic fishes (the first dietary descriptions reported for some of them) of different size and DVM behaviour (migrant vs. non-migrants). They show that all species have a similar carbon source, most of them from epipelagic food resources. However, shifts in δ^{15}N signals with increasing body size revealed ontogenetic changes in diet and trophic position. Finally, Contreras *et al.* (2019) provide novel information on the contrasting trophic ecology of the early life stages of six species of mesopelagic fish, including their diel patterns of feeding and how these change during ontogeny. They also report a general lack of dietary specialization in terms of prey size, mainly composed of copepods, although the diversity of the diet increased during ontogeny.

Most prey extracted from predator stomachs are unidentifiable by visual inspection. A more complete characterization of predator diets depends on molecular techniques that are now rapidly being applied to reveal trophic interactions among mesopelagic organisms (Clarke *et al.*, 2019) and to indirectly obtain information on other important species using genetic screening of the stomach content of mesopelagic fish (e.g. *Anguilla anguilla* in the Sargasso Sea, Jensen *et al.*, 2018). For example, DNA metabarcoding and environmental DNA are supporting rapid increases in knowledge about biodiversity, habitat distribution, and community structure, as well as providing new insights into the evolutionary history of colonization of the mesopelagic realm. A recent gene sequencing study shows that Southern Ocean myctophids are from at least three distant subfamilies, suggesting that colonization has occurred repeatedly, and that spatial divergence of myctophids is rare, likely owing to their enormous abundance and the homogenizing force of ocean currents (Christiansen *et al.*, 2018). Despite the promise in these techniques, they do not as yet support quantitative estimates of biomass or population size.

Quantification of carbon fluxes from primary production to mesopelagic fish and other organisms is one of the main challenges in assessing the role of mesopelagic organisms in the biological carbon pump (BCP), as well as their influence in regulating climate in the coming decades (Yool *et al.*, 2013).

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Anderson *et al.* (2019) approach this question by investigating carbon transfer via three groups of copepods: detritivores that access sinking particles, vertical migrators, and species that reside in the sub-surface layers. They compared a world ocean model (between 40°N and 40°S) with acoustics-based estimates of mesopelagic fish production. Their study demonstrates the paramount role of migrating organisms in transferring carbon from the surface to the mesopelagic zone. However, they also reveal that their estimates are highly sensitive to the (mostly assumed) trophic pathways within the mesopelagic food web. They explicitly stress that a deeper understanding and parameterization of these linked processes is required to support sustainable management of mesopelagic fish as a harvestable resource. Pakhomov *et al.* (2019) report a similar exercise (at a local scale) that focuses on the role of pelagic decapods, including large migrators, partial migrators, and non-migrators. They provide estimates of both active and passive carbon transport during the day and night that are not generally included in carbon flux models. In addition, recent studies show that co-occurring mesopelagic fish and crustacean species respond differently to the physical properties and biological factors defining mesopelagic ecoregions (Judkins and Haedrich, 2018), highlighting the contrasting spatial dynamics and dispersal pathways of different groups of mesopelagic organisms and the need to look beyond fish to understand the dynamics of the mesopelagic.

The extensive DVMs undertaken by members of the mesopelagic community play a key role in the transfer of material and energy (energy transfer efficiency, ETE) from the sub-surface to demersal and bottom ecosystems (e.g. Proud *et al.*, 2017). This vertical transfer of materials and energy that, at least in the open ocean appears to be higher than expected (Irigoien *et al.*, 2014; Proud *et al.*, 2017), is also a pathway through which the effects of climate change at the surface is transferred to the deep ocean, at a rate much higher than would be the case without the extensive vertical movement of mesopelagic biomass (Smith *et al.*, 2013). Global simulation exercises predict that global warming will increase ETE and result in shallowing of the deep scattering layer (DSL) and a 17% increase in its biomass (Proud *et al.*, 2017). An increase in species richness of mesopelagic zones away from equator is also predicted (Costello and Beyer, 2017). However, Koslow *et al.* (2019) call for caution when it comes to these future scenarios pending a more complete modelling approach that takes into account additional variables relevant for regional mesoscale processes, such as oxygen concentration.

Biomass estimates

More global and regional estimates of mesopelagic production are needed (e.g. Irigoien *et al.*, 2014; Proud *et al.*, 2017, 2019), but the various methods currently being used to obtain these estimates have produced wildly different numbers. While estimates based on acoustic surveys range from 14.3 to 19.5 Gt (Irigoien *et al.*, 2014), ten times higher than previously reported (1 Gt, Gjøsæter and Kawaguchi, 1980), estimates based on food-web models yield values around 2.4 Gt (Anderson *et al.*, 2019). Given these hugely different estimates, it is crucial to identify the main uncertainties in each approach-model, quantify them, and present them explicitly. Proud *et al.* (2019) apply a mesopelagic fish biomass model using acoustic backscatter from the DSL to assess the impact of different sources of uncertainty on estimates of global mesopelagic fish biomass. Their study reveals that there are still considerable sources of uncertainty associated with fish swimbladder volume, length distribution, species morphology, and the proportion of the backscatter that might be from siphonophores vs. fish. Taking these sources of uncertainty into account, they estimate mesopelagic fish biomass could range between ca. 1.8 and 16 Gt. In addition, spatial and temporal changes in these uncertainties could considerably alter the biological reference points that would potentially be used to design harvesting approaches for mesopelagic fish.

Although acoustic backscatter is easy to measure, converting it into a species-specific size spectrum and, thereby, into biomass, remains challenging. Most regional estimates of mesopelagic fish are based on acoustic surveys, which are calibrated using samples from mesopelagic trawls. However, catchability of mesopelagic organisms is one of the main limitations in their sampling. Peña (2009) reports a survey-based experiment to assess the influence of vessel lights and noise from the dynamic positioning (DP) system on mesopelagic fish behaviour and vertical distribution. She shows that light triggered a disperse diving of mesopelagics, and this effect was even stronger in response to DP system noise. New technological developments in gear and acoustics, that increase catchability such that it is more representative of what is present in the mesopelagic, are needed.

Other articles in this them set focus on the regional scale, making use of information available from monitoring programs. Sassa (2019) present an integrative exercise applying the daily egg production method to estimate spawning stock biomass of an important myctophid in the East China Sea, combining information from fish larval surveys and reproductive parameters available from the literature (i.e. sex ratio, back fecundity, and spawning fraction). These methods could be applied to analogous survey data in other regions in order to generate indirect assessments of myctophid biomass (at a regional scale) when other methods, such as acoustics, are not available or underestimate it.

While most approaches to estimating the abundance of mesopelagic organisms assume that biomass is static in space and time, production surely fluctuates on different temporal scales in conjunction with changes in spatial distribution. Fock and Czudaj (2019) compare the size structure of the mesopelagic fish community along a transect from the Equator to the Bay of Biscay during two periods; the 1970s and a survey conducted in 2015. Their study demonstrated that the size structure of 20 out of the 28 species studied had changed (although in different directions), with 8 species showing a greater dominance of small size classes in 2015 compared with earlier, 10 species showing a reduced dominance of older size classes, and 2 showing a clear shift in the modal length of size distributions. Because biomass estimates are dependent on the size structure of mesopelagic fish populations (something that is not easy to accurately determine), better information on the variability of population and community size structure is needed to decrease the uncertainty of these estimates.

Improved coordination and integration of food web modelling and DSL-based estimates is needed to better understand the temporal and spatial variation of mesopelagic production, ETE, and their implications on, for example, predation on zooplankton or the role of upper trophic levels, both of which are often omitted by mass balance and end-to-end ecosystem models. Complex models, such as Atlantis (Fulton *et al.*, 2011) and SEAPOYDM (Lehodey *et al.*, 2008, 2015), are starting to include depth integrated processes and associated diel variability, such as the relationship between DSL structure and depth of the euphotic

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zone. Accurate representation of the BCP in ecological models is important because it feeds directly into climate and earth-system models in which it plays a key role in estimating the transfer of climate forcing from the ocean surface to deep sea ecosystems.

Extracting and sustainably managing mesopelagic resources

Bioeconomic modelling of possible exploitation scenarios, coupled with alternative management strategies and harvest control rules, are needed to guide the management of mesopelagic resources, particularly for those species for which the present market is undeveloped. Prellezo (2019) presents a case study that assesses the technical, financial, and market viability of mesopelagic resources in the Bay of Biscay. While exploitation is technically possible, it is not a viable alternative to the existing commercial fisheries because of the lower profitability of the landings. However, in the context of the new landing obligation of the EU Common Fisheries Policy, exploitation of mesopelagic resources could have a narrow economic potential because catch quotas of commercial species (and fishing effort) will be limited, leaving the possibility for excess capacity to be used to harvest mesopelagic species. Additional studies such as this are needed, and will have to be updated, if/as the market for mesopelagic species changes.

Knowledge gaps and challenges

Mesopelagic resources, particularly lanternfish, represent one of the last high biomass groups of fish that is as yet unexploited. If even a small percentage of the estimated biomass of this group is extracted (e.g. 1% of 9 Gt), it would double the present global landings from capture fisheries (=ca. 90 million tonnes, as drawn from Fig. 1 in FAO, 2018). Given the forces alluded to at the beginning of this introduction, it seems likely that it is only a matter of time until this taxonomic group, and other mesopelagic resources, will be exploited. There is an opportunity here to learn from the mistakes (and successes) of the past to sustainably exploit these resources. To achieve that we will need much more information than what is currently available on key aspects of mesopelagic species and systems. Some of these knowledge gaps are mentioned above, others below. Although most of those that follow have been identified earlier (Irigoien *et al.*, 2014; St. John *et al.*, 2016; Proud *et al.*, 2017), they bear repeating.

St. John *et al.* (2016) listed five areas in which more knowledge is needed to inform the sustainable management of the mesopelagic zone: (i) population vital rates, which represent the basics for stock assessments and population dynamic modelling to predict the impact of fishing; (ii) development of stock assessment tools, harvest control rules, etc., adapted to data poor situations; (iii) the interaction between oceanographic scenarios and mesopelagic biomass and biodiversity that enable future projections including those associated with climate change impacts; (iv) food web implications of mesopelagic resource depletion; and (v) the role of mesopelagic species and communities in the sequestration of greenhouse gases. Additionally, there is a need to (vi) develop technology (ships, gear, real-time species identification and biomass estimation, fishing strategies to efficiently capture a diffuse and transboundary resource) to support efficient extraction of mesopelagic species, with minimal bycatch (e.g. Peña, 2019 and references therein); (vii) increase the application of the next generation of genetic tools (e.g. metabarcoding and environmental DNA) to provide a more complete characterization (including quantification) of the biodiversity and ecology of the mesopelagic; (viii) add to our knowledge and understanding of the possible ecosystem consequences of extracting mesopelagic organisms. Although it could be argued that knowledge of how other marine ecosystems react to the removal of large chunks of their biomass can guide us, that is true only to the extent that the food webs of those systems are known, which is often not at all well. Even less is known of the interconnectivity of mesopelagic organisms; (ix) better define how much energy is recycled within the mesopelagic, that is, how important is the "mesopelagic loop?"; (x) given the relative stability of the mesopelagic environment, assess the capacity of mesopelagic organisms to adapt to conditions that will change more rapidly as a result of climate change); and (xi) conduct socioeconomic receptiveness studies and develop market opportunities. There is a general lack of industrial-scale processing technology for these species, and markets for them will have to be developed (IMR *et al.*, 2017; Prellezo, 2019, and references therein). The fact that mesopelagic resources are generally present in regions beyond national jurisdiction presents another challenge in terms of agreeing upon, and implementing, legally binding instruments to govern their exploitation (O'Leary and Roberts, 2018).

The sustainable management of the services provided by the mesopelagic ecosystem requires an ecosystem-based framework that balances benefits, risks, and trade-offs (St. John *et al.*, 2016). That is, harvesting this ecosystem can produce more food for human consumption, but the potential consequences associated with the effect of biomass extraction on the (poorly known) role of the mesopelagic in climate regulation, conservation, biodiversity, and ecosystem stability must be carefully considered.

Given the present limits on our knowledge of the mesopelagic, and of the effects that large-scale extraction of biomass might have, a precautionary approach has been adopted by some management councils to protect forage fish species such as mesopelagic fish. For example, the Pacific Council, supported by a Comprehensive Ecosystem-Based Amendment (CEBA 1), "*prohibits the development of new directed fisheries on forage species that are not currently managed by the Council, or the States, until the Council has had an adequate opportunity to assess the science relating to any proposed fishery and any potential impacts to our existing fisheries and communities.*" In contrast, as stated in their "Blue Growth Strategy," the European Commission is currently open to the exploration and exploitation of new ocean horizons such as the mesopelagic (European Commission, 2018).

Global research output on topics such as "ocean acidification" and "marine plastic," or species such as "Atlantic salmon" and "Atlantic cod," is 500–900 primary research articles per year (quotation marks identify the search terms used in the Web of Science to obtain these numbers). The present output on "mesopelagic" research topics of about 150 primary research articles per year (Figure 1a) will not produce (on a reasonable timeline) the information needed to meet the challenge of sustainably managing this resource, particularly given the technical and logistic challenges associated with obtaining such information. Although the European Commission (and other agencies) have recently funded projects to investigate some of the questions raised here, considerably more resources will be required to conduct the research needed to support knowledge-based management of mesopelagic resources. Finally, large-scale

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exploitation of the mesopelagic should not begin until that information is incorporated into management tools.

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Disclaimer

The opinions and positions taken in this article are those of the authors and do not necessarily reflect those of their employers.

Conflict of interest statement

H.I.B. and M.H. work, respectively, for the Institute of Marine Research, Norway, and the Spanish Institute of Oceanography (IEO, Spain), both of which are government research institutes charged with generating science and providing advice in support of the sustainable use of marine resources. None of the directed funding that he has received to date has been related to the mesopelagic or mesopelagic organisms. H.I.B. is also Editor-in-Chief of this Journal (and M.H. a member of the editorial board), which is owned by the International Council for the Exploration of the Sea (ICES), a global intergovernmental organization that develops science and advice to support the sustainable use of the oceans. The authors declare no conflicts of interest.

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