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A global biogeographic classification of the mesopelagic zone

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ABSTRACT

We have developed a global biogeographic classification of the mesopelagic zone to reflect the regional scales over which the ocean interior varies in terms of biodiversity and function. An integrated approach was necessary, as global gaps in information and variable sampling methods preclude strictly statistical approaches. A panel combining expertise in oceanography, geospatial mapping, and deep-sea biology convened to collate expert opinion on the distributional patterns of pelagic fauna relative to environmental proxies (temperature, salinity, and dissolved oxygen at mesopelagic depths). An iterative Delphi Method integrating additional biological and physical data was used to classify biogeographic ecoregions and to identify the location of ecoregion boundaries or inter-regions gradients. We define 33 global mesopelagic ecoregions. Of these, 20 are oceanic while 13 are 'distant neritic.' While each is driven by a complex of controlling factors, the putative primary driver of each ecoregion was identified. While work remains to be done to produce a comprehensive and robust mesopelagic biogeography (i.e., reflecting temporal variation), we believe that the classification set forth in this study will prove to be a useful and timely input to policy planning and management for conservation of deep-pelagic marine resources. In particular, it gives an indication of the spatial scale at which faunal communities are expected to be broadly similar in composition, and hence can inform application of ecosystem-based

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management approaches, marine spatial planning and the distribution and spacing of networks of representative protected areas.

1. Introduction

The open oceans and deep seas (> 200 m depth) cover the majority of the Earth's surface area and habitat volume. Within these, the vast deep-pelagic habitat between the sunlit layers (upper 200 m) and the seafloor is the largest and least-understood environment on our planet (Webb et al., 2010). This habitat contains the mesopelagic (200–1000 m depth) and bathypelagic (water column > 1000 m depth) zones, though the precise depth at which these zones transition is variable, and vertical connectivity across this transition appears to be the rule rather than the exception at larger spatiotemporal scales (Sutton, 2013).

The importance of pelagic ecosystems to services supporting life on Earth, such as carbon cycling, are widely acknowledged but poorly understood (Robinson et al., 2010; St. John et al., 2016). Our limited knowledge of these ecosystems is increasingly problematic as they may be vulnerable to global issues such as climate warming, deoxygenation, acidification, commercial fishing, seabed mining, and other threats with unknown potential for feedback to the climate system (Sarmiento et al., 2004; Koslow et al., 2011; Ramirez-Llodra et al., 2011; Mengerink et al., 2014).

That the deep pelagial represents a critical gap in our knowledge of global ocean biodiversity has become abundantly clear as various international initiatives attempt to identify important or sensitive areas in the open oceans and deep seas-such as Ecologically or Biologically Significant Areas (EBSAs) in the high seas (CBD, 2009; Dunn et al., 2014), Vulnerable Marine Ecosystems in relation to deep-sea fisheries (FAO, 2009) and Particularly Sensitive Sea Areas in relation to shipping (IMO, 2005). The value of global biogeographies as a key first step in meeting targets for representative protection of the world's oceans is recognized (Lourie and Vincent, 2004), but such initiatives have primarily focused on benthic habitats or the epipelagic zone, necessitated by the limited availability of data and synthetic analyses of deep-pelagic ecosystems (Webb et al., 2010). Such classifications concentrate on the upper water column (Longhurst, 1998, 2007; Spalding et al., 2012) or the seafloor (UNESCO, 2009; Watling et al., 2013). As stated in the Global Open Oceans and Deep Seabed (GOODS) biogeographic classification, which was developed in 2007, "available information on taxonomic patterns or even of the abiotic drivers of such patterns remains so poor that it is unlikely that any distinct and global scale classification of deep-pelagic biogeography is possible at the present time" (UNESCO, 2009). However, as more data become available on deep-pelagic communities there are opportunities for new global biogeographic analyses to support these policy processes.

Based on present knowledge and available biotic and abiotic datasets on deep-pelagic ecosystems, we here propose a biogeographical classification schema for the mesopelagic zone, with the explicit proviso that the sparsity and spatiotemporally biased nature of mesopelagic data are why expert maps are still required in under-sampled areas of the ocean. We present this as a 'current state of knowledge' framework against which future data/analyses can be used to: 1) refine boundary locations and dynamics as spatiotemporal information accumulates; 2) investigate these dynamics to better understand the mechanisms underlying pelagic boundaries; and 3) provide a guide to the regional scales over which the deep-pelagic ocean varies in terms of biodiversity and function, thereby informing global conservation efforts. Also, the ecoregions proposed in this study could be used as a biogeographical framework in further studies to quantify potential anthropogenic perturbation in deep-pelagic ecosystems.

2. Methods

Rigorous quantitative analyses of taxonomic and environmental data for the deep-pelagic zone on a global scale are currently impeded by the spatially patchy and inconsistent manner of data collection over large areas, and because less than 1% of this enormous habitat has been sampled (Webb et al., 2010; Mora et al., 2011; Appeltans et al., 2012; Costello et al., 2012; Higgs and Attrill, 2015; St John et al., 2016). Hence this classification was accomplished by collating expert knowledge on distributional patterns of pelagic fauna or regions relative to environmental data felt to be important ecological drivers. A modified Delphi Method (Linstone and Turoff, 2002) was employed during a workshop held in July 2013 in Glasgow, Scotland, where a panel of experts provided information regarding the biogeography of various regions of the world's oceans, facilitators provided a summary of information, and panelists as a group reviewed this summary. The overall goal of the Delphi process as applied to this study was to lead the expert panel to consensus by an iterative exchange of information via a process coordinator. During this exchange, a GIS was used to display data and project a map on to a white board where the experts could interact with it when describing potential boundaries. This process mimicked the one used in the Convention on Biological Diversity's regional workshops to describe Ecologically or Biologically significant areas (Bax et al., 2016) and other expert-driven stakeholder processes. Higher weight was given to information produced from time-series data as opposed to shorter duration studies.

The panel constituency represented expertise in a suite of requisite disciplines: descriptive and numerical physical oceanography, geospatial mapping, marine ecology, organismal biology, and deep-pelagic taxonomy. Panel taxonomic/ecological expertise in a broad spectrum of taxa was encompassed (e.g., gelatinous zooplankton, chaetognaths, molluscs, crustaceans, and fishes), as different pelagic taxa exhibit different distributional dynamics; more mobile, longer-lived animals generally have larger ranges than smaller, more planktonic organisms (van der Spoel, 1994). Also, biogeographical boundaries can be asymmetrical/semi-permeable with respect to specific assemblage components. For example, subpolar fronts can be sharp distributional boundaries for warm-water pelagic fishes, whereas cold-water pelagic fishes can extend across these boundaries via subtropical submergence (e.g., Sutton et al., 2013).

In order to align this effort with the GOODS classification and subsequent updates (UNESCO, 2009; Watling et al., 2013), the mesopelagic biogeography was based on ecoregions. Ecoregions are areas of ocean that contain geographically distinct assemblages of natural communities and species (Spalding et al., 2007). These ecoregions host distinct species assemblages that are presumed to share a common history of co-evolution. This unit of biogeographic classification should not be equated with individual faunal ranges or distribution patterns, the latter being defined as the occupation of a range by two or more species. The biogeographic classification presented here relates to the daytime distribution of large-scale mesopelagic faunal communities. We consider daytime distributions as defining the mesopelagic fauna, given that a large portion of this fauna occurs in the epipelagic at night due to diel vertical migration. This classification does not consider the biogeography of the epipelagic fauna. Though we present ecoregion boundaries as static lines on a map, we wholly acknowledge the potential for seasonal movement of the transition zones based on epipelagic plankton dynamics (e.g., spring blooms at high latitudes) and seasonal water column stratification/destratification. The strength of seasonality at mesopelagic depths at specific locations is unknown for

most of the worlds' oceans, so the lines placed here were guided by concordance with mean annual physical oceanographic characteristics.

2.1. Data used for the biogeographic classification

2.1.1. Water masses

A core understanding among oceanic biogeographers is that meso-pelagic faunal distributions and boundaries are influenced by environmental conditions within water masses and circulation distributions. Although very few pelagic species are restricted to one water mass, studies of pelagic biogeography have consistently shown the concordance of large-scale pelagic assemblage distributions and the distribution of water masses (e.g., McGowan, 1974; Backus, 1986; Goetze and Ohman, 2010; Olivar et al., 2017). Temperature, salinity and dissolved oxygen data from the World Ocean Atlas (2009) and the CARS model (CARS, 2009) were used, as these parameters adequately delineate large-scale water masses and have been among the most consistently measured globally. The data were extracted at 200, 500, 750, and 1000 m depths, based on parameters of known biophysical significance, including light environment (Menzel and Ryther, 1959), depth of permanent thermocline (Lewitus and Broenkow, 1985), and depths of diel vertical migration (Vinogradov, 1997), respectively. In addition to being readily available on a global scale, these variables are thought to be key ecological drivers, or proxies for faunal community structure or abundance. Other variables are likely to be important at smaller spatial scales, but the focus here is on the broader ecoregion scale.

Investigation of individual variables at specific depths and cluster analyses of multiple variables across multiple depths were used to help identify biogeographic ecoregion boundaries. In ArcGIS, a non-hier-archical, iterative self-organizing clustering procedure (ISODATA; Ball and Hall,1965; Richards, 1986) was used to identify groups of cells with similar temperature, salinity and dissolved oxygen characteristics across a range of depths (200, 500 and 750 m, Fig. 1). The depths were chosen *a priori* based on known biophysical significance (e.g., light environment, permanent thermocline, diel vertical migration). The number of clusters was limited to 10 to avoid "over-splitting" the data at greater depths where there is lower variability in oceanographic parameters. The algorithm iteratively designated an arbitrary mean for each cluster and then assigned each 0.5° gridcell from the CARS dataset to the cluster with the closest mean. A new cluster mean was calculated based on all the gridcells assigned to a given cluster. The process was repeated until the number of pixels migrating between iterations was small. The final clusters were mapped and displayed on a whiteboard for discussion by workshop participants. Existing water mass classifications (e.g. Talley et al., 2011), based largely on global-scale hydrographic programs such as the World Ocean Circulation Experiment Hydrographic Program, were referenced when interpreting the cluster

results. An adaptive process based on discussions around the projected ArcGIS maps produced subsequent cluster analyses. This process was particularly useful as a starting point for discussion of the location of ecoregion boundaries.

2.1.2. Oxygen minimum zones (OMZs)

Extreme OMZs were regarded as one of the strongest environmental drivers of certain biogeographical ecoregions (e.g., Stramma et al., 2008). An OMZ ecoregion was defined by values of less than 0.5 ml l^{-1} dissolved oxygen concentration, a value that limits the distribution of many mesopelagic taxa (Vinogradov, 1997; Childress and Seibel, 1998). OMZs were extracted from the CARS and WOA in ArcGIS by delineating the 0.5 ml l^{-1} contour at 500 m depth (near the mid-point of the mesopelagic zone), although considerable variability is seen in the horizontal extent of OMZs as a function of depth within the mesopelagic zone (Fig. 2).

2.1.3. Temperature extremes

It is well-established that temperature plays a key role in the evolution and establishment of faunal distribution patterns. Extremes of temperature were defined by values less than 0.5 °C ('below normal,' Vinogradov, 1970) and greater than 10 °C. These low and high extremes are proxies for faunal communities that have origins or associations with polar and equatorial region water masses, respectively. Similar to the oxygen minimum zones, these areas were delineated in ArcGIS by extracting their respective contour lines at various depths.

2.1.4. Surface water productivity

As for epipelagic ecosystems (Longhurst, 1995, 1998, 2007), primary production in surface waters is a demonstrated driver of mesopelagic community biogeography (e.g., Schmid et al., 2000a, 2000b). We used global-scale production characteristics to define oceanic domains, into which ecoregions were organized.

2.1.5. Biotic partitioning

Where participants knew of very strong faunal community breaks or regions, perhaps driven primarily by biotic interactions, these were included by delineating the breaks on the map displayed on the white board, and then georectifying pictures of the white board map. Examples are listed in the ecoregion accounts. The participants acknowledged the potential for unknown discontinuities which are not taken into account here; these would provide the impetus for future updates.

2.2. Caveats

There are several qualifications that are associated with the data used. Predominant among these are data gaps, both geographically
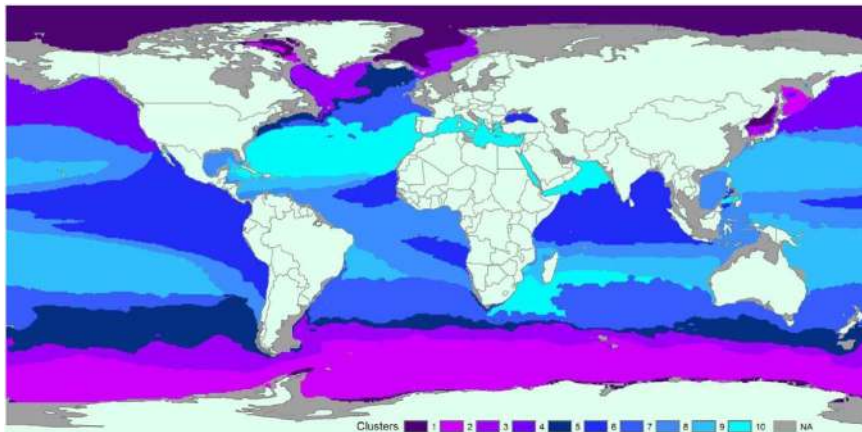

Fig. 1. Plot of 10 clusters values derived from the ISODATA analysis of global 0.5° resolution temperature, salinity and dissolved oxygen layers from the CARS (2009) model.
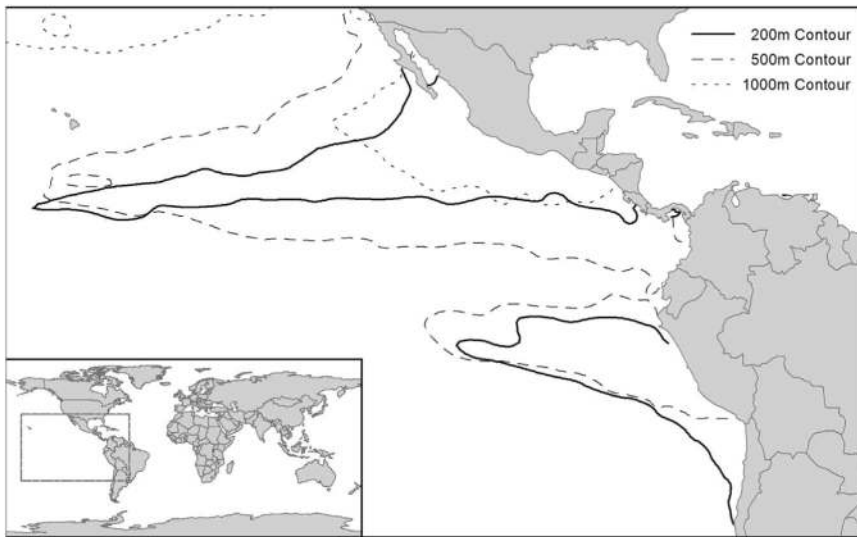
Fig. 2. Delineation of the OMZ region (0.5 ml l^{-1} O$_2$) in the eastern Pacific Ocean, extracted from the CARS (2009) model in ArcGIS at the 200 m, 500 m, and 1000 m depth horizons.

(e.g., Southern Pacific; www.iobis.org) and vertically (e.g., deeper than 200 m; Fig. 2 in Webb et al., 2010). For example, substantial areas within the ecoregions we propose are very poorly sampled, with little or no mesopelagic faunal data available (Fig. 3). Even in regions where research surveys have been conducted, sampling biases hamper syntheses of available data, as all midwater sampling techniques are inherently selective (e.g., Omori and Hamner, 1982; Robison, 2009; Heino et al., 2011). Seasonal life history cycles, especially ontogenetic depth zonation, obscure full knowledge of faunal distributions. Lastly, seasonal variations in both environmental conditions and sampling

intensity vary widely by region, with many databases (e.g., OBIS) heavily skewed toward summer sampling.

3. Results

The biogeographic classification presented here defines 33 ecoregions (Fig. 4, Table 1), depicting the daytime distribution of large-scale mesopelagic faunal communities. These are generally at the oceanic basin or sub-basin level which reflect the scale of oceanic water mass and current characteristics, although there are also more
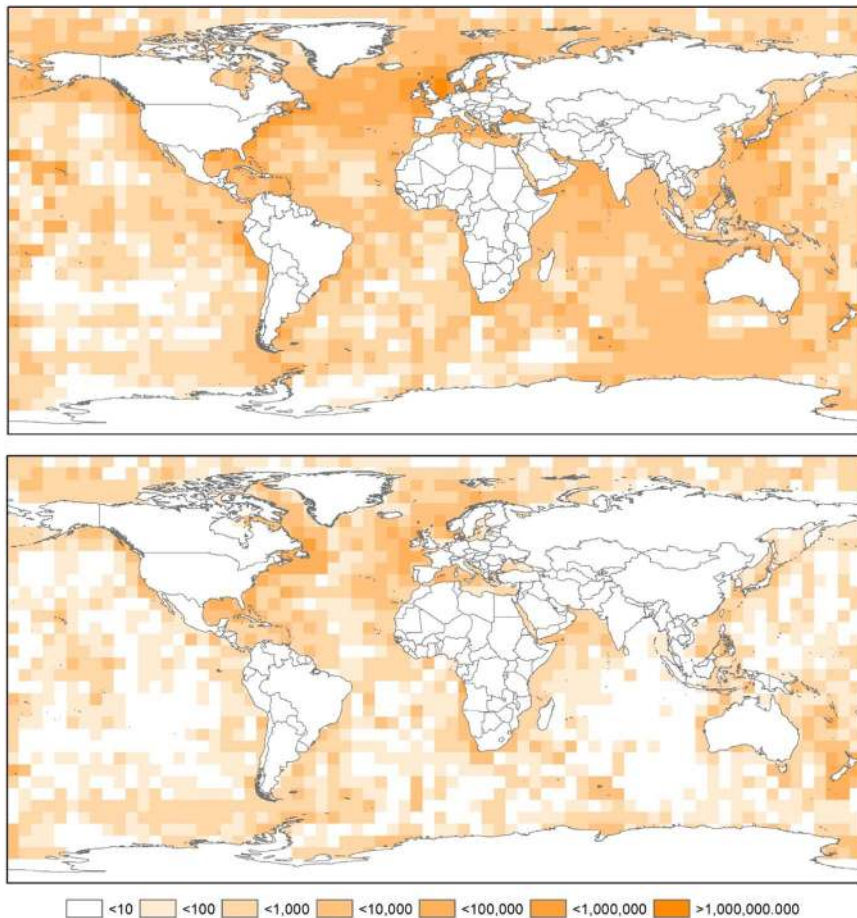

Fig. 3. Ocean Biogeographic Information System (OBIS) records aggregated to 5° cells in the world ocean by two depth zones: (a) 0–200 m, (b) 200–1000 m. Data from OBIS (2015). Heat map spectrum describes the number of records on a log scale: from light orange = > 10 to dark red (> 1,000,000).
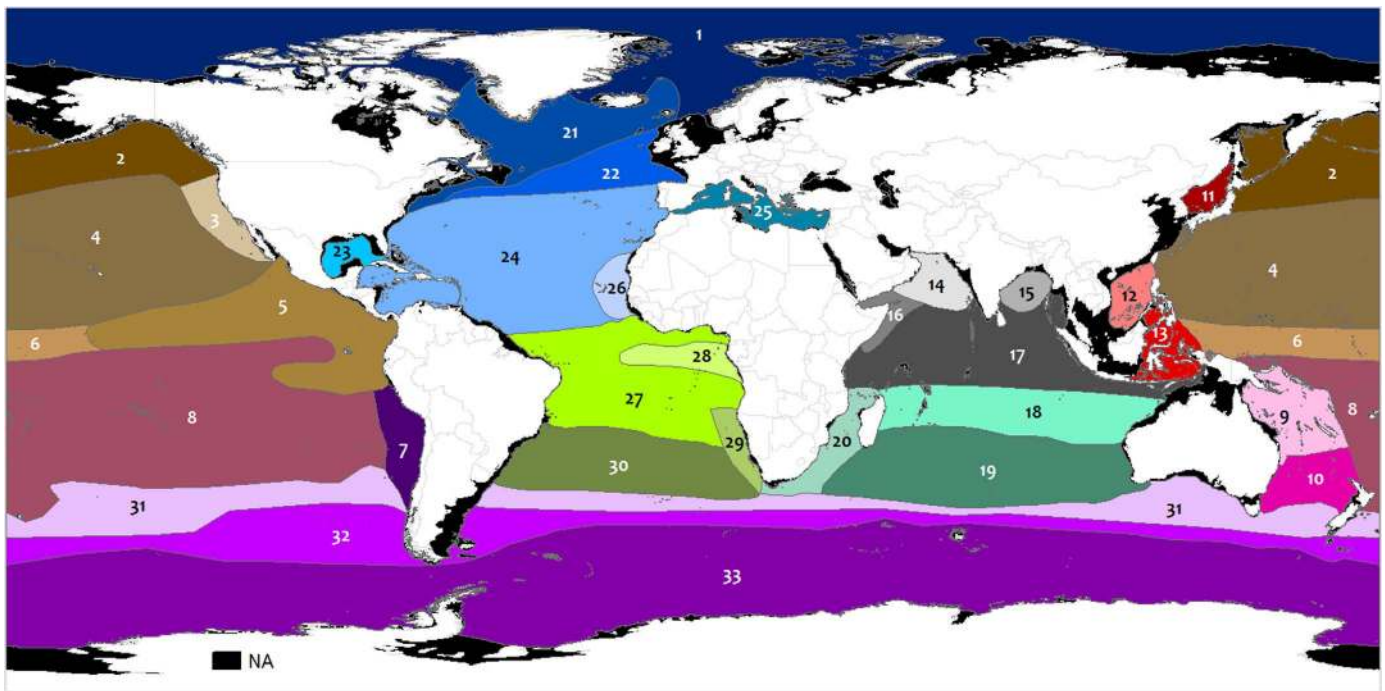
Fig. 4. Proposed mesopelagic ecoregions of the world's oceans. The numbers are simply for reference, and relate to the geographical names used in Table 1. Areas with depths less than 200 m shaded in black.

restricted ecoregions driven by a localized combination of factors. We have organized our ecoregions by oceanic biome (Beklemishev, 1971; Longhurst, 1995) in order to express the commonalities of the ecoregions on the largest scale before listing differences. These biomes (polar, westerly winds, trade wind, distant neritic) are based primarily on seasonal biophysical coupling of turbulence, stratification, and irradiance, all of which define primary productivity dynamics which drive ecosystem structure. Of the 33 ecoregions recognized, 20 are oceanic while 13 are distant neritic (i.e., oceanic assemblages associated primarily with continental shelf breaks, *sensu* Beklemishev, 1971). Biome characteristics and included ecoregions are given below (with ecoregion numbers listed as in Table 1, Fig. 4).

3.1. Polar biome – 3 ecoregions

In this biome the depth of water column mixing in winter is constrained by ice cover. A shallow pycnocline in spring/summer promotes algal blooms, while light limitation keeps primary productivity low the rest of year. The polar domain includes the Arctic (1), Northwest Atlantic Subarctic (21), and Southern Ocean/Antarctic (33) ecoregions. Each ecoregion contains a distinct cold-water mesopelagic fauna (e.g., fishes, squids, and crustaceans) that is depauperate relative to adjacent, lower latitude waters.

3.2. Westerly winds biome – 10 ecoregions

This biome is characterized by large seasonal changes in mixed layer depth due to high westerly wind stress in winter. Within this biome there are two groups of ecoregions based on the timing of maximum primary productivity. Two ecoregions, the Subarctic Pacific (2) and North Atlantic Drift (22), exhibit large spring and secondary late summer/autumn algal blooms, with light and/or nutrient limitation over the remainder of year. Eight ecoregions exhibit maximum algal production in winter, with nutrient limitation only. These include the South Central Pacific (8), Coral Sea (9), Tasman (10), Southern Indian Ocean (19), Mediterranean (25), South Atlantic (30), Circumglobal Subtropical Front (31) and Subantarctic (32) ecoregions.

Seasonality is weak to moderate in all of these except the Subantarctic ecoregion.

3.3. Trade wind biome – 7 ecoregions

This biome is characterized by small amplitude responses to trade wind variability. Seasonality is weak and primary production is low. A deep chlorophyll maximum is a persistent feature. This biome includes the Northern Central Pacific (4), Eastern Tropical Pacific (5), Equatorial Pacific (6), Southeast Asian Pocket basins (13), Gulf of Mexico (23), Central North Atlantic (24), and Tropical/West Equatorial Atlantic (27) ecoregions. The ecoregions included here contain the most diverse mesopelagic assemblages in the world's oceans (detailed in following ecoregion descriptions).

3.4. Distant neritic biome – 13 ecoregions

In this biome oceanic circulation is modified by interaction with continental topography and associated coastal winds. Algal blooms are produced by terrestrial runoff, upwelling, tidal rectification, and other oceanic margin effects. Three groups of ecoregions are included. The California Current (3), Peru Upwelling/Humboldt Current (7), Agulhas Current (20), Mauritania/Cape Verde (26), Guinea Basin/East Equatorial Atlantic (28), and Benguela Upwelling (29) ecoregions are sites of pulsed production at coastal divergences when winds are favorable for upwelling. The Arabian Sea (14), Bay of Bengal (15), Somali Current (16), Northern Indian Ocean (17), and Mid-Indian Ocean (18) ecoregions exhibit large amplitude responses to tradewind reversals which drive monsoon reversals. In these ecoregions rapid responses to nutrient pulses are due to upwelling and/or offshore Ekman suction. The last group includes the Sea of Japan (11) and China Sea (12) 'marginal sea' ecoregions, each with unique features due to surrounding topography. The ecoregions included here contain a high proportion of 'pseudoceanic' mesopelagic species, i.e. species from primarily mesopelagic families whose distributions are centered along continental shelf breaks.

Table 1

Summary of mesopelagic ecoregion descriptions (ecoregion numbers as in Fig. 4).

Ecoregion number	Ecoregion name	Physical geography	Biotic characterization
1	Arctic	Cold, low salinity water. Circulation restricted by land masses.	20% endemic zooplankton fauna; depauperate micronekton/nekton fauna
2	Subarctic Pacific	Productive waters, permanent halocline in offshore regions.	Very few species in common with Pacific Central gyres. Low diversity
3	California Current	Productive system driven by seasonal coastal upwelling.	Distinctive fauna, some endemism. Faunal change at tip of Baja Peninsula.
4	Northern Central Pacific	Gyre system bounded by North Equatorial and Kuroshio Currents.	Oligotrophic; fauna distinct from that of central Equatorial Pacific.
5	Eastern Tropical Pacific	Extensive stratification, shallow thermocline and very low oxygen.	Eutrophic; endemic species adapted to low oxygen.
6	Equatorial Pacific	Complex of both eastward and westward currents; zones of convergence and divergence, semi-permanent upwelling.	Mesopelagic fauna differs markedly from gyres to north and south. Dominant species rare in gyres.
7	Peru Upwelling/Humboldt Current	Northward flow of surface waters of subantarctic origin; strong upwelling.	Highly productive zone. Sharp faunal transition at western edge of Peru Current.
8	Southern Central Pacific	Gyral analog to that of North Pacific.	Oligotrophic; fauna distinct from N. Pacific gyre, lower biomass.
9	Coral Sea	Core associated with North Queensland Current and the Coral Sea gyre.	Distinct mesopelagic fish fauna, notably lanternfishes.
10	Tasman Sea	Semi-enclosed circulation bounded by the Tasman Front.	Fish fauna includes temperate species, with greater diversity than Coral Sea ecoregion.
11	Sea of Japan	Atidal; very cold deep waters (0.5 °C).	Depauperate mesopelagic fauna.
12	South China Sea	Deep, warm marginal sea, exchanges with Kuroshio.	Very speciose fish fauna, with species not found in the east.
13	Southeast Asian Pocket basins	Very deep (> 4000 m) basins of the Indo-Malayan Archipelago, Sulu, Celebes, and Banda Seas. Complex oceanography due to topography.	Unique Indo-Pacific fauna. Celebes Sea and Sulu Sea may constitute distinct ecoregions.ecoregions. Mesopelagic fauna includes epipelagic taxa due to high temperatures. Mesopelagic fauna includes epipelagic taxa due to high temperatures.
14	Arabian Sea	Highly seasonal: upwelling during the SW Monsoon, convective overturn during the NE Monsoon. OMZ region.	Very productive; biodiversity intermediate, but abundance, biomass and dominance of few species is extremely high.
15	Bay of Bengal	Smallest of four major OMZ regions, separated from Arabian Sea.	Mesopelagic fauna adapted to low oxygen concentrations; some endemism.
16	Somali Current	Seasonal monsoon conditions, with strong upwelling.	Southern boundary based on mesopelagic fish transition.
17	Northern Indian Ocean	Gyre system affected by complex seafloor topography.	Fish fauna distinct from Southern Indian Ocean; endemic crustacean species.
18	Mid-Indian Ocean	Broad frontal band with a characteristic TSO signature.	More productive than the Northern Indian Ocean ecoregion, with diverse mesopelagic fish fauna.
19	Southern Indian Ocean	Broad band of subtropical surface waters north of Subtropical Front. Well oxygenated.	Oligotrophic; mesopelagic fish diversity and biomass are lowest here relative to the rest of the Indian Ocean
20	Agulhas Current	Largest western boundary current in the world ocean, drives upwelling to the south.	Enhanced productivity; fauna reflects combination of subantarctic and tropical spp.
21	Northwest Atlantic Subarctic	Only major ocean region with deep-water connection with the Arctic.	High seasonal productivity; distinct cold-water assemblages.
22	North Atlantic Drift	Eddy field region, expanding eastwards as the continuation of the Gulf Stream.	Transition ecotone with admixture of boreal and subtropical species.
23	Gulf of Mexico	Enclosed, deep sea; flow dominated by the Loop Current.	Extremely diverse ecotonal fauna of tropical, subtropical and temperate taxa.
24	Central North Atlantic	Broad area of warm and consistent TSO conditions, including the Sargasso Sea.	Faunal composition distinct from the North Atlantic Drift and Equatorial Atlantic.
25	Mediterranean	Landlocked, with single shallow strait; deep waters uniformly warm and highly saline.	Depauperate mesopelagic fauna. 2nd-most abundant mesopelagic fish species is endemic.
26	Mauritania/Cape Verde	Upwelling region.	Discrete faunal communities, including endemics and relict populations of "cool water" taxa.
27	Tropical and West Equatorial Atlantic	Easterly winds cause divergence and upwelling.	Oligotrophic except for regions of upwelling. Distinct cephalopod fauna.
28	Guinea Basin and East Equatorial Atlantic	Trade wind reversal causes shoaling of pycnocline (Atlantic monsoon analog). Marked OMZ at about 400 m.	High diversity of mesopelagic fish and cephalopods except in OMZ areas.
29	Benguela Upwelling	Strong upwelling system, severe seasonal OMZ.	Highly productive; fauna strongly pseudo-oceanic. High cephalopod diversity.
30	South Atlantic	Gyral system of complex circulation affected by local topography (e.g., Walvis Ridge and Rio Grande Rise).	Mostly oligotrophic except for borders. Fauna includes sister species of North Atlantic gyre taxa.
31	Circumglobal Subtropical Front	Broad convergence band of subtropical and subantarctic waters. Frontal zone highly variable.	Highly productive with distinct deep-pelagic micronekton and zooplankton assemblages.
32	Subantarctic waters	Zone between the Antarctic Polar and Subtropical Fronts, characterized by cold, low salinity waters.	High productivity; deep-pelagic fauna either confined to, or centered within the Subantarctic Front; high number of endemic species.
33	Antarctic/Southern Ocean	Cold, dense bottom water. The Polar Front is a strong barrier (and may be a separate ecoregion).	Highly productive seasonally; high zooplankton endemism, mesopelagic micronekton diversity is low, no endemics.

3.4.1. Mesopelagic ecoregions and their description
3.4.1.1. Arctic.

About half of the area of the Arctic is represented by shallow seas, which generates the most obvious faunal community separation between the oceanic fauna inhabiting the central basins and the neritic fauna found in shelf habitats. Primary communication with other oceans at mesopelagic depths occurs via the Northeast Atlantic. Circulation is restricted by the Eurasian and American land-masses, such that exchange with other ocean basins is limited (Bluhm et al., 2011). Studies of zooplankton communities have found the Arctic ecoregion as a whole resembles that of the inflowing Atlantic, but with 15–20% of Arctic mesopelagic species being endemic (e.g., Kosobokova and Hirche, 2000). With respect to mesopelagic micronekton and nekton, the Arctic ecoregion is a depauperate version of the North Atlantic. This nature is exemplified by the absence in the core of the Arctic of the lanternfish family Myctophidae, a ubiquitous mesopelagic fish taxon found in all other oceans (Backus et al., 1977; Catul et al., 2011). Within the Arctic, temperatures at 200 m appear to be a better predictor of mesopelagic faunal distributions (Błachowiak-Samołyk, 2008).

3.4.1.2. Pacific Subarctic.

This ecoregion includes the northern and western North Pacific, plus the Bering Sea, Alaskan gyre, and northern California Current. The offshore oceanic part of the Subarctic is a large HNLC (high nitrate low chlorophyll) region. Temperature and salinity minima are found at the surface (Willis, 1984), with a permanent halocline near 110 m. Light and iron limit phytoplankton growth. There is a strong seasonal (spring) productivity peak, but in contrast to the North Atlantic subarctic spring bloom there are short term phytoplankton oscillations rather than a single seasonal chlorophyll biomass peak. Phytoplankton abundance is kept in check by protozoan grazers that are in turn grazed on by large copepods. Some of these copepods have large seasonal diapausing populations at mesopelagic depths, with young stages shoaling to feed on products of the spring bloom (summarized in Miller and Wheeler, 2012). The southern boundary is the Subarctic front, with steep horizontal gradients of salinity, temperature and chlorophyll (Park et al., 1967; Roden, 1972, 1977), sound scattering layers, copepod species, and animal biomass (Donaldson and Pearcy, 1972). The Pacific Subarctic has very few mesopelagic fish species in common with central Pacific gyres, equatorial waters, or the Eastern Tropical Pacific (Barnett, 1984). It is strongly dominated by a few species, such as the lanternfish *Stenobrachius leucopsarus*, whose relative abundance appears remarkably consistent in the western North Pacific over decades of study (50% of total assemblage; Willis, 1984; Sinclair and Stabeno, 2002). In addition, deep-sea smelts (Bathylagidae) such as *Leuroglossus schmidti*, *Bathylagus pacificus* and *Pseudobathylagus milleri* are very abundant (Sinclair and Stabeno, 2002). Within the Subarctic front, denser Subarctic water subsides under lighter Central waters, and this is reflected in the fish fauna taken from various depths (Willis, 1984). This vertical difference in biogeographic affinity highlights the complexity of determining pelagic biogeographic schemes in a truly three-dimensional environment.

In the western North Pacific there are transitional waters located between the subarctic and subtropical fronts, i.e. the Oyashio and Kuroshio fronts, respectively (Roden, 1991; Oyashio-Kuroshio interaction region of Longhurst, 1998), with extremely complex hydrography. These conditions sustain high productivity (and thus are included in this ecoregion and in the Subarctic water ecoregion of Brodeur and Yamamura (2005)) into which highly migratory pelagic fishes migrate in spring/summer for spawning and nursery habitat (Sassa and Kawaguchi, 2004). In general, transition waters in the western North Pacific appear to be more diverse than Subarctic waters with less dominance (e.g., dominant lanternfish, *Diaphus theta*, a typical subarctic species, represented ∼ 16% of total fish assemblage; Sassa et al., 2002). In contrast with the west, eastern North Pacific transition waters are

much less complex, except during El Niño conditions (Hernandez-Trujillo, 1999; Hood et al., 1990).

3.4.1.3. California Current.

This is a productive system driven by seasonal coastal upwelling (Hickey, 1979, 1998; Checkley and Barth, 2009) and strong interannual variability of horizontal advection of cold, low salinity, waters rich in nutrients from the north (Bernal and McGowan, 1981; Bernal, 1981; Chelton et al., 1982). Surface flows are to the south but a deep northward, strongly seasonal undercurrent probably assists in maintaining some populations in this ecoregion (Johnson and Checkley, 2004). The northern boundary of this ecoregion is marked by the intersection of the 7 °C isotherm with the top of the permanent halocline in the region of the Subarctic Current. There is a zone of faunal change at the southern tip of Baja Peninsula as cool, lower salinity water is warmed and mixed with subtropical water (Sverdrup et al., 1942; Brewer, 1973). Behaving almost as an "ecotone" of three other distinct biogeographic ecoregions, the assemblage composition of this ecoregion is much less spatiotemporally predictable than those of the central gyres (Barnett, 1983).

Several species of fishes and invertebrates are endemic to either the California Current ecoregion (Krygier and Pearcy, 1981; Jefferts, 1982) or the Subarctic/California Current ecoregions (Brinton, 1962; Ebeling, 1962). The northern section represents the southern limit of many Subarctic Pacific species (Brewer, 1973; Wasmer, 1972). Likewise, the southern region of this ecoregion represents the northern limit of many Eastern Tropical Pacific species (Brewer, 1973). For example, the dragonfish *Tactostoma macropus* occurs almost exclusively to the north of Point Conception, while its ecological counterpart *Stomias atriventer* is only found to the south (Robison, 2004). In contrast, two additional stomiids, *Chauliodus macouni* and *Idiacanthus antrostomus,* occur in abundance throughout the California Current ecoregion. The Transitional Zone waters (*sensu* Dodimead et al., 1963) off California contain faunal components of Pacific Subarctic, North Central Pacific, and Equatorial waters (Lavenberg and Ebeling, 1967; Brewer, 1973). Some faunal components of the basins and canyons off California may be non-reproductive, expatriate populations from both the north and south. The Gulf of California deep-pelagic fish fauna is abundant but with relatively low species diversity and a largely ETP affinity (Robison, 1972). Environmental parameters in the Gulf, particularly its well-developed oxygen minimum zone (Gilly et al., 2013), may be limiting for a number of Northern Central Pacific and California Current species (Brewer, 1973).

3.4.1.4. Northern Central Pacific.

This ecoregion largely corresponds to the oligotrophic (40 g C m^{-2} yr^{-1}) Northern Pacific gyre system. It is bounded to the south by the North Equatorial Current and to the north by the Kuroshio Current and Kuroshio Extension. Mesopelagic fish species diversity is high, with low intra- and interannual variability in assemblage composition (Barnett, 1983), suggesting limited advective processes and a high degree of biological regulation. Dominance of the fish genus *Cyclothone* is pronounced (Maynard et al., 1975). The fauna differ from that in the central Equatorial Pacific band along the equator (White, 1994; Clarke, 1987) and differ markedly from that found in the Subarctic waters to the north (Brodeur and Yamamura, 2005). Copepods in the gyre also show high diversity (over 200 species) and stable vertical distributions and community structure (McGowan and Walker, 1979).

3.4.1.5. Eastern Tropical Pacific.

The Eastern Tropical Pacific (ETP) ecoregion is characterized by high productivity and extensive layering of water masses, especially by a shallow, abrupt thermocline and an OMZ with very low oxygen at mesopelagic depths (Fiedler and Talley, 2006). There is also substantial variability associated with ENSO and other climatic cycles that

influences the shoreward extent of the low oxygen water (Chavez et al., 2003; Chavez and Messié, 2009). While warm-water epipelagic taxa are widely distributed across the entire equatorial and subtropical region, ETP midwater taxa and diel vertical migrators must be adapted to these extreme and abrupt depth gradients (McGowan, 1974). Consequently, ETP mesopelagic faunal distributions are characterized by many endemic taxa which are usually very rare in oceanic waters (Pierrot-Bults and Angel, 2012) or by hiatuses in the distribution of tropical species (e.g. Reid et al., 1978; Brinton, 1979; Fernández-Älamo and Farber-Lorda, 2006). There are also vertical associations with oxygen gradients (e.g. Longhurst, 1967; Sameoto, 1986; Vinogradov et al., 1991; Saltzman and Wishner, 1997; Escribano et al., 2009; Wishner et al., 2013). The ETP ecoregion blends beyond about 130°W with characteristic Equatorial ecoregion conditions. There are several euphausiid species (Brinton, 1962) as well as lanternfishes such as *Diogenichthys laternatus* that are present in the gyres but are dominant in the ETP ecoregion (Brodeur and Yamamura, 2005; Evseenko and Shtaut, 2005).

3.4.1.6. Equatorial Pacific.

This ecoregion is characterized by a complex of both eastward and westward currents, with zones of convergence and divergence (Kessler, 2006). A narrow productive band exists between equatorial current and counter-current conditions to the north and south, sustained by semi-permanent upwelling. Due to its planetary forcing the central equatorial Pacific is distinctive in being the only truly oceanic area in the world ocean where upwelling and concomitant high primary production are not strongly seasonal. Mesopelagic fauna of this ecoregion differ markedly from gyral assemblages found in the Northern and Southern Central ecoregions (Barnett, 1984). Grandperrin and Rivaton (1966) studied the deep-pelagic fishes taken in a transect along the equator from the Galapagos (~ 92°E) to 160°E and reported four longitudinal faunal zones, belying a complex equatorial system with variations in dissolved oxygen and primary productivity as principal environmental drivers. Vertical migration between opposing currents may maintain the geographic integrity of this ecoregion. Three deep-pelagic fish species in this ecoregion, *Cyclothone signata, C. acclinidens,* and *Sternoptyx obscura,* are rare or absent from the oligotrophic central gyres but are abundant in the California Current (Ebeling et al., 1970) and the Peru Current (Craddock and Mead, 1970), where surface temperatures are lower than at the equator or in the gyres, but where temperatures at depth are equivalent, and productivity is high (Barnett, 1984).

On a finer scale, Hartmann and Clarke (1975) and Clarke (1987) suggested the presence of a distinct change in the mesopelagic fish faunas within the Equatorial Pacific, between Hawaii and Tahiti, with a North Equatorial component occurring between 14.5°N and 7°N and an Equatorial component between 7°N and 3°S. The former contained species endemic to the eastern Pacific, with most of these occurring in the core of the Eastern Tropical Pacific, and many also in the California and Peru Currents. The latter component contained species of Indo-Pacific affinity. The faunal division between the two components did not seem to be related to currents, as the boundary occurred in the middle of the equatorial water mass. The authors suggested that the North Equatorial component contained species adapted to low oxygen, and the Equatorial component contained species adapted to high productivity.

3.4.1.7. Peru Upwelling/Humboldt Current.

This ecoregion has a predominant northward flow of surface waters of subantarctic origin and strong upwelling of cool nutrient-rich subsurface waters of equatorial origin. Along the coast of Peru and northern and central Chile, upwelling is localized and its occurrence changes from being mostly continuous in Peru and northern Chile to a more seasonal pattern in southern-central Chile (Thiel et al., 2007). Low oxygen waters are present at depth due to high surface

productivity that is two to three orders of magnitude higher, and an oxygen consumption rate that is an order of magnitude higher, than that of oligotrophic waters offshore (Packard et al., 1983). Primary production rates along the Chilean coast are estimated as similar to those of Peru (4000 mg C m^{-2} d^{-1}; Walsh, 1981) and about 2-fold higher than those of the California upwelling system (1000–2500 mg C m^{-2} d^{-1}; Olivieri and Chavez, 2000). The depth and shoreward extent of the low oxygen water varies with the ENSO cycle. It is a highly productive zone for epi- and mesopelagic fishes and there is some faunal continuity with the Equatorial Pacific. Craddock and Mead (1970) described the faunal change along an east-west transect from the Peru Current toward the central South Pacific at 34°S, in the southern part of the South Central Pacific ecoregion. They showed a change from a species assemblage found in southern mixed waters of high productivity to a central water assemblage. The faunal break centers at about 80°W, roughly the western edge of the Peru Current.

3.4.1.8. Southern Central Pacific.

This ecoregion is broadly defined as the oligotrophic southern Pacific gyre system. Like the Northern Central Pacific, this southern ecoregion is rich in mesopelagic fish species, with low intra- and interannual variability in assemblage composition (Barnett, 1983), suggesting limited advective processes and a high degree of biological regulation. Dominant fish species are similar to the Northern Central Pacific, but the rank order of abundance is shifted on a scale greater than that seen within either area alone (Barnett, 1983). It has been estimated that approximately half of the total mesopelagic species of both Central ecoregions are shared, the remainder being unique to either ecoregion (Barnett, 1984). Overall biomass is also significantly lower in the Southern Central Pacific relative to the Northern Pacific (Barnett, 1984).

On a finer scale, Bertrand et al. (1999) found a maximum abundance of deep-pelagic micronekton (fishes, shrimps and cephalopods) between 11 and 14°S in the French Polynesian region, a zone of weak convergence where oxygen is no longer limiting at depth (see their Fig. 12).

3.4.1.9. Coral Sea.

This ecoregion occurs off the northeastern sector of Australia. The core is associated with the North Queensland Current and the Coral Sea gyre (Dennis et al., 2001; Schiller et al., 2008). It has a characteristic lanternfish fauna, with approximately half of the species being restricted to tropical waters and not extending past the Capricorn boundary (~ 25°S; Flynn and Marshall, 2013). The Capricorn boundary, identified for a range of marine taxa (Last et al., 2005; Hooper and Ekins, 2005), corresponds to a zone of formation and intensification of the East Australian Current (Weeks et al., 2010).

3.4.1.10. Tasman Sea.

Deepening of the Tasman Seaway was one of four major tectonic events during the Cenozoic Era that had a major impact on ocean circulation and pelagic biogeographical patterns (Angel, 1997). The Tasman Front is an asymmetric zoogeographic boundary off eastern and southeastern Australia, being semi-permeable to northern species but strong for southern species. The lanternfish fauna differs from that of the Coral Sea ecoregion (Flynn and Marshall, 2013), having more species (including temperate species) and extending south to the Tasman Front (33–35°S). There is a gradient in lanternfish biomass across the Tasman Sea from west to east, and indications that there is greater recycling of nutrients in eastern areas of the Tasman Sea, but this sub-basin gradient is not sufficient to split the ecoregion longitudinally (Flynn and Kloser, 2012).

3.4.1.11. Sea of Japan.

The Sea of Japan lies between the Asian mainland, the Japanese

archipelago and the Russian island of Sakhalin. It has almost no tides due to its nearly complete enclosure from the Pacific Ocean, being shielded from the Kuroshio and Oyashio Currents by the landmasses of Japan. Its salinity is lower (~ 34 psu) than the Pacific, but its dissolved oxygen is elevated, though the oxygen content has decreased over the past 60 years (Chen et al., 1999). Surface temperatures vary greatly (> 20 °C) between regions and seasons, while deep layers are very cold (0.5 °C). It is the second-coldest sea in the world with an average water temperature of 0.9 °C, compared to that of the Arctic Ocean at 0.7 °C.

Because of the shallow straits connecting the sea with the Pacific (< 140 m), the mesopelagic fauna is depauperate (Ikeda and Hirakawa, 1998). Only seven copepod species, two euphausiids, one mysid, two hyperiid amphipods, one chaetognath, one micronektonic fish, and one ostracod species regularly inhabit the extremely cold mesopelagic depths (Ikeda and Hirakawa, 1998). The giant squid *Architeuthis* apparently moves regularly into the Sea of Japan and resides at mesopelagic depths (Wada et al., 2015). Most of the deep-sea fauna are boreal or sub-boreal species that are only now evolving into a deep-sea mode of life – so-called "secondary deep sea species." Surveys using nets and more recently submersibles (Lindsay and Hunt, 2005) have revealed that the species diversity of both midwater gelatinous meso- and macro-plankton is also extremely low. Vinogradov (1970) reported 'disturbed' vertical distributions of fauna, with deep-pelagic organisms found shallower than usual.

3.4.1.12. South China Sea.

The South China Sea is one of the deepest and largest marginal seas in the Western Pacific Ocean. It is connected to the Pacific Ocean by the Bashi Channel, Taiwan and Mindolo Straits, etc., and to the Indian Ocean by the Strait of Malacca. It is mostly in the tropical zone and exchanges warm water of the Kuroshio Current through the Bashi Channel. The mesopelagic fish fauna is species-rich (e.g., 62 species of lanternfishes; Yang and Huang, 1986) and of tropical/subtropical affinity, sharing a majority of species with the Central and Eastern Tropical Pacific, though with a number of species not found to the east (Yang and Huang, 1986). Only a few South China Sea fish species are found in the Subarctic Pacific.

3.4.1.13. Indo-Pacific "Pocket" Basins.

This ecoregion encompasses the deep (> 4000 m) basins of the Indo-Malayan Archipelago, the Sulu, Celebes (Sulawesi), and Banda Seas. It is bounded by the Philippines, New Guinea, Indonesia and Borneo and has the largest density of islands on Earth. Between the island groups are pocket basins, areas of the seafloor that are thousands of meters deep, yet isolated from each other by islands and submerged ridges. The sill depths of some of these seas reach to within a few hundred meters of the surface, effectively restricting the exchange of some deep-living fauna. The deeper layers are hydrographically distinct and hold a unique Indo-Pacific fauna (Briggs, 1974; Robison and Hamner, 2009). This ecoregion is characterized by low productivity (< 150 g C m^{-2} yr^{-1}) and complex oceanography within the basins due to strong currents, trench topography, seamounts and active volcanic islands (US NOAA,1991). The shallow sill depths of the Sulu Sea (400 m) prevent the inflow of cold deep water from the Pacific and Indian Oceans, resulting in high temperatures (10 °C) at great depth. As with the Mediterranean and Red Seas, where water temperatures at depth are also elevated, many usually common deep-sea taxa are absent (Grossmann et al., 2015). The closed nature of the Sulu Sea in particular is reflected in the characteristic temperature-salinity-oxygen signature of its water as well as the presence of distinct 'morphotypes' of cosmopolitan species in this basin, such as the viperfish, *Chauliodus sloani* (Haffner, 1952). The Sulu Sea likely comprises an ecologically distinct habitat within the Indo-Malayan region, and may warrant separation as a separate ecoregion on a global scale. Although the species rosters of the other basins are not as

distinct, these basins none-the-less comprise a distinct biogeographic ecoregion, in part due to their complex oceanography and semi-closed nature. This oceanographic complexity and isothermal nature have been cited to explain the unusual presence of meso- and bathypelagic organisms in the epipelagic zone (Gordon et al., 1994). van der Spoel and Schalk (1988) reported both meso- and bathypelagic fauna occurring in the upper 100 m of the eastern Banda Sea and Aru Basin during both Southeast and Northwest Monsoon seasons, which they ascribed to the effect of deep mixing (Gordon, 1986) and deviating temperatures at depth. As a large, complex marine ecosystem in total, this ecoregion holds a unique Indo-Pacific fauna, including endemic species (Gopalakrishnan, 1975; Pietsch, 1979) and inter-ecoregion species (Nafpaktitis et al., 1995), though inter-basin differences are notable.

3.4.1.14. Arabian Sea.

The Arabian Sea is one of the most productive oceanic areas in the world (Ryther et al., 1966), but production is highly seasonal and associated with the monsoonal cycle. Productivity and vertical flux peak during the summer Southwest Monsoon as a result of wind-driven upwelling but are also surprisingly high during the Northeast Monsoon as a result of deep convective overturn (Barber et al., 2001). This seasonality causes unique and highly variable circulation systems (Wyrtki, 1973; Qasim, 1982). A five-fold increase in zooplankton displacement volumes has been reported during the Southwest Monsoon relative to the Spring Intermonsoon in the western Arabian Sea, but at mesopelagic depths there was little seasonal change in zooplankton biomass during the JGOFS (Joint Global Ocean Flux Study) year of sampling in 1995 (Wishner et al., 1998). There is a strong onshore-offshore gradient in zooplankton biomass, however. Seasonal severe OMZ intensification occurs (Herring et al., 1998), with oxygen levels less than 1.0 ml l^{-1} as far south as 10°N. The northern Arabian Sea encompasses the thickest of the major oxygen-poor layers, with values below 0.1 ml l^{-1} from 100 m to 1000 m (Qasim, 1982). Mesopelagic fish diversity is intermediate in the Arabian Sea relative to equatorial waters of the Northern Indian Ocean (Cohen, 1986), but fish abundance and biomass, particularly the lanternfish *Benthosema pterotum*, can locally be very high (Gjøsaeter, 1984). The nearshore areas of the Arabian Sea hold nearly one half of the mesopelagic fish biomass recorded from the western Indian Ocean (Gjøsaeter and Kawaguchi, 1980).

3.4.1.15. Bay of Bengal.

This ecoregion is the smallest of the four extensive regions with oxygen levels below 0.1 ml L^{-1} (the others being the California Current, the Arabian Sea and the ETP, listed in increasing size). The ecoregion is bounded in the south by equatorial waters, and has separate low oxygen levels from the Arabian Sea Ecoregion. Both the Bay of Bengal and the Arabian Sea share a limited deep-pelagic endemic fish fauna, such as *Chauliodus pammelas*, (Gibbs and Hurwitz, 1967) and *Astronesthes lamellosus* (Goodyear and Gibbs, 1969).

3.4.1.16. Somali Current.

The Somali Current ecoregion is affected by seasonal monsoon conditions and has strong seasonal upwelling and productivity. The deep-diapausing copepod *Calanoides carinatus* comes to the surface to feed and reproduce during the Southwest Monsoon (Smith et al., 1998). Its boundary coincides with the western edge of its namesake current, where the dominant mesopelagic fish species (*Benthosema fibulatum*) transitions to that of the Arabian Sea (*Benthosema pterotum*) (Gjøsaeter, 1984). Overall mesopelagic fish abundance and biomass is much lower than those of the Arabian Sea and Bay of Bengal, but higher than those of the oceanic Indian Ocean (Gjøsaeter and Kawaguchi, 1980). One of the dominant fishes in this ecoregion, *Diaphus watasei,* usually caught near the bottom day and night, is among the largest lanternfishes known (Nafpaktitus, 1978).

3.4.1.17. Northern Indian Ocean.

This ecoregion is the northern gyre system of the Indian Ocean, ~10˚N–4˚S, affected by various currents at depth and complex seafloor topography. Primary productivity is fairly low except in localized areas of upwelling. Mesopelagic fish faunal composition is distinctive relative to that of the Southern Indian Ocean. Mesopelagic fish diversity is highest in equatorial waters, but offset to the south, coincident with the interface between the South Equatorial Current and the Central water masses (Wyrtki, 1973; Cohen, 1986), an area that also supports enhanced seabird and tuna abundance.

3.4.1.18. Mid-Indian Ocean.

This ecoregion encompasses a broad frontal band of the Indian Ocean near the equatorial region, ~ 4–20˚S, with a characteristic temperature-salinity-oxygen (TSO) signature, and shoaling of the 10 ˚C isotherm (above 500 m). Primary productivity is higher in this ecoregion than in the Northern Indian Ocean ecoregion. This ecoregion is well- oxygenated relative to the Arabian Sea, but less oxygenated than the Southern Indian Ocean. This ecoregion contains a diverse mesopelagic fish fauna (Craddock and Haedrich, 1973).

3.4.1.19. Southern Indian Ocean.

This ecoregion encompasses a broad band of subtropical surface waters, ~ 20–40˚S, north of the Subantarctic Convergence. Primary production in this ecoregion is very low, less than $0.10 \text{ g C m}^{-2} \text{d}^{-1}$ (Craddock and Haedrich, 1973). The waters are well oxygenated, with values exceeding 5.0 ml l^{-1}. Mesopelagic fish diversity and biomass are lowest here relative to the rest of the Indian Ocean (Cohen, 1986). Fish biomass, but not diversity, increases around 40˚S, where water column stratification eases and the thermocline shoals (Cohen, 1986). Ebeling (1962) surveyed 135 species of circumglobal deep-pelagic fishes and found that species living in this and the Mid-Indian Ocean Ecoregions have a 45% overlap with the South Atlantic and 75% overlap with the South Central Pacific. The pelagic fauna of the southwestern Indian Ocean is influenced by seamounts and continental slopes of the Southwest Indian Ocean Ridge. From Socotra Island at 12˚N to Walters Shoals at 33˚S, 50–80% of the mesopelagic biomass at night may be accounted for by benthopelagic shrimps of the genera *Janicella, Pasiphaea, Challengerosergia,* and the lophogastrid genera *Lophogaster, Paralophogaster,* and *Echinomysis* (Vereshchaka, unpubl.). As shown for invertebrates in areas of the Pacific (Vereshchaka, 1990), the water column at night in areas of the Southern Indian Ocean is dominated by a specific benthopelagic fauna at distances of tens of kilometers around topographic features (Vereshchaka, 1995), and thus this ecoregion contains punctured areas where mesopelagic assemblages significantly differ from those in the surrounding waters.

3.4.1.20. Agulhas Current.

The Agulhas Current (AC) is the western boundary current of the southwest Indian Ocean, and is considered the largest western boundary current in the world ocean (~ 100 Sv). It flows down the east coast of Africa from 27˚S to 40˚S, where it is narrow and strong. The zone of departure from the South African Coast is characterized by complex patterns of vigorous fronts and eddies, the effects of which extend below 1600 m depth (Bang, 1970; Lutjeharms, 1981). The AC acts as a convergence zone, driving upwelling south of the current, resulting in enhanced primary productivity (Mann and Lazier, 2006). The faunal composition within this ecoregion reflects a combination of deep-living subantarctic species and broadly tropical species whose southern limit is extended by the AC (Hulley, 1989). The AC is one of the likely dispersal routes between the temperate Pacific and Atlantic habitats (Cermeño and Falkowski, 2009).

3.4.1.21. Northwest Atlantic Subarctic.

This ecoregion extends from the Arctic Circle to the North Atlantic Subpolar Front. It is the only major ocean region that has a deep-water connection with the Arctic. This is the "subarctic" region of Backus (1986), though his is much smaller. On smaller spatiotemporal scales there is evidence that the Northwest Atlantic Subarctic has eastern and western mesopelagic components, particularly on each side of the relatively shallow Reykjanes Ridge (Sutton and Sigurðsson, 2008), where wholesale changes of species abundance and dominance in the fish fauna occurs. It has also been known for quite some time that the northern boundary of many warm-water species varies considerably in the eastern and western parts of this ecoregion (Krefft, 1976), being much farther north on the eastern side.

3.4.1.22. North Atlantic Drift.

This ecoregion encompasses an eddy field region, expanding eastwards and tracking the flow of the Gulf Stream. It is a weak transition zone for northern species due to tropical submergence, but a strong boundary for southern species (Sutton et al., 2013; Vecchione et al., 2015). The Subpolar Front is the northern boundary, though this boundary becomes quite weak east of about 25˚W (Krefft, 1976). This ecoregion corresponds to the "northern temperate" region of Backus et al. (1977), though their region was much larger and contained six ecoregions (Slope Water, Northern Gyre, Azores/Britain, Mediterranean Outflow, Western Mediterranean, and Eastern Mediterranean). In the far western North Atlantic, the Slope Water fauna described in Jahn and Backus (1976) appears to be an oceanic rim ecotone between the Northern Sargasso Sea region of the North Atlantic Drift ecoregion and the Labrador region of the Northwest Atlantic Subarctic ecoregion.

3.4.1.23. Gulf of Mexico.

The Gulf of Mexico (GoM) is physically distinct from the Caribbean Sea and the Central North Atlantic due to geography (the 'American Mediterranean'), the influence of tropical waters *and* winter cooling, and the influence of a large river system (Mississippi River). The GoM has been called a place of 'special interest' to pelagic biogeographers (Backus et al., 1977; Backus, 1986; Bangma and Haedrich, 2008). It is a faunal region of high diversity with respect to mesozooplankton (Hopkins, 1982), and mesopelagic micronekton: fishes (Gartner et al., 1988), macrocrustaceans (Flock and Hopkins, 1992; Hopkins and Sutton, 1998; Judkins, 2014), and molluscs (Passarella and Hopkins, 1991; Judkins et al., 2009). Bangma and Haedrich (2008) found the GoM to be higher in abundance, biomass, and richness than adjacent oceanic regions (Caribbean and Sargasso Sea), supporting the classification of the GoM as a unique biogeographic ecoregion (Backus et al., 1977; Gartner et al., 1989). The 794 fish species collected in deep-pelagic surveys after the *Deepwater Horizon* oil spill rank the GoM as one of the four most-speciose oceanic ichthyofaunas known in the World Ocean (Sutton et al., 2017).

3.4.1.24. Central North Atlantic.

This ecoregions encompasses a broad area of consistent TSO conditions across the northern Atlantic. Its faunal assemblage composition is distinct from the North Atlantic Drift and Equatorial Atlantic ecoregions, but with regional variation in relative abundances. At its northern extent the borders of cold- and warm-water species occur close together near 42˚N (Backus et al., 1977). On the western side the ecoregion includes the Caribbean Sea ('Atlantic Tropical Region' of Backus et al., 1977) and the Sargasso Sea ('Atlantic Subtropical Region' of Backus et al., 1977). On smaller spatiotemporal scales Backus et al. (1977) classified northern and southern subtropical regions within the Central North Atlantic, The former geographic border is detectable but weak relative to ecoregion borders, especially when one considers deep-mesopelagic and bathypelagic taxa (Sutton et al., 2010). Fasham and Foxton (1979), in an analysis of pelagic decapod crustacean distribution in the eastern North Atlantic, did not detect this faunal boundary in their datasets. Hulley and Krefft (1985) also questioned this subdivision based on results of the 1979-Sargasso Sea Expedition of the R/V *Anton Dohrn*,

finding differences in species abundances rather than faunal composition. There is evidence of east/west regional differences within the Central North Atlantic, with some species restricted to one side or the other (e.g., *Maurolicus weitzmani* in the western North Atlantic, *Argyropelecus olfersi* in the eastern). The Azores Front, a permanent southerly return branch of the Gulf Stream, has been reported as a biogeographic boundary separating Eastern and Western Atlantic Water (Gould, 1985; Domanski, 1986), though the effect is primarily on abundance and rank order versus presence/absence of species.

3.4.1.25. Mediterranean.

The Mediterranean is the youngest of our ecoregions, formed about 5.3 million years ago when a narrow strait opened to the Atlantic flooding the then nearly dry Eastern and Western basins (Garcia-Castellanos et al., 2009) to an average depth of 1500 m. Now a nearly land-locked sea, it is connected to the Atlantic by the shallow (300 m) Strait of Gibraltar. Evaporation greatly exceeds precipitation and drives the circulation. The deep waters of the Mediterranean are universally warm (12–13 °C) and of relatively high salinity. The mesopelagic plankton is much sparser than that of the Atlantic, likely due to the warm temperatures that result in low survival of immigrants (Casanova, 1986). The larger fauna is depauperate relative to the North Atlantic Drift and Mauritanian ecoregions (see below), an observation typified by both lanternfishes (Myctophidae) and pelagic decapod shrimps (Judkins, 2014). The Mediterranean has 17 resident lanternfishes and 10 decapod species compared to 44 lanternfishes (Sutton et al., 2008) and 44 shrimp in the mid-North Atlantic, 53 lanternfishes (McEachran and Fechhelm, 1998) and 35 decapods in the Gulf of Mexico, and 67 lanternfishes in the South Atlantic subtropical region (Backus et al., 1977). The biomass of mesopelagic fishes is low, even more so in the Eastern Basin than in the Western (Goodyear et al., 1975). The second- most abundant mesopelagic fish species (*Cyclothone pygmaea*; Badcock, 1984) and a deep-living decapod (*Sergestes eximia*; Judkins, 2014) are endemic.

3.4.1.26. Mauritania/Cape Verde.

This ecoregion encompasses an area around the Cape Verde Plateau with the Canary Current at the surface. Two production regimes exist within this ecoregion, based on the source of upwelled water: north of Cape Blanc is North Atlantic Central Water, which is less nutrient-rich; south of Cape Blanc is South Atlantic Central Water, which is 'older' and more nutrient-rich (Gardner, 1977). Backus (1986) recognized this ecoregion as a 'special biogeographic region.' It has discrete mesopelagic faunal communities, including relict populations of far northern Atlantic deep-pelagic species (euphausiid *Meganyctiphanes norvegica* and lanternfish *Benthosema glaciale*), Mediterranean species (Badcock, 1981), as well as other eastern Atlantic "cool water group" lanternfishes (Badcock, 1981; Hulley, 1981; Zelck and Klein, 1995) and pelagic decapods (Judkins, 2014). Olivar et al. (2017) analyzed samples from 12 stations across the tropical and equatorial Atlantic (NW Africa to Brazil), and found that the mesopelafc fish species richness off the Cape Blanc upwelling was the highest for the entire survey, reflecting the mixed faunas of tropical and subtropical and even temperate origins. This ecoregion also contains endemic species, such as the lanternfish *Lampadena pontifex* (Backus et al., 1977) and, along with the Benguela Upwelling ecoregion (see below), the decapods *Sergia manningorum, DeoSergestes pediformis, ParaSergestes diapontius* and *Gennadas brevirostris* (Judkins, 2014). The two ecoregions also share a strong on-slope component, with obligatory and facultative pseudoceanic lanternfish species as dominants (e.g., *Diaphus taaningi* and *Diaphus dumerilii*; Badcock, 1981). Morphological analyses of fish species co-occurring in the Mediterranean and Canary Current regions suggest that gene flow between these ecoregions must be strongly maintained, much more so than that between the Mediterranean and the North Atlantic (Badcock, 1981).

3.4.1.27. Tropical and West Equatorial Atlantic.

In this ecoregion easterly winds cause divergence and upwelling, creating a narrow band of high productivity. This ecoregion is influenced by the northern boundary of the South Atlantic subtropical gyre, the effect of which is noticeable from the surface down to 1500 m (Schmid et al., 2000a, 2000b), and the south equatorial current and counter current system. Marked differences in the combination of TSO characteristics from adjacent areas are evident and this mesopelagic ecoregion is in general alignment with epipelagic boundaries. There is some differentiation of water properties at around 30°W, the eastern part being cooler, of lower salinity and having less dissolved oxygen than the western part (Backus et al., 1977). This ecoregion is mostly oligotrophic, with mean productivity lower than 90 g C m^{-2} yr^{-1} (Rosa et al., 2008). Over the Mid-Atlantic ridge mesopelagic fish and cephalopod assemblages were found to be of lower abundance and species-poor compared with adjacent areas (Kobyliansky et al., 2010; Perez et al., 2012).

Hygophum reinhardtii, H. taaningi, Lobianchia gemellarii and *Myctophum selenops* were the only lanternfishes of Atlantic tropical distribution found in this region, as were the squids *Cycloteuthis sirventi* and *Neoteuthis thielei*. This cephalopod fauna impoverishment was also reported by Rosa et al. (2008), and attributed to the low primary productivity at the surface. Over the slope of the Brazilian margin (500–2000 m), Haimovici et al. (2007) differentiated two pelagic cephalopod assemblages to the north and to the south of 18°S, roughly the boundary between this ecoregion and the South Atlantic ecoregion.

3.4.1.28. Guinea Basin and East Equatorial Atlantic.

This ecoregion is characterized by a summer phytoplankton bloom induced by the intensification of the Southeast trade winds that cause the deepening of the thermocline in the West Equatorial Atlantic while shoaling in the East (Longhurst, 1993). Surface chlorophyll *a* concentrations vary between 0.66 and 1.28 mg m^{-3} between June and December and the region is also influenced by the coastal upwelling system off Namibia and the plume produced by the Congo River runoff (Pérez et al., 2005). The western boundary of this ecoregion is based on the distribution of dissolved oxygen, as there is a marked OMZ in the equatorial eastern Atlantic at about 400 m. The mesopelagic fish species richness of this ecoregion is high; the lanternfish species number equals that of the Gulf of Mexico (Backus et al., 1977). Diverse and abundant assemblages of mesopelagic fishes and cephalopods occur over the Romanche Fracture Zone (00°34′N–04°48′S), with a strong sound-scattering layer (Kobyliansky et al., 2010; Perez et al., 2012). Among the dominant taxa of this region are the fish species *Cyclothone alba, Sternoptyx diaphana* and *Vinciguerria nimbaria,* and the cephalopods *Liocranchia reinhardti* and *Vitreledonella richardi*.

3.4.1.29. Benguela Upwelling.

The Benguela Ecoregion is a strong upwelling system supporting highly productive pelagic fisheries and severe seasonal OMZ formation. The mean annual primary productivity exceeds 300 g C m^{-2} y^{-1} (Rosa et al., 2008). Its mesopelagic fauna has a strong pseudo-oceanic component (Hulley and Lutjeharms, 1989) owing to the proximity of the frontal system to the shelf break in the southern region of the ecoregion. The dominant pseudo-oceanic lanternfish, *Lampanyctodes hectoris*, is so abundant it has been fished commercially and at one time accounted for over 9% of the annual pelagic catch by the South African purse-seine fishery (Hulley and Prosch, 1987). Some deep-pelagic crustacean taxa (e.g., *Euphausia hanseni* and *Nyctiphanes capensis*) appear to have life cycles that retain the populations within the upwelling cells (Barange and Pillar, 1992). This ecoregion contains the highest diversity of oceanic cephalopods in the Atlantic (Rosa et al., 2008) and the diversity of pelagic decapods, with 46 of 91 Atlantic species, is likewise high (Judkins, 2014). The landward distribution of oceanic species and the seaward distribution of pseudo-oceanic species

in the central and southern Benguela regions (28–35°S) largely coincide with the 800-m isobath. The areal extent of the Benguela Upwelling ecoregion is seasonal, being pinched during summer and early autumn between the Angola and Agulhas Current systems (Shannon, 1985, 1986), and expanding in the winter.

3.4.1.30. South Atlantic.

This ecoregion is a region of complex circulation features. Circulation at depth is affected by local topography (e.g., Walvis Ridge and Rio Grande Rise), potentially deeper than 1000 m. The ecoregion mostly contains oligotrophic waters of the South Atlantic subtropical gyre, except for borders with the Subtropical Convergence zone (to the south) and the Benguela upwelling zone (to the east). Nesis (2003) defined this zone as "south subtropical," citing the Atlantic distribution limits meso- and bathypelagic squid species (e.g., *Teuthowenia pellucida* and *Histioteuthis macrohista*). Zooplankton communities are distinctive across the southern Atlantic. Mesopelagic fish and shrimp faunas differ from those of the Central North Atlantic, though the difference often is manifest as "sister species" (i.e., within a genus or closely related genera) replacements. For example, the caridean shrimp *Acanthephyra kingsleyi* is replaced at about 18°S by *A. quadrispinosa,* which in turn is replaced by *A. pelagica* at about 35°S (Fasham and Foxton, 1979; Judkins, 2014). Deep-pelagic (*meso-* and *bathypelagic*) species richness is higher in the South Atlantic Central waters than in the North Atlantic (Fock, 2009), possibly a function of paleo-ecology; the deepwater pathways between the Pacific and Atlantic ~50 million years ago channeled through the South Atlantic before entering the North Atlantic (Mironov, 2006). Kobyliansky et al. (2010) reported high mesopelagic fish diversity in the vicinity of the Walvis Ridge, both over abyssal depths and the summits of a large guyot. In the latter, samples comprised a mixture of tropical, subtropical and subantarctic lanternfish species. These authors attributed the increased fish diversity (and abundance) to the proximity of a transition zone, the highly productive subtropical convergence. Similar results were shown for the cephalopod fauna with a high diversity of Atlantic tropical-subtropical species, including *Stigmatoteuthis arcturi, Histioteuthis corona, H. meleagroteuthis* and *H. reversa* (Perez et al., 2012).

3.4.1.31. Circumglobal Subtropical Front.

This ecoregion encompasses a broad band in the Southern hemisphere where there is convergence of subtropical and subantarctic waters. The Subtropical Convergence is associated with strong horizontal gradients in the upper 400 m, with associated high hydrographic variability (Sokolov and Rintoul, 2002; Hamilton, 2006). At some places and times the frontal zone is relatively permanent and intense (e.g., south of Africa), while in others it can be ephemeral and weak (e.g., mid-Atlantic sector; Barange et al., 1998) or highly dynamic (e.g. the eddy-filled region in SW Atlantic; Stramma and Peterson, 1990). This ecoregion is highly productive; in the South Atlantic satellite-derived mean annual estimates of primary productivity exceed 190 g C m^{-2} yr^{-1} (Rosa et al., 2008), with associated high diversity of oceanic cephalopods in the Atlantic. In the Pacific sector, Bekker and Evseenko (1986) defined the southern boundary between 40 and 42°S, determined from an analysis of the shift in species composition of mesopelagic fishes and their larvae.

Pakhomov et al. (1994) identified distinct deep-pelagic micronekton and zooplankton assemblages in the Subtropical Convergence and Subantarctic Front (their Antarctic Polar Front) off Southern Africa. Robertson et al. (1978) and McGinnis (1982) also identified the Sub-tropical Convergence as a biogeographic boundary off New Zealand and south of 30°S, respectively. In all areas of the Subtropical Convergence cross-frontal mixing of subtropical and Antarctic species across a wide range of trophic levels is prevalent (Barange et al., 1998).

3.4.1.32. Subantarctic.

This ecoregion encompasses an oceanographic zone ("notalian"

zone of Parin et al., 1974; "Westwind Drift" of Krefft, 1974) between the Antarctic Polar and Subtropical Fronts (Condie and Dunn, 2006). The zone is characterized by cold, low salinity waters. This ecoregion contains deep-pelagic fauna either confined to, or centered within the Subantarctic Front and extending south into the Southern Ocean (Krefft, 1976; Flynn and Marshall, 2013). In the Pacific sector, Bekker and Evseenko (1986) defined the southern boundary between 50 and 54°S (depending on longitude) and the northern boundary around 40–42°S, determined from an analysis of changes in species composition of mesopelagic fishes and their larvae. For zooplankton, the subantarctic waters are the only truly oceanic region with substantial endemism (Pierrot-Bults and Angel, 2012). Across taxa, the high number of species endemic to the ecoregion corroborates its distinctiveness. Krefft (1976) postulated that the speciose, circumglobal Southern Ocean midwater fish fauna originated in the subantarctic water mass. In the Australasian region, species with Subantarctic affinities may extend north into the Subtropical and Tasman Sea ecoregions if they occupy deeper strata (i.e., "tropical submergence"; Thorne, 1972; van der Spoel and Schalk, 1988).

3.4.1.33. Antarctic/Southern Ocean.

This ecoregion is characterized hydrographically by cold, dense water, and a strong eastward circumpolar current south of Antarctic Convergence, which is the largest pelagic boundary of the world ocean (Sournia, 1994). Some consider the Southern Ocean water mass to include the waters listed in the previous two biogeographic ecoregions; in this treatment we regard the seasonally fluctuating Antarctic Convergence as separating the Southern Ocean biogeographic ecoregion from those of other oceans due to the distinctive faunal composition of the former relative to those of the latter. Unlike its northern counterparts, where phytoplankton growth is primarily limited by nitrate, the Southern Ocean is characterized by strong iron limitation (Moore and Abbott, 2000; Cermeño and Falkowski, 2009), which in turn affects the distribution of higher trophic levels. As with the Arctic, temperatures at 200 m appear to be a better predictor of mesopelagic faunal distributions within the Southern Ocean than surface temperature (Hulley, 1998; Koubbi et al., 2011). A similar finding was indicated for Arctic zooplankton (Błachowiak-Samołyk, 2008). In general the mesopelagic fish species richness of the Southern Ocean is low compared to other ocean basins (e.g., Macpherson (2002) for Atlantic Ocean). When primarily benthic or benthopelagic taxa are excluded (e.g., Notothenoidei, Zoarcidae, Liparidae), there appears to be no exclusively Antarctic midwater fish fauna. However, the relative contribution of deep-pelagic fishes to the total Antarctic fish fauna is high, ~ 25% (Kock, 1992), and in areas outside the influence of seasonal pack ice, i.e., areas not dominated by *Euphausia superba* (Hempel, 1987), nekton diversity can be relatively high (Piatkowski et al., 1994). Though early reports confirmed the circumpolarity of Southern Ocean plankton species (Baker, 1954), more recent studies have prompted the subdivision into "ecoregions." For example, Koubbi et al. (2011) suggested up to three pelagic ecoregions of the Indian sector between the Subantarctic Front and the Subtropical Convergence based on modelling of lanternfish distribution.

4. Discussion

In this paper we have integrated new and previous efforts to develop a global biogeographical classification of the *meso*pelagial, designed to mesh with the epipelagic and deep-benthic classifications developed as parts of the GOODS biogeographic classification (UNESCO, 2009; Spalding et al., 2012; Watling et al., 2013). In considering a biogeo-graphic division of the global mesopelagial, given the data gaps we have listed, one may ask, "Why now, and why is this important?" The reasons are many, and relate to an increasing awareness of the im-portant role of mesopelagic animals in the structure and function of the global ocean. Mesopelagic fishes dominate the world's total fish

biomass and constitute a major component of the global carbon cycle. Gjøsaeter and Kawaguchi,1980 estimated their biomass at 1000 million tons, but acoustic surveys now suggest that mesopelagic fish biomass may be an order of magnitude higher (Kaartvedt et al., 2012). This biomass, when combined with findings that energy transfer efficiency from phytoplankton to fishes in the open ocean is higher than typically assumed (Irigoien et al., 2014), suggests that mesopelagic fishes in oceanic ecosystems may be respiring as much as 10% of the primary production in the deep pelagial. The increased biomass estimate has recently spawned increased interest in mesopelagic fisheries, with Norway and Pakistan issuing new licenses to fish there (The Economist, 2017). Lastly, in terms of global biogeochemistry, marine fishes may contribute up to 15% of total oceanic carbonate production in their intestines (Wilson et al., 2009), while vertical migrators (fish, crustaceans, cephalopods) play a major role in the active transport of carbon to deeper waters (Steinberg et al., 2002; Bianchi et al., 2013).

A critical element of the biogeographical classification was consideration of variability in both horizontal and vertical dimensions, as illustrated in Fig. 2. The panel approach enabled and expert-opinion consideration of this variability to produce a general scheme that we believe will prove reasonably sound. Nevertheless, both vertical and horizontal boundaries should be regarded as transitional zones (sometimes characterized by fronts, eddies and other mixing phenomena, varying with depth and location) and not abrupt borders (Vecchione et al., 2015). Ecoregion boundaries in some cases are thought to be highly dynamic, such as the changing position of the Sub-Polar Front in the North Atlantic. In addition to physical mixing processes, many pelagic taxa can persist for appreciable periods of time when advected into regions beyond their reproductive ranges (e.g., lanternfishes and deep-sea smelts; Sassa et al., 2004). Thus, these diffuse and often asymmetrical biogeographical boundaries apply primarily to 'typical' assemblages, rarely to individual species. It is also clear, as more data on depth distributions of a range of taxa become available, that the depth ranges encompassed by epi-, meso-, and bathy-pelagic zone definitions are not borders, and species patterns vary with depth and taxa. Our understanding of how trends may change within the *meso*pelagial will no doubt evolve as more information is gathered on the deeper bathyal fauna. Developing genetic approaches also offer considerable promise for determining geographical relationships, and discovery of cryptic species (e.g., Kulagin et al., 2014).

4.1. Comparisons with existing schema

Few global mesopelagic biogeographic classifications are directly comparable to the one presented here. Most mesopelagic treatments are confined to ocean basins or smaller scales, and most are taxon-specific. Hoving et al. (2014) reviewed the state of biogeographical knowledge of deep-sea cephalopods, but their account was structured by ocean basin, and highlighted obvious geographical gaps in cephalopod studies. Vereshchaka et al. (2014) reviewed the global distribution of mesopelagic shrimps (Sergestidae) and found that species of most mesopelagic genera are restricted to a single ocean. Brodeur and Yamamura (2005) developed a biogeography for mesopelagic micronekton in the North Pacific, and their divisions are similar to those presented here at the largest scale. In their schema they divided our Subarctic ecoregion into a northern Subarctic zone and southern Transition zone. Such 'zonal' and 'regional' discrimination within our ecoregion biogeographical level is also reflected in the delineation of 10 pelagic 'regions' in the North Atlantic by Backus et al. (1970). In a follow-on paper, Backus and Craddock (1977) refer to these same delineations as 'provinces,' which were defined as 'open waters of the deep ocean in which the fauna is thought to be reasonably homogeneous.' In this and later works (Backus et al., 1977; Backus, 1986) the two terms were purposely undefined, other than to say that 'provinces' were subdivisions of 'regions.' The resulting schema based on Atlantic lanternfish distributions delineated seven faunal regions subdivided

into 20 provinces. Aligning this with our structure, the 10 Atlantic ecoregions conform reasonably well to their seven pelagic regions, with some exceptions: we recognize the Mediterranean, Guinea/East Equatorial, and Benguela Upwelling ecoregions as being biogeographically distinct, and our Atlantic subtropical gyre ecoregions are delimited by equatorial upwelling. Judkins (2014) provides a perspective on taxonomic specificity; his study of pelagic decapods from the same collections as those of Backus et al. (1977) recognized only five biogeographic patterns.

In considering the global distribution of 135 species of 'warm-water' deep-pelagic fishes, Ebeling (1967) described two main patterns: 1) that of the equatorial water masses, and 2) that of the vertically stable central water masses. In total, he recognized seven "primary zoogeographical regions": Gulf of Mexico, Mediterranean, Atlantic Subarctic, Circum-central/Tropical, Eastern Pacific Equatorial, Subarctic and North Pacific Subarctic/Transitional. Aligning Ebeling's (1967) schema with ours, he recognized 14 of our 33 ecoregions, with the primary differences being our discrimination of eight marginal seas and upwelling regimes, and our georeferenced ecoregion boundaries.

Parin (1984) summarized previous studies of mesopelagic fish biogeography, citing the concordance of many species' distributions with the principal large-scale circulations, and with the transitional zones of their interactions. He further described 12 types of ranges of mesopelagic fishes, many of which spanned multiple ecoregions listed in this paper (e.g., 'broadly tropical,' 'equatorial-central type'). He noted, "*It seems, however, that the recognition of water masses by temperature-salinity indices is not sufficiently sensitive for revealing all pelagic habitats.*" This statement reiterated that of Backus et al. (1970): "*Were the water mass hypothesis sufficient, however, the zoogeography of the North Atlantic pelagial would be very simple, for it consists solely of one water mass – the North Atlantic Central Water. Our data indicate a far greater complexity.*" The classification presented here further refines this notion; the interplay between seasonality, export production, water column aerobic respiration, proximity to continental shelves/topography, and the nature of primary production (i.e., "new" vs. "recycled" production; Dugdale and Goering, 1967) are likely drivers of biogeographical ecoregion extent.

Proud et al. (2017) defined over 60 distinct provinces of mesopelagic organisms based on acoustically sensed deep-scattering layer (DSL) characteristics (depth, vertical extent, and acoustic backscattering intensity). These authors chose a ten-class acoustic model (36 provinces) as corresponding most closely to existing mesopelagic biogeography. In large areas of the Pacific and Indian Oceans the 36-province model has many of the same features as the present scheme, but lack of data in the Atlantic Ocean, North Pacific and Northern Indian Ocean, along with their schema having no taxonomic component, limit its comparability with a global mesopelagic biogeography. Their acoustic schema, like our 33-ecoregion schema, revealed a biogeographic structure with more complexity than simple latitudinal banding patterns. Given the disparate methodologies used, the biogeographic patterns revealed by the two studies were similar in many regards, emphasizing the importance of surface ocean processes on deep-pelagic community structure.

Recent work by Sayre et al. (2017) stratified the ocean into physically and chemically distinct areas, based on analysis of temperature, salinity, oxygen, nitrate, phosphate and silicate. They identified six mesopelagic and seven bathyal pelagic "Ecological Marine Units" (EMU) at 1000 m depth. The remaining 24 EMUs were epipelagic. This schema has some similarities to the one we present, but has fewer regions, and the same units often comprise several discrete areas which may not include the same faunal communities because of geographical separation.

An important element of the current work lies in the combination of physical environmental data and biological information. Different environmental variables could have been used (as per Sayre et al., 2017) but we felt that defining core water masses by temperature, salinity and

oxygen was appropriate and biologically meaningful for mesopelagic depths. Biological data were not specifically analyzed, but the knowledge of panel members was used to synthesize patterns of a wide range of taxa from both published studies and their familiarity with unpublished datasets. There remains a major problem with gaps in sampling, but with time it is to be hoped more formal analyses can be undertaken to test our classification.

4.2. Management applications

The first analytical step in any effort toward systematic conservation planning is the consideration of the biogeographical context of the region in question (Roberts et al., 2003). It is fundamental to the application of ecosystem-based management approaches, marine spatial planning, and the development of representative networks of protected areas (Rice et al., 2011). However, when we began this work no mesopelagic biogeography was available to the various ongoing intergovernmental efforts aimed at global or regional conservation, though Proud et al. (2017) recently used a hybrid of their and Longhurst's biomes to predict future changes in biomass. While work remains to be done to produce a truly three-dimensional, dynamic, mesopelagic biogeography, we believe that the classifications set forth in this study will prove a useful, timely, and novel input to policy planning and management for conservation and sustainable use of deep-pelagic marine biodiversity. In particular, it gives an indication of the spatial scale at which faunal communities are expected to be broadly similar in composition, and it provides a contextual structure for prediction of future changes resulting from climate change, environmental fluctuations, and human-induced impacts. This mesopelagic biogeography extends the depth range of our current global biogeographic knowledge, improves our understanding of the nature of oceanic boundaries, and should fundamentally shift the discussion over what is included when considering representative protection of the world's oceans.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2017.05.006.

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