



A proposed biogeography of the deep ocean floor

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ABSTRACT

While there are many generalized schemes representing the biogeographic distribution of life in the deep sea, reviewed here, a comprehensive analysis has not been undertaken since Vinogradova (1979, 1997) for the abyssal and Belyaev (1989) for the hadal. The purpose of this paper is to propose global biogeographic provinces for the lower bathyal and abyssal benthos (>800 m depths) in order to aid high seas management efforts. Biological samples from these depths are sparse so delineation of biogeographic provinces was initially hypothesized using oceanographic proxies, and examined with documented locations of select benthic marine species. These biogeographic provinces were first developed in 2009 via an expert consultation workshop to delineate biogeographic provinces in offshore regions – the Global Open Ocean and Deep Sea (GOODS) classification. We have refined the GOODS deep-sea classification by incorporating additional high-resolution hydrographic and organic-matter flux data for the seafloor. Water mass characteristics (temperature and salinity) and particulate organic flux to the seafloor were the strongest determinants in the final delineation of provincial boundaries. This process resulted in the delineation of 14 lower bathyal and 14 abyssal provinces. The bathyal and abyssal classifications presented here should be used with other management tools and analyses (e.g., predictive habitat modeling, seamount classifications, etc.) to help determine where marine protected areas should be placed and to minimize the negative impacts of commercial activities in the high seas.

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1. Introduction

Biogeographic distributions of marine organisms have fascinated biologists since the earliest days of ocean exploration. The first major synthesis of marine organism distribution was that of Forbes and Godwin-Austen (1859) for the North Atlantic seas bordering western Europe. Forbes and Godwin-Austen identified five areas of endemism in an area extending from the Arctic Ocean to the Mediterranean Sea. They also noted that as depth increases life becomes more tenuous and suggested the sea floor below 550 m was most likely azoic due to the lack of light, low temperatures, high pressure, and general decrease of animal life with depth (Anderson and Rice, 2006).

The concept of a biogeographic province was first proposed by phytogeographers (reviewed in Lomolino et al., 2010) and refers to an area of species occurrence with a certain level of endemism. Valentine (1973) proposed that Earth's biota is organized in a hierarchical manner with species occurring in associations or assemblages which are then aggregated into ecosystems. Provinces are

associations of ecosystems and have the capacity to change over time as the underlying communities change. Lomolino et al. (2010) summarize this in a more modern fashion by suggesting that a province is not just a place with some level of endemism, but that these endemic species must have a shared history of “having long been isolated by some combination of unique ecological conditions and barriers to dispersal...” (p. 375). However, as noted by Lomolino et al., most biogeographic units have not been analyzed to show they consist of assemblages with such a shared history.

The oceans of the world extend to great depths with the deepest ocean trench being deeper than Earth's tallest mountain is high (Fig. 1). Changes in faunal composition with depth is a well-documented phenomenon (e.g., Carney, 2005), but drawing depth-related provincial boundaries is difficult because faunal changes are not abrupt and vary with latitude and ocean basin (see also Bouchet et al., 2008). Carney conducted a detailed analysis of zonation patterns at 34 sites in the Atlantic, Pacific, Arctic, and Antarctic Oceans, and concluded:

“The depths at which faunal boundaries are found for a broad range of taxa may coincide with sharp local changes in bottom and water column conditions. Boundaries marking gradual shifts in species composition are expected at a shelf-slope zone

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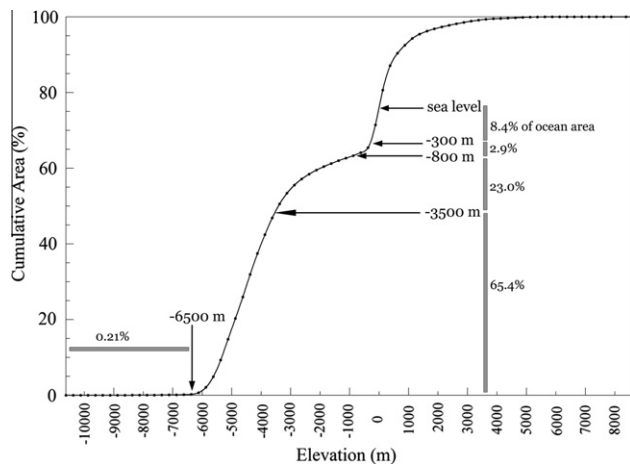


Fig. 1. Hypsometric curve of global topography, areas calculated using ETOPO2 data. Analysis provided by P. Wessel, University of Hawaii at Mānoa.

of transition (300–500 m), at an upper slope depth (1000 m) and at a lower slope zone of transition (2000–3000 m). These blurred zonal boundaries become even less distinct with increasing latitude and depth due to widening of the depth ranges of individual species” (p. 262).

The most recent comprehensive analysis of zoogeographic distributions was conducted by Briggs (1974, 1995) and modified by Briggs and Bowen (2011), who delineated continental-shelf provinces. There have been only a few attempts to delineate seafloor biogeographic provinces at depths beyond the continental shelf. Especially notable are compilations by Vinogradova (1979, 1997) for the abyssal zone, Zezina (1973, 1997) for the bathyal zone, Belyaev (1989) for the hadal zone, and Menzies et al. (1973) primarily focusing on the abyssal zone.

The bathyal and abyssal zones include a variety of topographic features, such as seamounts, as well as localized areas of chemo-synthetic habitat (hydrothermal vents and cold-seeps). Certain habitats, such as vents and seeps, have ecological forcing factors and evolutionary histories distinct from the surrounding deep sea and are not covered in this paper. The biogeography of hydrothermal vents has been considered recently by Van Dover (2000) and Bachraty et al. (2009), and that of cold-seeps by Sibuet and Olu (1998) and Levin (2005).

Here we review existing classifications and data for the lower bathyal and abyssal zones. We have adopted the concept that changes in key ecological (chemical, physical, environmental) parameters, as well as water-mass connectivity, drive the turnover and distribution of marine species and communities. This allows us to formulate hypotheses and draw biogeographic province boundaries based on our understanding of oceanographic and paleoceanographic conditions across space and time. This approach is much like the ecological geography of Longhurst (2007) for surface waters of the ocean but differs from the approach taken by those who looked strictly at patterns in physiographic data and subdivided distributions of physical variables at various arbitrary levels to create manageable “seascapes” (e.g., Harris and Whiteway, 2009; Roff et al., 2003).

1.1. Objectives

The purpose of this study is to hypothesize centers and boundaries of benthic biogeographic provinces at depths greater than 800 m and to provide a classification of deep sea areas that can be used for high seas management purposes (e.g., CBD, 2009; GOBI,

2010). Biotic data for these depths are very limited geographically (i.e., many areas of the deep sea remain to be sampled), many species collected from these depths remain undescribed, and many others are known only from single sampling stations and so are not amenable to biogeographic analyses. In light of these facts, oceanographic proxies were developed to predict areas where the fauna was likely to be different. The initial impetus came from an expert consultation workshop carried out to delineate biogeographic areas in offshore regions – the Global Open Ocean and Deep Sea (GOODS) classification (UNESCO, 2009). This paper develops the classification further by: (1) using detailed hydrographic and organic-matter flux data to hypothesize the position and extent of deep-sea provinces and (2) examining some of the proposed biogeographic provinces using studies of selected benthic species.

In this paper we are primarily concerned with biological distributions that are important for global efforts to balance human exploitation and ecosystem conservation. Hence we focus on bathyal and abyssal zones. The hadal zone, at depths exceeding 6000 m, comprises trench habitat with highly specific and specialized characteristics (e.g., Jamieson et al., 2010) and we utilize the classifications derived by Wolff (1970) and Belyaev (1989).

1.2. Historical background

The first explorations of the deep-sea benthos occurred off the coasts of Norway and Britain where the fauna proved to be remarkably similar, suggesting the deep-sea fauna was widely distributed (Koslow, 2007). However, following the Challenger Expedition, Murray and Hjort (1912) proposed there was, in fact, some heterogeneity in the distribution of animals over the deep-sea floor. Later expeditions (“Valdivia” from Germany and “Albatross” from the United States) showed that many families and genera were widely distributed, but species were not. Ekman (1953) noted that even though the deep-sea seemed to be relatively homogeneous in its physical features, the fauna of the abyss could be divided into four major groups: (1) Atlantic, (2) Pacific, (3) Arctic, and (4) Antarctic. Ekman also believed the geographical ranges of species increased with depth and those found at bathyal depths were more limited than those in the abyss.

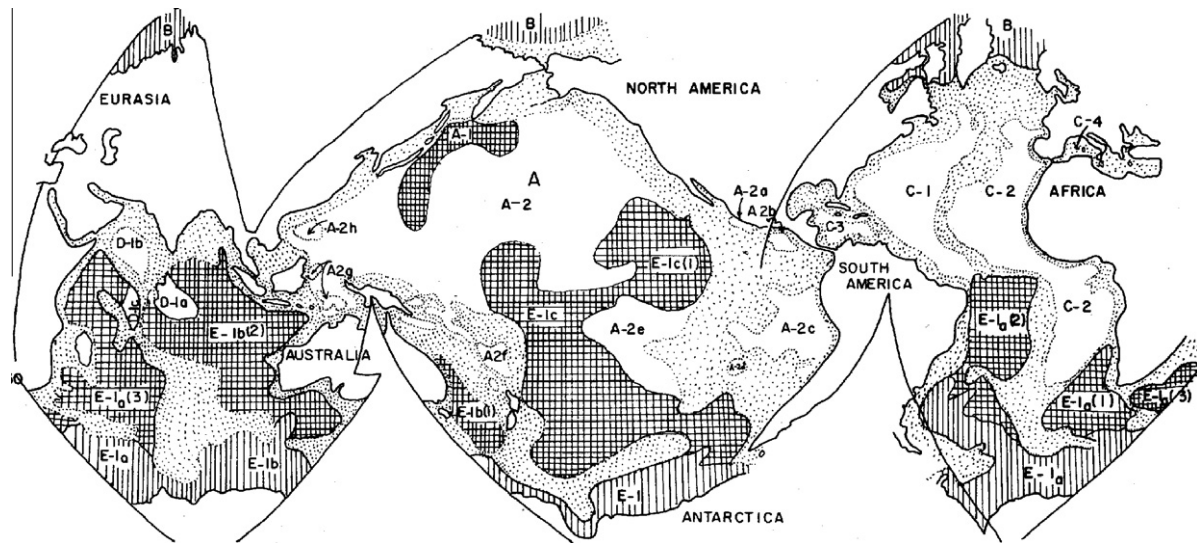
In the 1950s the idea of a cosmopolitan fauna existed among some investigators (e.g. Bruun, 1957). Following more detailed sampling by the “Galathea” expedition, some groups, isopods for example, were found to have no cosmopolitan species (Wolff, 1962), whereas others, such as the polychaetes, were thought to be widespread (Kirkegaard, 1995). Knudson (1970) also considered the Bivalvia to be widely distributed, but only three of 193 species appeared to be cosmopolitan (Vinogradova, 1997). Menzies et al. (1973) summarized the distributions of much of the larger deep-sea fauna as well as the smaller peracarid group, the isopods. They recognized five large zones in depths >4000 m, one in each ocean basin. The five zones were divided into 13 provinces and 17 regions/subregions (Table 1, Fig. 2). Their scheme used temperature and topography as determinants for province definitions and, though similar to that of Ekman (1953), was more finely subdivided.

Species endemism among isopods is relatively high, which prompted Kussakin (1973) to restrict comparisons to the genus level. His deep-sea classification included three regions (Table 1): Austral (from about the Antarctic Convergence southward), Indo-Pacific, and Atlantic. These regions were divided into 10 provinces according to the following scheme: Austral Region divided into Andean and Gondwanian Provinces; Indo-Pacific Region containing Indian, West-Pacific, East-Pacific, and North-Pacific Provinces; Atlantic Region including West-Atlantic, East-Atlantic, North-Atlantic, and Arctic Provinces.

Table 1

A summary of major classification schemes for the deep-sea benthos.

Author	Depth zone	Regions	No. provinces (areas)
Menzies et al. (1973)	Abyssal	Pacific	2 (8)
		Arctic	5
		Atlantic	4
		Indian	1 (3)
		Antarctic	1 (3)
Kussakin (1973)	Abyssal	Austral	2
		Indo-Pacific	4
		Atlantic	4
Vinogradova (1979)	Abyssal	Pacific-North-Indian	4
		Atlantic	4
		Antarctic	3
Belyaev (1989)	Hadal (ultra-abyssal)	Pacific	6
		North Indian	1
		Atlantic-Antarctic	3
Zezina (1997)	Upper upper bathyal (300–700 m)	Boreal-Arctic	5
		Amphi-Atlantic Tropical	4
		West-Indo Oceanic Tropical	1
		Indo-West Pacific Tropical	2
		South Brazilian-Uruguayan Subtropical	1
		South African Subtropical	1
		South Australian Subtropical	2
		New Amsterdamian Antiboreal	1
		New Zealandian-Kerguelenian Antiboreal	4
		Antarctic-South American	2
	Lower upper bathyal (700–2000 m)	Boreal	2
		Amphi-Atlantic	2
		West-Indo Oceanic	1
		West Pacific	2
		Antarctic	1

**Fig. 2.** Abyssal province scheme of Menzies et al. (1973).

Vinogradova's (1979) classification of the abyssal and hadal zones was based on common and easily identifiable species in the bottom fauna of deep-sea regions of the Pacific Ocean. She noted the ranges of species tended to contract, rather than expand, with depth and were restricted by deep-sea ridges yielding ocean basins with unique faunas. The Pacific contained 53% of the endemic species overall, but the lower abyssal fauna was 93% endemic. For the entire World Ocean, she found 85% of the species occurred in one ocean only and 4% were common to the Atlantic, Indian, and Pacific Oceans. Overall, she characterized the abyssal fauna as highly endemic at the species level, with a large number of endemic genera and families. Her classification of the abyssal included

three regions, six subregions, and eight provinces (Fig. 3). Vinogradova (1997), after reviewing the known deep-sea faunal studies, suggested there were three major schools of thought regarding deep-sea zoogeographic patterns: (1) the bottom fauna should be very widespread because of the lack of ecological barriers and relative homogeneity of conditions on the deep-sea floor; (2) the deep-sea fauna is fractionated by the presence of topographic features that divide the sea floor into ~50 separate ocean basins; and (3) species generally have much larger ranges at greater depth, but may be restricted to single ocean basins.

The distribution of tunicates taken in the Atlantic Ocean at depths greater than 2000 m by various expeditions over a 15 year

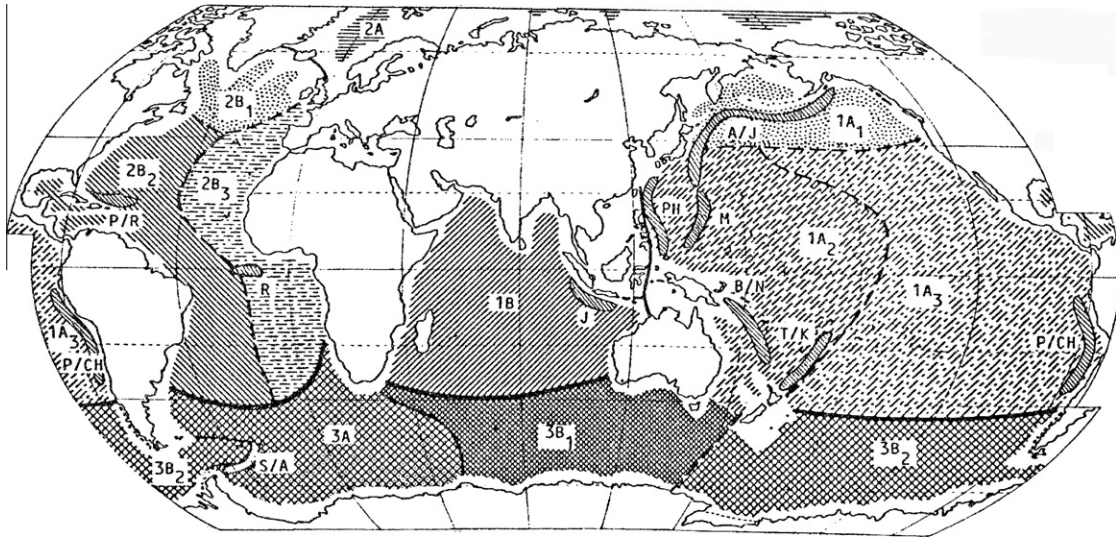


Fig. 3. Zoogeographic scheme of Vinogradova (1979) for the abyssal region with hadal scheme of Belyaev (1974). From Vinogradova (1997).

period was summarized in a short paper by Monniot (1979) who used the Kulczynski-2 index to compute the similarity of tunicate faunas among the basins. The northern and eastern Atlantic Basins had the strongest affinities with similarity coefficients above 40% for the Labrador, European, Angola-Guinea, and Cape Basins. The Surinam, Brazil, and Argentine Basins on the western side of the Atlantic had low affinities with each other and with the basins to the north and east, but these weak affinities could be the result of under-sampling.

Sibuet (1979) summarized all available data on deep-sea asteroids (sea stars) from more than 100 trawl samples taken from 1800 to 4500 m in seven Atlantic basins: European, Mediterranean, Labrador, Cape, Angola, Greenland, and Norwegian. The fauna was divided into species occurring above or below 3000 m and inter-basin comparisons made using the Kulczynski-2 index. From 1800 to 3000 m, the Norwegian and Greenland basins, and the European-Mediterranean-Angolan basins, were the most similar. This was true also at the level of genera, except that the Greenland and European basins were also quite similar. From 3000 to 5000 m, the Norwegian and Greenland basins had similar species and generic compositions, as did the European-Angola-Cape basins at the species level, with the addition of the Labrador basin at the generic level. The results were affected by different levels of sampling effort in the various basins.

The known faunal distributions of the ultra-abyssal (or “hadal”) seafloor areas were summarized by Belyaev (1989). He noted there were 37 seafloor areas >6500 m deep, 28 of which were in the Pacific. Most are part of recognizable trenches, but others are broad deep areas of the abyssal sea floor. In general, Belyaev found about 56% of the species were endemic to the hadal, but about 95% of those were found only in one trench. Of the non-endemic species, 22% were found in the abyssal area where the trench was located, suggesting the trench fauna originated from the surrounding abyssal province. Several areas had either not been sampled or the data not analyzed at the time of his monograph. Nevertheless, Belyaev suggested the abyssal classification scheme of Vinogradova (1979) be supplemented with hadal provinces as follows (these regions are indicated on the Fig. 3, from Vinogradova, 1979): Pacific Ocean Subregion with the hadal provinces Aleutian-Japan (Aleutian, Kuril-Kamchatka, Japan, Izu-Bonin Trenches), Philippine (Philippine and Ryuku Trenches), Mariana (Volcano, Mariana, Yap and Palau Trenches), Bougainville-New Hebrides (New Britain, Bougainville, Santa Cruz, and New Hebrides Trenches), Tonga-

Kermadec, and Peru-Chile. The North Indian Subregion contains only the Yavan hadal province. The Atlantic Subregion includes the Puerto Rico and Romanche Trench provinces. The Antarctic-Atlantic Subregion includes only the Southern Antilles hadal province.

Zeina (1997) reviewed the distributional studies of the bathyal fauna, but mainly classified bathyal regions according to the distributions of brachiopods. She considered the bathyal fauna to be divisible into four main latitudinal climatic belts: (1) those corresponding to the distributional limits of tropical (low latitude) species; (2) the limits of northern and southern subtropical species; (3) the limits of low boreal and antiboreal species; and (4) the limits of most cold-water species. Zeina's (1973) scheme for classifying the geographical distribution of the bathyal fauna primarily followed latitudinal zones. The scheme for shallower depths included the sublittoral, upper bathyal, and greater depths of the lower bathyal. There were few data on brachiopods from lower depths which resulted in a more generalized schema. For depths <700 m (sublittoral to upper bathyal) the ocean was divided into 10 broad areas, some of which are further subdivided into subareas and occasionally into provinces (see Fig. 2 in Zeina, 1997).

Parin et al. (1997) reviewed studies conducted on the Nazca and Sala y Gomez Ridges located on the Nazca Plate in the South Pacific. The Nazca Ridge is a deep, narrow plateau containing seamounts with summits from 200 to 850 m. In contrast, the Sala y Gomez Ridge consists of a chain of guyots with summit depths of 200–500 m. Samples were taken by trawl and baited traps at depths of 200–550 m, with one station at almost 800 m. Endemicity and species relationships were investigated for echinoids, shrimp, tanaids, and fish species. Among the echinoids, 15 of the 17 genera were found both in the Pacific and the Atlantic. However, 8 of the 19 species were endemic to the ridge. Only one species was cosmopolitan. The 29 shrimp species had very broad distributions, many being found across the Pacific (10) and in other oceans (7). Two (of nine) tanaids were endemic and six were common to the North Atlantic. Fish were widespread, with 74% of the fish genera found in Hawaiian waters and 85% in Japanese waters. However, 51% of the fish species were endemic to the seamounts of the two ridges. Faunal similarity (using the Hacker-Dice index) among 22 seamounts based on 155 genera showed a clear separation of seamounts located eastward of 83°W and northward of 23°S. The fauna of this region was distinct from the fauna found to the west and south.

The biogeographic position of these two ridges could not be agreed to by the three authors of Parin et al. (1997). Mironov accepted the idea that the fauna of the ridges divides at 83°W, with the portion to the west of this line belonging to the Indo-West Pacific Region and the portion to the east being part of the Peru–Chile Province of the Eastern Pacific Tropical Region. Parin and Nesis, on the other hand, considered the whole of the two ridges as belonging to a separate unit that they named the Nazcaplatensis Province, after the Nazca Plate on which the ridges sit. They consider the Nazca Ridge, the portion to the east of 83°W, to be merely an impoverished section of the province as a whole. In general, the composition of the fauna in this region could be explained by eastward dispersal of the western Pacific fauna across a biogeographic barrier (the relatively mountain-less abyssal area) (well known for shallow species; Grigg and Hey, 1992) and active speciation in situ (Parin et al., 1997).

The Southern Ocean has generally been considered to be a zoogeographic unit of its own and the source of species for the deep-sea wherever Antarctic Bottom Water has spread. Linse et al. (2006) investigated the distributions of the two largest classes of molluscs (gastropods and bivalves) at both local and regional scales throughout the Southern Ocean. Patterns of endemism were very different between bivalves and gastropods. On the basis of distributional ranges and centers of radiation of evolutionarily successful families and genera, three biogeographic provinces in the Southern Ocean were defined: (1) the continental, high Antarctic province excluding the Antarctic Peninsula; (2) the Scotia Sea province which includes the Antarctic Peninsula; and (3) the Sub-Antarctic province comprising the islands bathed by the Antarctic Circumpolar Current. A multivariate analysis of the combined gastropod and bivalve data showed that at all levels, from family to species, the areas within the Antarctic Convergence form one biogeographic unit with closest affinities to the islands of the Sub-Antarctic, with the exception of the shelf and islands around New Zealand. The southern part of South America is very closely related to the Southern Ocean fauna at the level of family, but less so at the level of genus and species.

Allen and Sanders (1996) used hierarchical cluster analysis to summarize the zoogeography of the protobranch bivalves, using data from 38 stations in 6 basins of the Atlantic Ocean at depths from 1000 m to 5800 m sampled by epibenthic sled. Two major patterns were found: a segregation of stations into two depth zones (1000–3000 m and 3300–5200 m) and clustering of stations within depth zones, for example, at 1000–3000 m, the Argentine and Cape Basins formed their own separate clusters whereas the stations from the remaining basins all grouped into one large cluster. Within the Argentine Basin, the bathyal station was in a separate cluster from the abyssal. Basins nearest to each other shared more species than basins further apart, but Allen and Sanders also noted that the protobranch fauna of the Norwegian Basin and Southern Ocean share no species with the other Atlantic basins.

At the point of Zezina's (1997) summary, the bathyal was the least analyzed biogeographically of all areas of the ocean. It is characterized by its highly heterogeneous physiography and hydrography (Levin and Sibuet, 2012). The bathyal of the Reykjanes Ridge was recently sampled by Russian scientists and the results compiled in a volume edited by Mironov et al. (2006). Mironov and Gebruk (2006) noted corals, barnacles, brachiopods, sea urchins and sea stars found at depths from 1000 to 3000 m were a mix of eastern and western Atlantic species with a few Pacific and Antarctic species also present. Of 24 bivalve species taken on seamounts in the Horseshoe and Meteor groups in the northeastern Atlantic, 10 were also known from the western Atlantic (Krylova, 2006). Molodtsova (2006) summarized the known distribution of 33 antipatharian (black coral) species currently known from the northeastern Atlantic. Almost half of the species were known from

other parts of the Atlantic, but about 40% of the species from open ocean rises were endemic to the northeastern Atlantic.

Mironov and Gebruk (2006) noted that faunistic boundaries were areas where the boundaries of the ranges of several species tended to be close together. Following early (1800s) authors, they referred to these boundaries as “zones of crowding” and outlined several methods to estimate where these boundaries might be found. In particular, they noted two major vertical crowding zones when data on echinoids were pooled. One occurred at 800–900 m and, citing data on sea stars, bivalves, and asellote isopods, they suggested that the boundary of the upper and lower bathyal should be at about 800–1000 m in the North Atlantic. Further, a deep boundary at about 2500–3500 m, with an average at about 3000 m was also noted, dividing the bathyal from the abyssal.

Cairns and Chapman (2001) used hierarchical cluster analysis and multi-dimensional scaling (MDS) to investigate the distributions of 134 North Atlantic deep water scleractinian coral species. They subdivided the North Atlantic into 38 geographic regions from the Arctic to the tropics, including West Indian, Azores, and Canary Islands as well as the seamounts of the northeastern Atlantic. Their analysis showed the corals to be distributed in three major groups: I, encompassing the West Indies and Florida; II, the northwestern Atlantic from Cape Hatteras northward and the northeastern Atlantic from the English Channel northward; and III, the northeastern Atlantic from the English Channel to off West Africa. The northeastern Atlantic island slopes and seamounts belonged also to this last group. They suggested the biogeographic provinces established for the continental shelves extended to bathyal depths for hard corals.

This literature review suggests understanding of deep-sea biogeography has changed steadily over time and will probably continue to change as more detailed studies are conducted, especially at bathyal depths. Some of the bathyal consists of sea floor that is volcanic in origin and is extremely rough, and therefore has been very difficult to sample without the use of remotely operated vehicles (ROVs) or submersibles. Recent studies using these tools are underway now for the seamounts of the northwestern Atlantic, the Aleutian Ridge, the Northwestern Hawaiian Archipelago, and the southwest Indian Ocean. Trawling studies at bathyal depths have also recently been conducted around New Zealand and in the region of New Caledonia. While a seemingly large number of samples of many types have been collected from bathyal and abyssal depths, the deep-sea benthos is still very poorly sampled compared to the enormous size of deep-sea ecosystems, i.e., covering >60% of the Earth's solid surface (e.g., Ebbe et al., 2010). Most of the fauna remains undescribed because of high species richness and very limited taxonomic descriptions of the fauna (e.g., Rex and Etter, 2010). For example, >90% of the abyssal macrofaunal species sampled at any single site in the abyssal Atlantic and Pacific typically are new to science (Ebbe et al., 2010). Recent deep-sea sampling programs have targeted abyssal depths and bathyal depths within the Census of Marine Life program, but detailed species descriptions and biogeographic analyses, even for the abyssal plains, are very limited (Ebbe et al., 2010). With the advent of global biogeographic databases, such as the Ocean Biogeographic Information System (OBIS, www.obis.org), detailed global biogeographic analyses, based on species distributions, should eventually become possible as species descriptions and distributional data are published.

2. Materials and methods

We have used physical and chemical proxies thought to be good predictors of the distributions of organisms at the deep-sea floor. These variables were depth, temperature (T), salinity (S), dissolved

oxygen (O), and particulate organic carbon flux (POC) to the seafloor. Depth (or more specifically hydrostatic pressure) and temperature, operating on a range of physiological processes, are postulated to be important determinants of the bathymetric distributions of deep-sea organisms (see Carney (2005) for a detailed review). In fact, piezo-thermal thresholds have been postulated to set the upper depth limit of many deep-sea species (Carney, 2005). Large variations in temperature along isobaths are also expected to limit fauna distributions, again through a host of temperature-dependent physiological processes. It is well documented that oxygen availability can limit faunal distributions in the deep sea (Levin, 2003; Stramma et al., 2010). POC flux to the seafloor, which ultimately controls food availability in the detritus based deep-sea, is also expected to limit the distributions of deep-sea species (e.g., Carney, 2005; Smith et al., 2008a). Most of the deep-sea is considered to be “food limited,” with differences in POC flux related to (1) changes in body size (e.g., McClain et al., 2010; Collins et al., 2005), (2) species turnover (Glover et al., 2002; Carney, 2005; Collins et al., 2005; Rex et al., 2005), (3) population densities (and hence the abundance of potential prey and/or mates) (Rex et al., 2005), (4) life-history characteristics (Grassle and Sanders, 1973; Gage and Tyler, 1991), (5) trophic structure, (6) community composition, and (7) a variety of ecosystem functions (e.g., Smith and Rabouille, 2002; Smith et al., 2008a). Declining POC flux has been postulated to set the lower depth limit of many deep-sea species (Collins et al., 2005; Carney, 2005), and the large variations in POC flux observed along isobaths in the deep sea are correlated with species turnover and limits of distribution (e.g., Glover et al., 2002; Ebbe et al., 2010). We acknowledge that depth, temperature, oxygen availability, and POC flux are a subset of factors that can potentially limit species distributions on a biogeographical scale, and that a combination of factors will often be important (e.g., Carney, 2005). Nonetheless, in cases where these environmental parameters are not the main drivers of species distributions, we expect that they are generally correlated with regional drivers.

An additional major determinant of species distributions, and biogeographical boundaries, is connectivity, i.e., the ease with which dispersal occurs across various “boundaries” and spatial scales. We have used the distributions of water masses to infer certain levels of connectivity; seafloor regions within a particular water mass (e.g., Antarctic Bottom Water) are more likely to share species, and thus fall within a biogeographical province, than regions bathed by different water masses.

ETOPO2 bathymetric data were downloaded from the National Geophysical Data Center (NGDC) and used initially to determine biogeographic province boundaries (Smith and Sandwell, 1997). Srtm30 bathymetry was used to further refine the biogeographic provinces (Becker et al., 2009). Temperature, salinity, and oxygen (ml l^{-1}) data were obtained by download from the National Oceanographic Data Center (NODC) World Ocean Atlas (WOA) web site. Only annualized means were used because maps of the standard error, also available from WOA, indicated that for most depths of concern here the s.e., was less than 0.1. Particulate organic carbon (POC) flux to the seafloor was obtained from Lutz et al. (2007).

All hydrographic and bathymetric data were entered into ArcGIS and converted to shapefiles and raster grids. All data were initially binned into 0–300, 301–800, 801–2000, 2001–3500, 3501–6500, and >6500 m layers. In this paper we adopt a simple bathymetric scheme similar to that outlined by Carney (2005), originally proposed by Vinogradova (1979, 1997) and Zezina (1997), and modified by Mironov and Gebruk (2006): continental shelf, 0–300 m; upper bathyal, 301–800 m; lower bathyal, 801–3500 m; abyssal, 3501–6500 m; and hadal, >6500 m. Because our focus here is on international waters, the 0–300 and 301–800 m layers were discarded as they are almost exclusively within the

exclusive economic zones (EEZs) of various nations. In addition, the 0–300 m layer comprises the continental shelf provinces already outlined by Briggs (1995) and Briggs and Bowen (2011). For the hadal zone, we used the biogeography proposed by Belyaev (1989) so no additional analysis of the hadal zone was carried out.

Province centers and approximate boundaries were initially hypothesized by L. Watling, M. Clark, C. Smith and others at a workshop in Mexico City using expert knowledge of hydrographic data, POC flux estimates, and biotic information when the latter was present, and reported in UNESCO (2009). A later review by the current authors resulted in modifications of some of the province boundaries. We then analyzed province depth, temperature, salinity, dissolved oxygen, and POC flux characteristics on data gridded at $1 \text{ km} \times 1 \text{ km}$ spacing using a bathymetric grid obtained from the srtm30 dataset (Becker et al., 2009). All environmental, chemical, and physical data were resampled to $1 \text{ km} \times 1 \text{ km}$ resolution and the environmental data values from WOA05 and POC extracted for seafloor cells based on the seafloor bathymetry value (approach described by Davies and Guinotte, 2011). Masks for each province were created in ArcGIS and used to calculate summary statistics (min, max, mean, median, range, standard deviation, and areal extent) of T, S, O, and POC flux. These summary statistics were used to assess overall similarity of the physiography and hydrography of the provinces.

3. Results

3.1. Bathymetric patterns

The bathyal regions have characteristically been divided into upper and lower portions. With few exceptions, the upper bathyal (300–800 m) (Fig. 4) follows the continental margins, the major exception being the large plateau areas off New Zealand and the Kerguelan Islands. Virtually all of the upper bathyal is within national EEZs.

The lower bathyal (plotted as 801–3500 m) (Fig. 5) consists almost entirely of three physiographic categories: lower continental margins, isolated seamounts and oceanic island slopes, and mid-ocean ridges. The lower bathyal of the continental margins is largely sediment covered, having accumulated large deposits from continental run-off. These areas may be part of the extended continental shelves of coastal nations. In contrast, seamounts, island flanks, and mid-ocean ridges may have varying amounts of sediment cover but also offer large expanses of hard substrate with attached megafauna. Seamounts and ridges provide heterogeneous substrata at lower bathyal depths in offshore regions dominated by abyssal plains. Bare rock surfaces can be common because of accelerated current flow scouring the often steep flanks. The physical structure of seamounts interrupts currents and creates hydrographic eddies and flows that can concentrate larvae and other plankton, and enhance production processes over the seamount (e.g., Clark et al., 2010a). Even though the area covered by ridges and seamounts may be small in relation to the surrounding seafloor, their geographic location may be very important as “stepping stones” in determining the distribution of bathyal species across the wider ocean basins (Rowden et al., 2010).

The abyssal (3500–6500 m) (Fig. 6) covers the bulk of the deep ocean floor (65.4%; Fig. 1). The ocean basins are dissected to various degrees by the mid-ocean ridge system and ridges associated with island arcs and seamount chains. There are, however, gaps in nearly all the ridges (the Walvis Ridge and East Pacific Rise being important exceptions), allowing some water flow at abyssal depths from one basin to another. In the Indo-West Pacific Region, there are a few small basins that are completely isolated from the rest of the abyssal ocean, but these are mostly within the EEZ of various

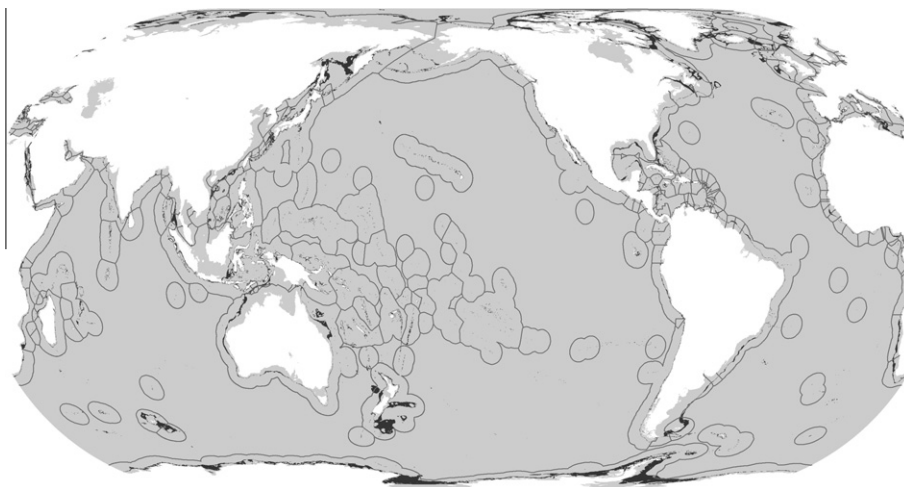


Fig. 4. Extent of the upper bathyal depth layer, 300–800 m (dark gray). Solid thin lines are EEZ boundaries. Note there are only a few areas of upper bathyal outside areas of national jurisdiction.

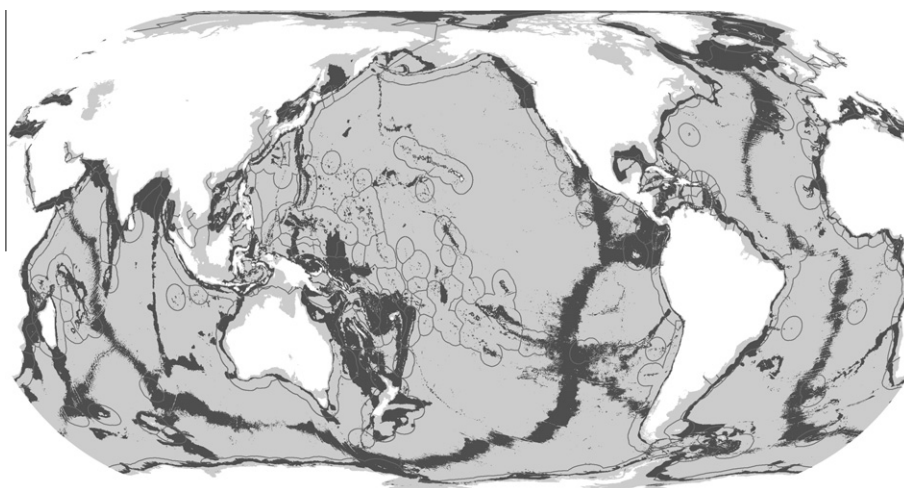


Fig. 5. Extent of the lower bathyal depth layer, 800–3500 m (dark gray). Solid thin lines are EEZ boundaries. Most of the bottom area at this depth comprises ridges and seamount systems.

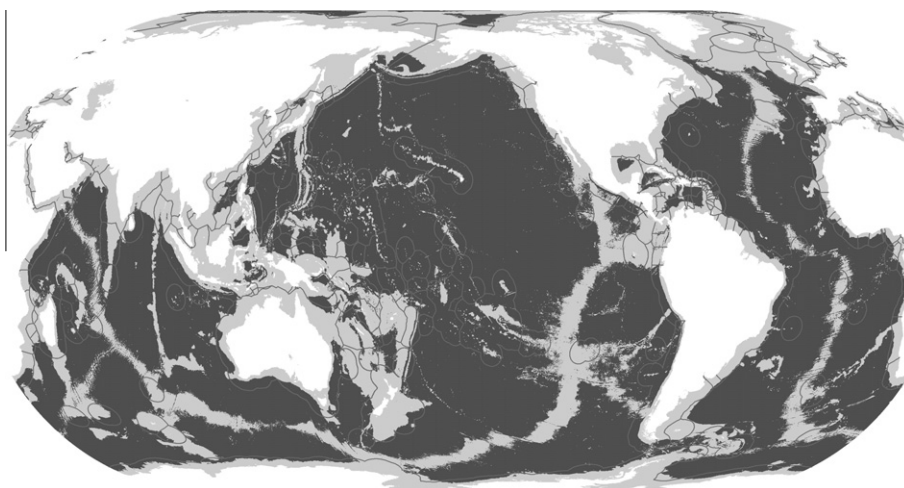


Fig. 6. Extent of the abyssal depth layer, 3500–6500 m (dark gray). Solid thin lines are EEZ boundaries.

nations. These basins are warmer at the bottom because they are isolated from the influence of Antarctic Bottom Water which otherwise spreads over the abyssal and hadal regions of the Pacific Basin. On the eastern side of the equatorial Pacific, the Guatemala Basin is also mostly isolated and most of its area is outside of any country's EEZ.

The hadal (ultra-abyssal) areas (>6500 m) (Fig. 7) are mostly restricted to plate boundaries where deep ocean trenches are formed by subduction of lithospheric plates. The exception is the Romanche Fracture Zone, a small depression in the equatorial Atlantic. Most of the trenches deeper than 6500 m are in the western Pacific, stretching from the Aleutians to Japan, the Philippines, Indonesia, the Marianas, and finally to the Tonga–Kermadec Trench north of New Zealand. The eastern Pacific contains only the Peru–Chile Trench, the Atlantic possesses the Puerto Rico, Cayman and South Sandwich Trenches, and the Indian Ocean only the Sunda Trench (Jamieson et al., 2010). All but the Romanche Fracture Zone and South Sandwich Trench are within the EEZs of various countries, with the latter being within the Antarctic management area (CCALMR).

3.2. Hydrographic and POC flux patterns

There have been many summaries of water mass characteristics of the World Ocean, one of the latest and most comprehensive being that of Tomczak and Godfrey (1994). However, variables important to our understanding of biogeography such as temperature and dissolved oxygen are given broadly only for the surface and abyssal waters with one meridional profile deemed sufficient to characterize an ocean-basin interior. Over the last decades, however, most of the hydrographic data taken during research cruises have been compiled by NOAA's National Oceanographic Data Center and are available online (<http://www.nodc.noaa.gov/OC5/WOA05/woa05data.html>).

Because of the coarse scale of biogeographic units within the World Ocean, we discuss only the major hydrographic features of the large ocean basins. In addition, since species distributions are limited vertically as well as horizontally, hydrographic patterns will be summarized at depths of 800, 2000, 3500, and 5500 m. These depths reflect the horizons of probable biogeographic change.

3.2.1. Temperature

At 800 m (Fig. 8) water temperatures differ significantly among the major ocean basins. The Arctic is very cold, below 0 °C, as is the Southern Ocean. A steep front exists along the northern border of

the Southern Ocean with temperatures rising 3–6 °C over a distance as short as 5° of latitude (~500 km). Particularly steep gradients occur north and west of the Kerguelen Plateau south of the Indian Ocean. The gradient becomes less steep entering the Pacific and extends over a long distance in the South Atlantic. At 40°S the Atlantic is the coldest ocean with water about 4 °C, the Pacific slightly warmer near 4 °C in the east and 7 °C in the west. North of the Subtropical Convergence, the Indian Ocean warms to around 9 °C at this depth. The Indian overall is warmer (6–10 °C) than the Pacific (3.5–6 °C). The Atlantic, however, is cold in the south, but due to the effects of the Gulf Stream and Mediterranean outflow, warms to more than 10 °C between 20°N and 40°N.

At 2000 m (Fig. 9) the water has cooled considerably in the Indian Ocean, being about 2.5–3 °C north of 40–45°S. The Pacific over most of its area at this depth is about 0.5° cooler, but the Atlantic shows a more complicated, and warmer, temperature pattern. At this depth the water is for the most part between 3 and 4 °C, flowing southward and incorporating some features of Labrador Sea Water and lower Mediterranean Outflow Water. The latter is particularly evident west of the Straits of Gibraltar. The Southern Ocean is coldest to the east of the Weddell Sea where Antarctic Bottom water is formed, and warmest south of the eastern Pacific. Temperatures below 2 °C are also prevalent in the northern part of the North Pacific.

The ocean basins become more subdivided by topography at 3500 m. While there is no noticeable change in the temperature regime in the Southern Ocean, the effects of Antarctic Bottom Water are clearly seen in both the Indian and Pacific Oceans, where temperatures are between 1.25 and 1.5 °C over most of the area (Fig. 10). Exceptions are the NW Indian Ocean and the southeastern Pacific where waters can reach 2 °C. The Atlantic remains the warmest of the major basins, being about 2.5 °C over most of its area. The coldest parts of the Atlantic are in the Namibia and Cape Basins on the east side and the Argentine Basin on the west side. They are more subject to Antarctic Bottom Water whereas all the basins northward (at 2–3 °C) are more influenced by the slightly warmer North Atlantic Deep Water.

The deepest parts of the ocean basins, at 5500 m (Fig. 11), reflect the temperature pattern seen at 3500 m, the major exception being the SW Atlantic, where the deep waters are under the influence of Antarctic Bottom Water, and the deep water in the southernmost parts of the Atlantic and Pacific Oceans, where bottom temperatures are below 0 °C.

Temperature gradients can also indicate the location of frontal zones, where water masses meet and mix. The major surface water

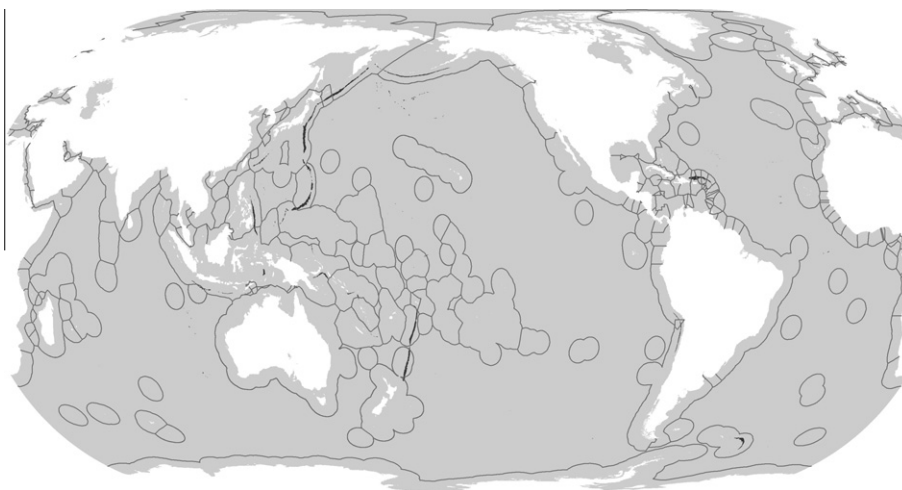


Fig. 7. Extent of the hadal zone, >6500 m (dark gray). Solid thin lines are EEZ boundaries. Almost all of the hadal is within national jurisdiction.

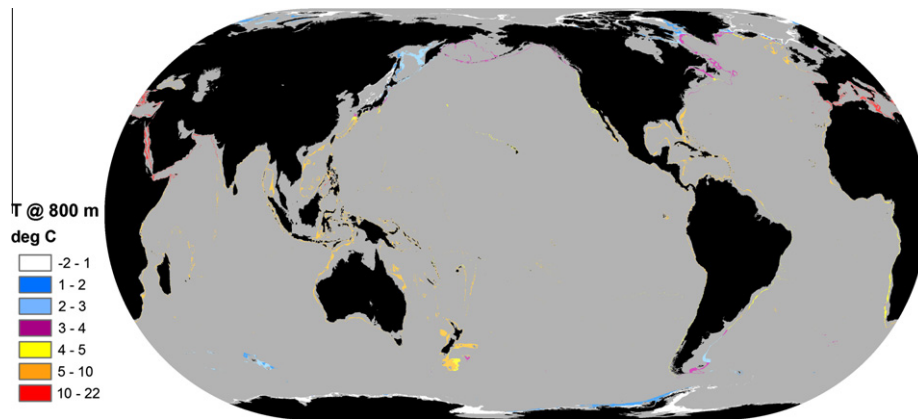


Fig. 8. Bottom water temperature at 800 m plotted on bottom depths of 300–800 m.

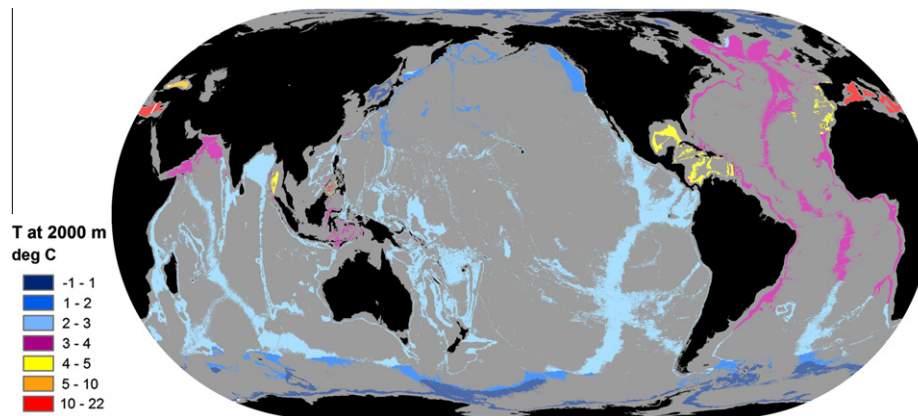


Fig. 9. Bottom water temperature at 2000 m plotted on bottom depths of 2000–3500 m.

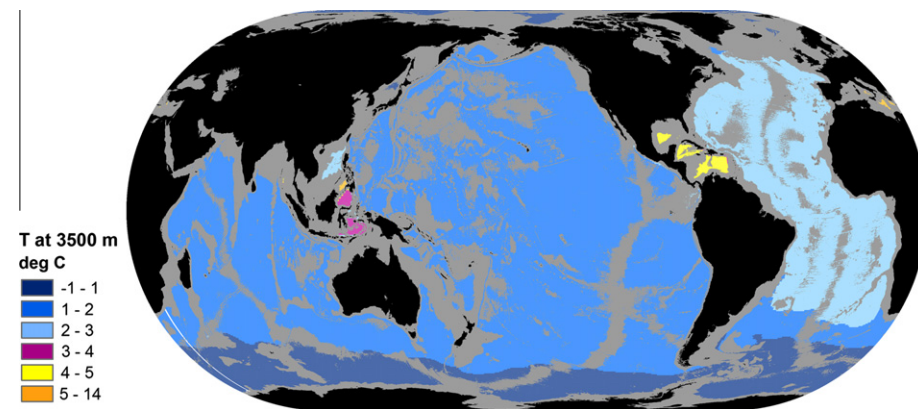


Fig. 10. Bottom water temperature at 3500 m plotted on bottom depths of 3500–5500 m.

convergence areas (e.g. Subtropical Convergence, Antarctic Convergence) signify large changes in water characteristics, such as between Antarctic, Temperate, and Tropical waters. Many shelf-depth species do not cross such boundaries because of physiological limitations to either adults or their early life stages. These convergence zones may not extend below upper bathyal depths but the “downstream” effects of factors such as increased productivity may well influence benthic composition or abundance.

3.2.2. Salinity

The salinity structure of the World Ocean does not vary by much more than 1 psu (practical salinity unit) over most of the area and at all depths. Salinity ranges and salinity gradients, along with temperature are indicators of water masses, which are connected by transport and mixing processes, potentially influencing species distributions. One of these water masses, Antarctic Intermediate Water, is characterized by a salinity minimum at around

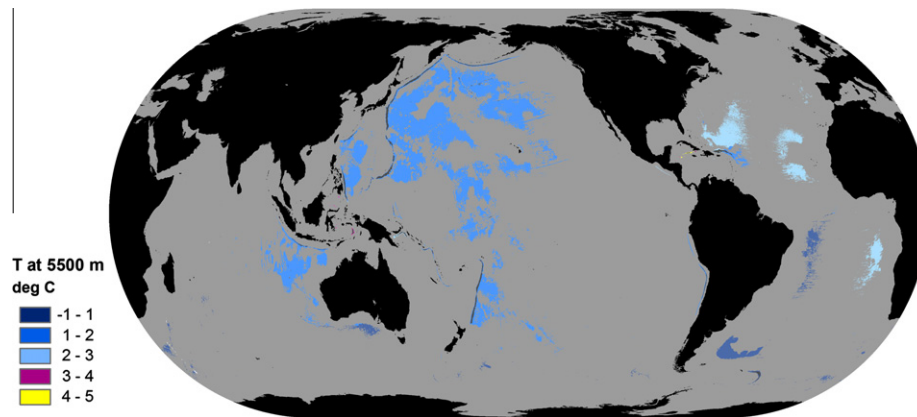


Fig. 11. Bottom water temperature at 5500 m plotted on bottom depths of 5500–6500 m.

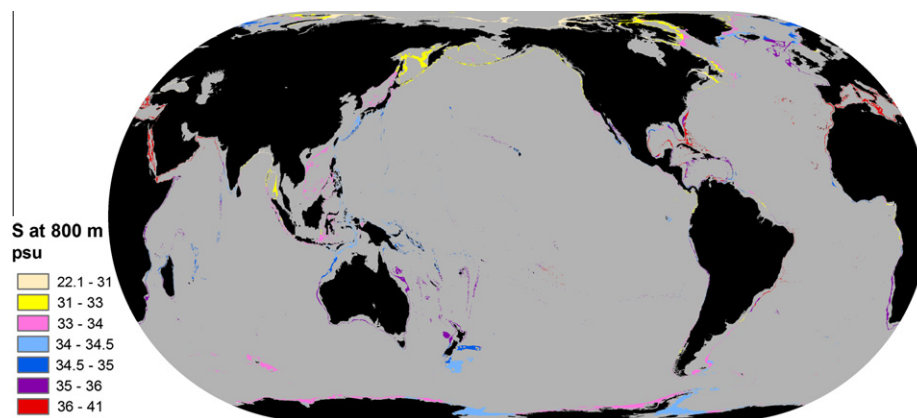


Fig. 12. Bottom salinity at 800 m. Plot as for Fig. 8.

1000 m in the South Pacific. The profile at 800 m (Fig. 12) shows that this water mass does not extend northwards into the North Pacific, and many deep-dwelling fish species associated with such water do not occur in the northern Pacific (e.g. orange roughy, oreos; Clark, 2009). Other areas of distinct salinity are at 800 m in the NW Indian Ocean where the salinity may exceed 36 psu, and in the North Atlantic where the salinity is influenced by saline Gulf Stream and Mediterranean outflows. Due to the Gulf Stream as well as the northward spreading Mediterranean Overflow Water, the high salinity water extends as far north as the Iceland-Faeroes Ridge on the eastern side of the Atlantic. In deeper water, the

salinity becomes more uniform, but at 2000 m (Fig. 13) there is still some influence of the waters above. The deep sea below 3500 m (Fig. 14) is nearly uniform with salinities between 34.5 and 35 psu, with only the marginal seas having saltier water.

3.2.3. Oxygen

Oxygen may be important to determining the presence of species in various parts of the ocean, but it seems to be truly limiting in the deep sea only in those areas where values fall below $\sim 1 \text{ ml l}^{-1}$, with hypoxic stress beginning at about 1.4 ml l^{-1} (Levin, 2003; Stramma et al., 2010). Oxygen values vary over a wide range,

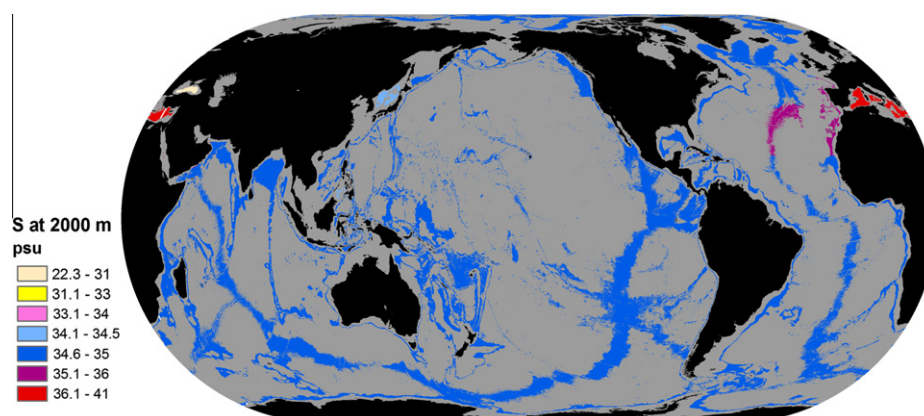


Fig. 13. Bottom salinity at 2000 m. Plot as for Fig. 9.

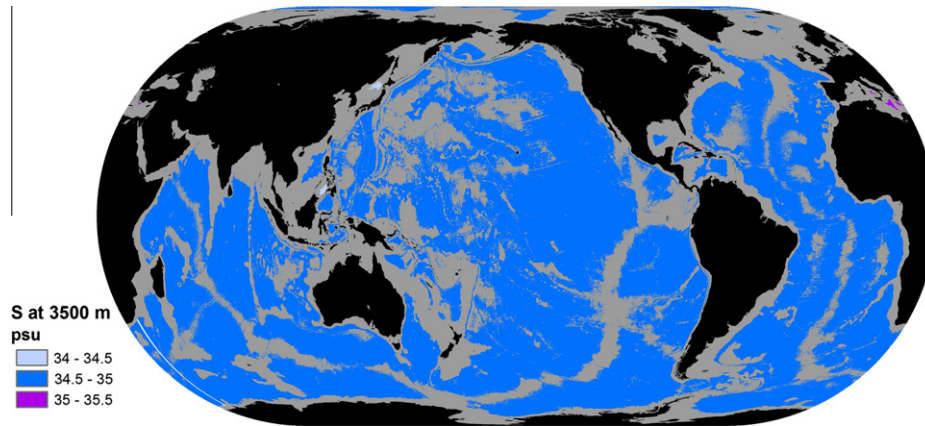


Fig. 14. Bottom salinity at 3500 m. Plot as for Fig. 10.

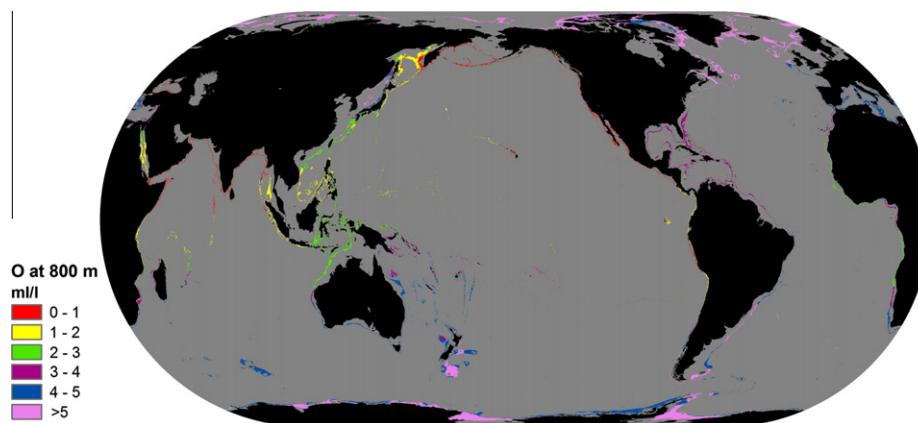


Fig. 15. Bottom dissolved oxygen at 800 m. Plot as for Fig. 8.

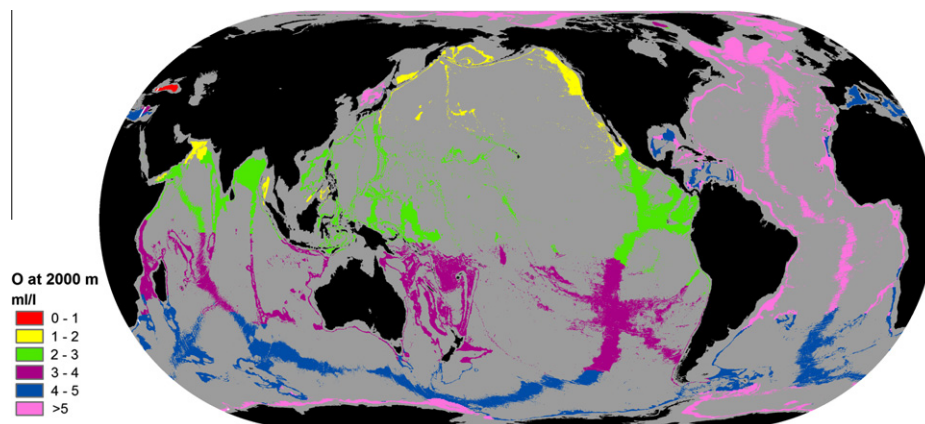


Fig. 16. Bottom dissolved oxygen at 2000 m. Plot as for Fig. 9.

with the highest values generally associated with the colder, deeper, and younger waters. At 800 m (Fig. 15) those waters are in the Arctic, which has dissolved oxygen concentrations at about 7 ml l^{-1} , and the Antarctic Intermediate Water in all three major basins where values are between 5 and 5.5 ml l^{-1} . Very strong oxygen minima ($<1 \text{ ml l}^{-1}$) occur at this depth in the northern Indian and eastern and northern Pacific Oceans. The Atlantic oxygen minimum occurs at much higher concentrations, i.e., about 2.5 ml l^{-1} off the coast of SW Africa.

At 2000 m, the influence of the upper Antarctic Bottom Water can be seen in both the Indian and Pacific Oceans where dissolved oxygen values are between 3 and 4 ml l^{-1} over most of the southern portions of both basins (Fig. 16). In the Pacific, oxygen is consumed by decomposition processes as the water moves slowly northward, resulting in values below 2 ml l^{-1} at 45°N and in the Indian when it moves NW to the Arabian Sea. In contrast, Atlantic waters at this depth are well oxygenated ($6.5\text{--}5.5 \text{ ml l}^{-1}$, north to south) due to the southward flowing North Atlantic Deep Water.

From 3500 m to the deepest parts of all the basins the pattern of dissolved oxygen follows that seen at 2000 m. However, in the Indian and Pacific basins, the better oxygenated Antarctic Bottom Water has spread all the way to the northern reaches, so that dissolved oxygen values are always more than 3 ml l^{-1} . The pattern established in the Atlantic at 2000 m carries all the way to the bottom where, except for the Argentine and Cape Basins, dissolved oxygen concentrations are at least 5.2 ml l^{-1} and are about 6 ml l^{-1} in the NW Atlantic basin.

3.2.4. Particulate organic carbon (POC) flux

With the exception of communities in the vicinity of chemosynthetic habitats (e.g., vents and seeps), the benthos at depths below about 200 m rely on deposition of POC produced in the photic zone of the water column for food input. Because POC flux drops off exponentially with ocean depth, deep-sea communities are widely considered to be “food limited”; i.e., community structure and function, life histories, body size, feeding types, species diversity, as well as biogeographic patterns, are thought to be heavily influenced by the flux of POC to the deep-sea floor (e.g., Smith and Rabouille, 2002; Carney, 2005; Rex et al., 2005; Smith et al., 2008a; Ruhl et al., 2008; Rex and Etter, 2010). Modeling the pelagic input to the seafloor has long been a problem with most information coming from widely scattered sediment traps (e.g., Lampitt and Antia, 1997). The advent of space-based remote sensing promised the possibility that phytoplankton production over the whole ocean could be estimated from ocean color data. We investigated two such remote-sensing models of POC flux, one from Yool et al. (2007) and the other from Lutz et al. (2007). Both estimated flux through the mesopelagic zone (spatial resolution was $500 \text{ m} \times 500 \text{ m}$ for Yool et al. and $1 \text{ km} \times 1 \text{ km}$ for Lutz et al.) but only Lutz et al. attempted to estimate the amount of material arriving at the seafloor. The latter is a valuable quantity for benthic biogeographic work since the distance to the seafloor of the bathyal is roughly half that for the abyssal. As a result, some bathyal areas (for example along the mid-ocean ridges and some island or seamount chains, see Lutz et al. Fig. 14d) receive much more POC input than adjacent abyssal areas. Plotting the Lutz et al. (2007) values using our bathyal and abyssal topographic bins (Figs. 17 and 18), it can be seen that areas downstream of upwelled water (eastern Pacific especially $20\text{--}30^\circ\text{N}$ and S of the Equator, southeastern Atlantic) and under strong currents (NW Pacific and NW Atlantic), as well as areas of strong fronts (Sub-Antarctic Convergence) all show high levels of POC flux to the benthos. At lower bathyal to abyssal depths, one might expect the benthic communities in these areas to have higher biomass and diversity (Rex and Etter, 2010) compared to areas in the same biogeographic unit where

organic matter input is less because at these depths deep-sea bottom communities are widely considered to be food limited (e.g., Rex et al., 2005; Carney, 2005).

3.2.5. Hydrography and POC flux summary

From a benthic biogeographical perspective it seems clear the hydrographic and environmental variables of primary importance are temperature and POC flux, and in certain areas dissolved oxygen content, although salinity can be used to help characterize the presence of certain water masses (and hence connectivity), e.g., Antarctic Intermediate Water. These factors differ considerably in various parts of all ocean basins. Much of the variability occurs between 800 and 2000 m, encompassing the upper part of the lower bathyal, especially the large mid-ocean ridges and seamounts, where temperatures and dissolved oxygen values differ from ocean to ocean, especially between the Indian, Pacific, and Atlantic, as well as among the smaller basins of the Atlantic. POC flux also varies dramatically within and between basins as a consequence of (1) dramatic differences in overlying productivity between eutrophic upwelling zones and oligotrophic central gyres, and (2) the negative exponential dependence of POC flux on water depth (Carney, 2005). Hydrographic and environmental factors thus provide insights into potential province distributions, which can be tested as more species distributional data become available.

3.3. Proposed benthic biogeographic units

The benthic biogeographic units proposed here start with the concepts regarding regions and provinces promoted by Menzies et al. (1973) and Vinogradova (1979) for the abyssal areas, Belyaev (1989) for the hadal (ultra-abyssal) areas, and Zezina (1973, 1997) for the bathyal. Some boundaries have been altered on the basis of more recent data, published and unpublished observations, or re-analyses of existing data.

Our proposed deep-sea benthic biogeographic classification encompasses two large depth zones: the lower bathyal, 801–3500 m, and the abyssal, 3501–6500 m. All of the provinces discussed below are to be considered as hypothetical, and need to be tested with species distribution data, especially for the lower bathyal where many of the provinces have few data. We expect that the deeper provinces, especially their core regions, are more likely to remain unaltered even with additional species distribution information, while the shallower provinces could change substantially because of the greater environmental heterogeneity of continental margins (Levin and Sibuet, 2012). In addition, all provinces need to be viewed primarily as centers of distribution of deep-sea faunal groups; i.e., the locations of boundaries are

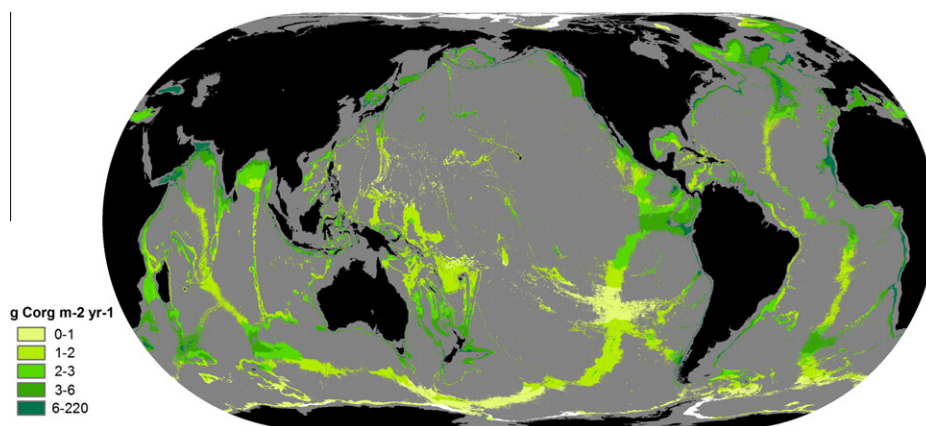


Fig. 17. POC flux to the bottom at depths between 800 and 3500 m. Data from Lutz et al. (2007).

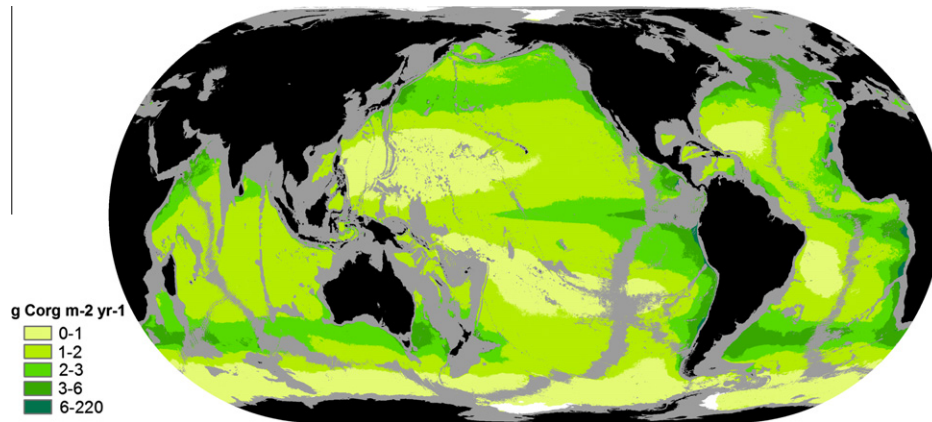


Fig. 18. POC flux to the bottom at depths between 3500 and 6500 m. Data from Lutz et al. (2007).

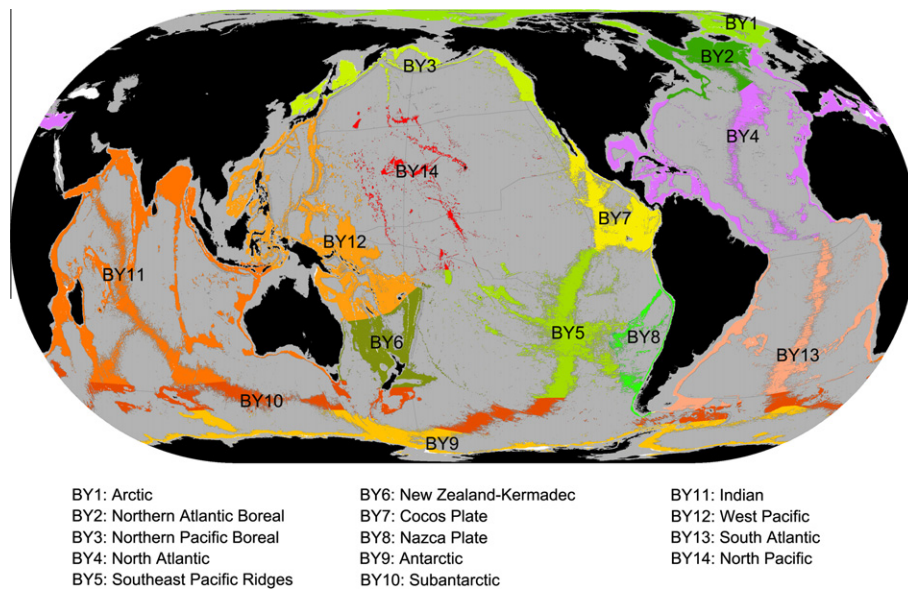


Fig. 19. Proposed Lower Bathyal Provinces.

particularly uncertain, and in most cases are more likely to be transition zones than absolute boundaries (see O'Hara et al., 2011, for an examination of one such transition area). We have marked these "transitional boundaries" with lines that approximately correspond to locations where oceanographic fronts or transitions in species and/or other environmental variables are known to occur.

3.3.1. Lower bathyal provinces (Fig. 19)

Proposed lower bathyal biogeographic provinces, their approximate coverage, and the features/parameters that define their boundaries are described below and summarized in Table 2. The lower bathyal includes both the slopes of continents as well as ridges, island slopes, and several thousand seamounts, about half of which extend upward into the bathyal zone (Clark et al., 2011); many of the latter are not readily evident on the maps presented here due to their small areal extent but are encoded in the GIS shapefiles available from the authors.

BY1. Arctic: includes the entire Arctic Ocean Basin and Norwegian-Greenland Sea in the east (bounded on the south by the Iceland-Faroe Ridge) and to the Bering Strait in the west; temperatures are very cold, average is $-0.6\text{ }^{\circ}\text{C}$, and POC flux is estimated to average $5.2\text{ g m}^{-2}\text{ yr}^{-1}$.

BY2. Northern Atlantic Boreal: from the Iceland-Faroe Ridge in the north, south along the Reykjanes Ridge, over the Newfoundland Seamounts and following the Western Boundary Undercurrent southward along the eastern slope of North America to off Cape Hatteras; temperatures average $3\text{ }^{\circ}\text{C}$, but salinity is slightly reduced to about 34.9 and POC flux, while moderately high on an annual basis ($6.6\text{ g m}^{-2}\text{ yr}^{-1}$) is dominated by spring bloom pulses (e.g., Lampitt and Antia, 1997).

BY3. Northern Pacific Boreal: covers the Aleutian Ridge in the North through the Gulf of Alaska to approximately the Mathematisians Seamounts in the eastern Pacific and including the Emperor Seamounts and the area off Hokkaido in the west; temperature averages about $1.8\text{ }^{\circ}\text{C}$ but salinities are a bit fresher than the normal range of Circumpolar Deep Water from which the water mass covering this province is derived; POC flux averages about $8.5\text{ g m}^{-2}\text{ yr}^{-1}$, higher than for any province, most likely because production is driven by deep water upwelling and continues for at least 4 months of the year (Hansell et al., 1993; Springer et al., 1996).

BY4. North Atlantic: extends southward along the Mid-Atlantic Ridge from the Reykjanes Ridge to approximately the equator, and along the eastern and western margins of the North Atlantic

Table 2

Summary of physiographic and hydrographic data for proposed deep-sea benthic provinces. Values are means obtained from analysis of rasterized variables for each province (data sources listed in Materials and Methods); area estimates derived from strm30 grid, spatial resolution of 30 arcsec (each pixel is approximately 1 km²).

Symbol	Province name	Area (km ² × 10 ⁶)	T (°C)	Depth (m)	POC (g C _{org} m ⁻² yr ⁻¹)	Salinity (psu)	Dissolved oxygen (ml l ⁻¹)
BY1	Arctic Bathyal	34.73	-0.53	2337	5.22	34.92	6.58
BY2	North Atlantic Boreal	7.27	3.19	2449	6.61	34.95	6.35
BY3	North Pacific Boreal	5.74	1.71	2381	8.57	34.49	2.25
BY4	North Atlantic Bathyal	11.48	5.58	2445	4.92	35.65	5.24
BY5	Southeast Pacific Ridges	10.12	1.82	3081	1.41	34.67	3.68
BY6	New Zealand Kermadec	5.95	2.76	2200	4.66	34.62	3.77
BY7	Cocos Plate	5.62	2.03	2939	4.11	34.66	2.59
BY8	Nazca Plate	1.70	2.07	2795	6.78	34.65	3.45
BY9	Antarctic Bathyal	17.36	0.23	2582	0.94	34.69	5.11
BY10	Subantarctic	13.93	1.22	2847	1.98	34.70	4.73
BY11	Indian Ocean Bathyal	18.35	2.52	2633	3.73	34.76	3.57
BY12	West Pacific Bathyal	12.20	2.52	2356	2.58	34.62	2.93
BY13	South Atlantic	8.56	2.51	2685	4.43	34.81	5.07
BY14	North Pacific Bathyal	1.72	1.96	2704	1.80	34.64	2.60
AB1	Arctic Basin	13.81	-0.62	3993	1.67	34.94	6.83
AB2	North Atlantic	35.59	2.35	4672	2.09	34.89	5.80
AB3	Brazil Basin	8.57	1.24	4659	1.13	34.77	5.33
AB4	Angola, Guinea, Sierra Leone Basins	9.20	2.38	4578	2.33	34.88	5.41
AB5	Argentine Basin	8.69	0.50	4770	2.77	34.69	5.11
AB6	Antarctica East	51.68	0.12	4487	1.03	34.68	5.38
AB7	Antarctica West	28.49	0.53	4314	0.74	34.70	4.91
AB8	Indian Ocean	52.34	1.18	4541	1.82	34.72	4.47
AB9	Chile, Peru, Guatemala Basins	17.99	1.75	4006	2.44	34.69	3.46
AB10	South Pacific	44.89	1.25	4623	1.23	34.70	4.47
AB11	Equatorial Pacific	21.56	1.41	4688	1.52	34.70	3.93
AB12	North Central Pacific	42.02	1.52	5154	1.38	34.69	3.71
AB13	North Pacific	23.63	1.54	4982	2.31	34.68	3.39
AB14	West Pacific Basins	1.47	3.17	4320	1.66	34.61	2.38

Ocean, including the Mediterranean Sea in the east and the Gulf of Mexico and Caribbean Sea in the west; inclusion of eastern and western Mediterranean seas results in high average temperature (5.58 °C) and very broad temperature range (std. deviation = 3.91 °C); POC flux is also moderately high and is quite variable (4.92 ± 5.1 g m⁻² yr⁻¹; mean ± 1 s.d.); further analysis may result in subdivision of this province.

BY5. Southeast Pacific Ridges: includes all the ridges and seamounts in the South Pacific Ocean to the west of the Nazca and Cocos Plate, reaching northward to about 2–8°S, west to about 165°W, and south to about 45°S where the influence of sinking Antarctic Intermediate Water will be felt; waters here represent the warmer (1.8 °C) end of Circumpolar Deep Water; POC flux is moderately low (1–2 g m⁻² yr⁻¹).

BY6. New Zealand-Kermadec: includes plateaus around New Zealand and extending northward along the Kermadec and Lau Ridges almost to Tonga and the seamounts of the Louisville Ridge; water mass is Antarctic Intermediate Water with temperatures averaging 2.8 °C; POC flux moderately high (4–6 g m⁻² yr⁻¹) due to mixing around the Chatham Rise and other banks to the southeast and northwest of New Zealand.

BY7. Cocos Plate: encompassing all the ridges and seamounts of the Cocos Plate, extends along 3°S from the South American slope out to about 110°W and north to the deeper parts of the Gulf of California; waters are derived from Antarctic Intermediate Water (T, 2.1 °C) and POC flux, due to eastern Pacific upwelling, is moderately high (4–6 g m⁻² yr⁻¹); most of this province is below the oxygen minimum zone, but some shallower bathyal areas experience dissolved oxygen values below 1 ml l⁻¹ and are likely to fall in a different province.

BY8. Nazca Plate: suggested by Parin et al. (1997) to encompass the ridges of the Nazca Plate, from the border with BY 7 to Tierra del Fuego along the western South American slope and westward to about 90°W; defined primarily by Antarctic Intermediate Water (~2 °C) with high POC flux (6–8 g m⁻² yr⁻¹) due to eastern Pacific upwelling; as with BY7, some areas of the shallow bathyal

experience very low dissolved oxygen levels, but average levels for all bottom areas is above 3 ml l⁻¹.

BY9. Antarctic: encompasses all the slope and ridge areas around the Antarctic continent connected by Circumpolar Deep Water; temperatures are very cold (average is 0.2 °C) and annual average POC flux is very low (1–3 g m⁻² yr⁻¹) although some areas experience very high levels due to localized high productivity.

BY10. Subantarctic: extends northward around the Southern Ocean, encompassing a 10–20° of latitude band from 40–45°S to 55–60°S; defined by the extent of 1–2 °C Circumpolar Deep Water; POC flux (1.5–3 g m⁻² yr⁻¹) is higher than in the Antarctic Province; further research may show this province to be a transition region between the Antarctic Province and the bathyal provinces to the north of 45°S.

BY11. Indian: includes all of the Indian Ocean northward from the Antarctic Convergence, and extends eastward to include southern slopes of Australia to Tasmania; temperatures average 2–3 °C over most of the area but can be very warm along the northern Indian Ocean slopes; POC flux is moderate (3–4 g m⁻² yr⁻¹) except under the northwest upwelling zone; more research may result in this province being further subdivided.

BY12. West Pacific: extends from 14 to 23°S northward to off Japan, west to the Indonesian Archipelago, and eastward to about 165–175°E; temperature and salinity are characteristic of Antarctic Intermediate Water that is moving northward along the western Pacific (Whitworth et al., 1999) at bathyal depths; POC flux is moderate (2–3 g m⁻² yr⁻¹).

BY13. South Atlantic: encompassing all of the South Atlantic from about the equator to the Antarctic Convergence (45–50°S), dominated by Antarctic Intermediate Water; POC flux is highly variable, 3–9 g m⁻² yr⁻¹ over most of the region, but some areas have very high values.

BY14. North Pacific: comprises exclusively seamounts, island slopes, and ridges of the northern Central Pacific from about 10°S northward to about 40°N; water temperatures are heavily influenced by Circumpolar Deep Water flowing northward; POC flux

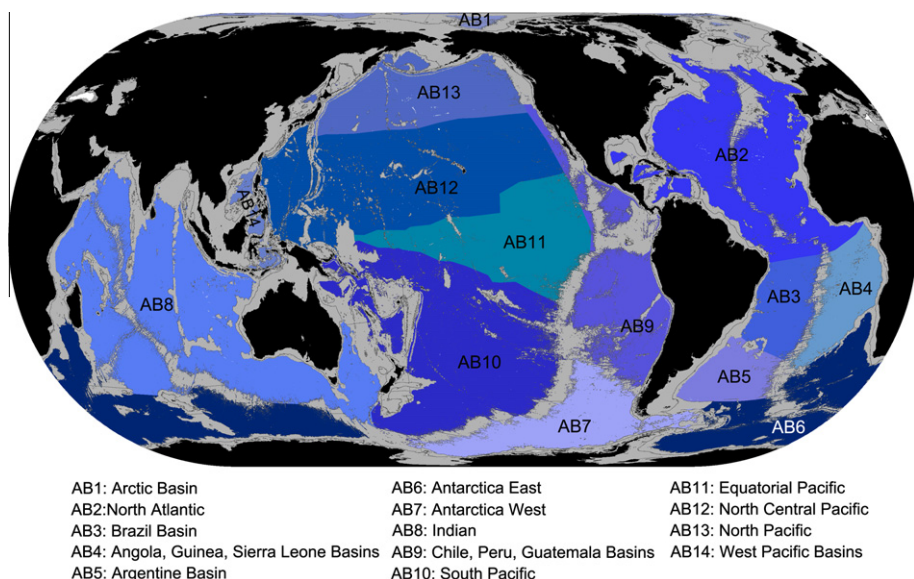


Fig. 20. Proposed Abyssal Provinces.

is moderately low ($1\text{--}2\text{ g m}^{-2}\text{ yr}^{-1}$), being higher closer to the equator.

3.3.2. Abyssal provinces (Fig. 20)

The abyssal provinces are separated by mid-ocean ridges and other bathyal topography creating deep basins and/or are distinguished by varying levels of POC flux to the seafloor (Table 2). The proposed abyssal provinces are as follows.

AB1. Arctic Basin: covers the northernmost abyssal region isolated from all other abyssal provinces by sills of about 800 m depth; mean temperature is $-0.6\text{ }^{\circ}\text{C}$, colder than for any other province, and mean POC is $1.7\text{ g m}^{-2}\text{ yr}^{-1}$.

AB2. North Atlantic: includes all areas north of the equator under the influence of North Atlantic Deep water; is divided by the bathyal depths of the Mid-Atlantic Ridge, and perhaps could be divided into eastern and western provinces. POC flux varies N to S, but averages $2.09\text{ g m}^{-2}\text{ yr}^{-1}$.

AB3. Brazil Basin: a region of low to moderate POC flux ($<1\text{--}2\text{ g m}^{-2}\text{ yr}^{-1}$), isolated by the bathyal depths of the Mid-Atlantic ridge to the east.

AB4. Angola, Guinea, and Sierra Leone Basins: three abyssal basins with primarily low to moderate POC flux ($1\text{--}3\text{ g m}^{-2}\text{ yr}^{-1}$) bounded to the west by the bathyal mid-ocean ridges; these basins are under the direct influence of North Atlantic Deep Water which has its southern boundary in the southeastern Atlantic at the Walvis Ridge.

AB5. Argentine Basin: a region of relatively high abyssal POC flux ($2\text{--}6\text{ g m}^{-2}\text{ yr}^{-1}$) largely bounded on all sides by bathyal depths; major water mass is Antarctic Bottom Water.

AB6. Antarctica East: includes the areas where very cold bottom water flows into Cape, Agulhas, Natal, Crozet, and South Indian Basins and perhaps the Tasman Sea to about 170°E ; is bounded on nearly all sides by bathyal depths; has uniformly low POC flux ($<1\text{ g m}^{-2}\text{ yr}^{-1}$), its boundary with the Argentine Basin defined by a transition from low to high POC flux, from very low to moderate abyssal temperatures.

AB7. Antarctica West: includes the Amundsen Plain in the region from the Ross Sea to the Antarctic Peninsula and north to the Antarctic-Pacific Ridge and the Southeast Pacific Basin; this is an abyssal basin bounded on all sides by bathyal depths and generally characterized by low POC flux ($<2\text{ g m}^{-2}\text{ yr}^{-1}$) and low abyssal temperatures (-1 to $1\text{ }^{\circ}\text{C}$).

AB8. Indian Ocean: includes all the basins north of approximately 45°S (this region is not well studied and some parts of this province may have species dispersed by Antarctic Bottom Water/Circumpolar Deep Water northward); is characterized mostly by low POC flux, with moderate levels on its margins; also includes a number of abyssal basins at least partially isolated by bathyal mid-ocean ridges; further study may well warrant designation of some of these basins as additional provinces.

AB9. Chile, Peru, Guatemala Basins: also includes the smaller Panama Basin and other minor deep areas east of the East Pacific Rise and north of the Chile Rise, and extending under the oxygen minimum zone of the western North American slope; this series of abyssal basins is connected by abyssal passages through the mid-ocean ridges, and is characterized by moderate-high abyssal POC flux ($2\text{--}6\text{ g m}^{-2}\text{ yr}^{-1}$) at the centers of the basins.

AB10–AB13. South (AB10), Equatorial (AB11), North Central (AB12), and North Pacific (AB13) Provinces: together, these encompass the Pacific from the Antarctic and East Pacific Ridges in the southeast to the Aleutian Ridge in the north and all of the abyssal depths in the western Pacific; divided into Provinces from north to south based on projections of POC flux to the seafloor; the centers of the South Pacific and North Central Pacific provinces underlie oligotrophic central gyres and are characterized by extremely low POC flux ($<1\text{ g m}^{-2}\text{ yr}^{-1}$); the core of the Equatorial Pacific province underlies high productivity related to equatorial upwelling and is characterized by moderate-high abyssal POC flux ($2\text{--}6\text{ g m}^{-2}\text{ yr}^{-1}$); the North Pacific province lies beneath the subarctic Pacific and is characterized by moderate seafloor POC flux ($2\text{--}3\text{ g m}^{-2}\text{ yr}^{-1}$); boundaries between these Pacific abyssal provinces are very likely to be characterized by gradual transitions from oligotrophic to eutrophic biotas.

AB14. West Pacific Basins: includes the basins of the Banda, Sulawesi, and Sulu Seas, and perhaps the South China Sea, that are isolated by shallow sill depths from the influence of Antarctic Bottom Water as it spreads northward; abyssal depths of these basins have very high temperatures ($4.8\text{--}5.25\text{ }^{\circ}\text{C}$) by abyssal standards (O'Driscoll and Kamenkovich, 2009).

3.3.3. Hadal (ultra-abyssal) provinces (Fig. 21)

No changes are made to the scheme presented by Belyaev (1989) for deep areas below 6500 m. The provinces comprise:

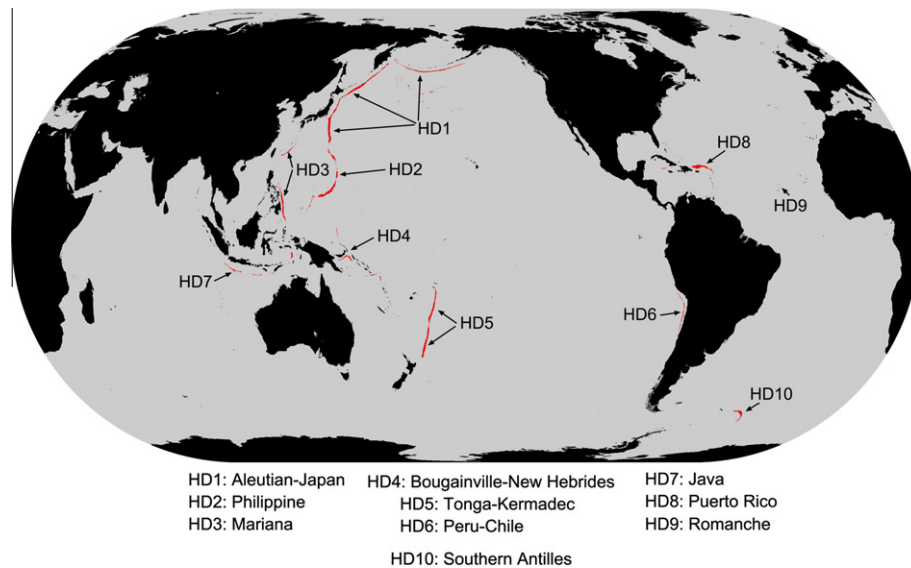


Fig. 21. Hadal provinces (after Belyaev, 1989).

HD1. Aleutian-Japan: includes the Aleutian, Kuril-Kamchatka, Japan, and Izu-Bonin Trenches.

HD2. Philippine: includes only the Philippine and Ryuku Trenches.

HD3. Mariana: comprising the Volcano, Mariana, Yap and Palau Trenches.

HD4. Bougainville-New Hebrides: a series of small trenches including the New Britain, Bougainville, Santa Cruz, and New Hebrides Trenches.

HD5. Tonga-Kermadec: includes the north-south trending Tonga and Kermadec Trenches.

HD6. Peru-Chile: includes only the Peru-Chile (Atacama) Trench.

HD7. Java: includes only the Java (Sunda) Trench extending along the southern margin of Indonesia.

HD8. Puerto Rico: includes the Puerto Rico and Cayman Trenches.

HD9. Romanche: this is a small deep in the equatorial Atlantic that reaches only to about 8000 m depth; whether it will stand as a province separate from the abyssal Atlantic will depend on further research.

HD10. Southern Antilles: includes the South Sandwich and South Orkney Trenches.

4. Discussion

4.1. Hydrographic and POC flux features of the provinces

The proposed provinces are based strongly on water-mass (or connectivity) characteristics, which are defined by temperature and salinity signals, and POC flux characteristics, which define food availability in these detritus-based deep-sea ecosystems. The mean T-S for the bathyal provinces is plotted in Fig. 22 in relation to the major water masses that occur between 500 and 1500 m (data from Emery and Meincke, 1986). Provinces BY2 and BY4, in the North Atlantic, are within the envelope of W and E Sub-Arctic Intermediate Water (W & ESAIW), the primary difference between the two provinces attributable to the influence of Mediterranean Water (MW) which is both warmer and saltier than most other Intermediate Waters of the world ocean. The Arctic Bathyal Province (BY1) is near the core of Arctic Intermediate Water (AIW). Some of the remaining bathyal provinces (BY9, BY10, BY5, and

BY7 in the Southern Ocean and Pacific) are connected by Circumpolar Deep water (CDW), which extends into the bathyal zone in the southern hemisphere, while others (BY6, BY8, BY11–14) are within the core of Antarctic Intermediate Water (AAIW), which forms north of the Polar Convergence and is a little warmer and fresher than CDW. AAIW extends north of the equator in the Atlantic and Pacific Oceans and covers at least the southern half of the Indian Ocean at depths of 500–1500 m (Emery and Meincke, 1986). Province BY3 is located along the rim of the northern end of the North Pacific, and is more characteristic of North Pacific Intermediate Water (NPIW), or perhaps its source water mass, Gulf of Alaska Intermediate Water (You, 2003, 2010).

In the abyss, most of the provinces are under the influence of (and ultimately connected by) Antarctic Bottom water (AABW) or CDW (Fig. 23). Only provinces AB1 in the Arctic, and AB2 and AB4 in the Atlantic show influences of other deep water masses (Arctic Bottom Water, ABW, and North Atlantic Deep Water, NADW, respectively). Abyssal Province AB14 is in the relatively warm waters of the Sulu, Sulawesi, and Banda Seas and is isolated from most of the bottom waters of the world ocean by shallow sills (Tomczak and Godfrey, 1994).

Oxygen levels low enough to deplete species numbers occur only in the bathyal of the eastern Pacific (Figs. 15 and 16) and northern Indian Oceans. Extensive regions of the 800–2000 m benthos in those areas are subject to dissolved oxygen levels below 0.5 ml l^{-1} , a level commonly considered to be limiting to many marine species (Levin, 2003). This value, based on studies on the Oman margin and other deep-sea oxygen-poor areas may be a reasonable threshold for many deep-sea benthic invertebrates in regions with an evolutionary history of low oxygen (Levin, 2003; Stramma et al., 2010). However, we note recent work by Vaquer-Sunyer and Duarte (2009) who investigated the effects of hypoxia in a number of shallow-water coastal sites and observed sublethal effects at higher oxygen values, especially for benthic-pelagic fishes. Although the overall mean threshold from their study was 1.1 ml l^{-1} , there was variability among taxa. It seems quite likely that for some taxa, especially active fishes, and in regions lacking an evolutionary history of oxygen stress (e.g., the North Atlantic), sublethal effects of oxygen stress could cause faunal turnover at concentrations significantly above 1 ml l^{-1} , so that low oxygen levels also yield transition zones.

POC flux to the seafloor influences body size, life-history characteristics, food-web complexity, and the diversity of species found

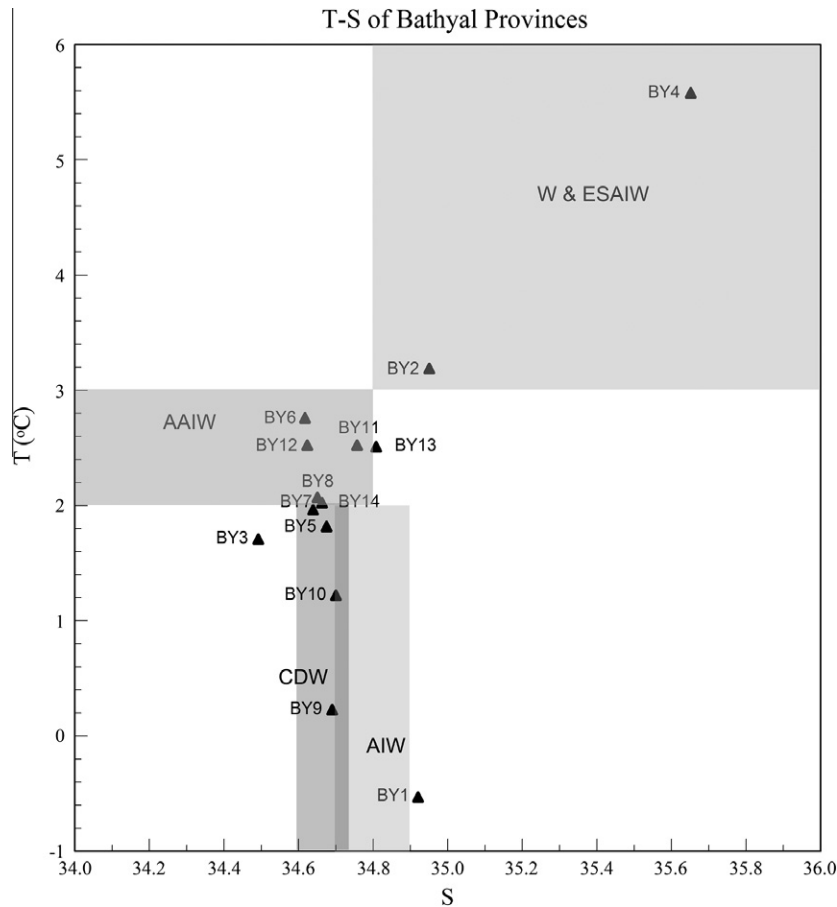


Fig. 22. Plot of mean temperature vs. mean salinity for each bathyal province. Bathyal water mass data (shaded areas) from Emery and Meincke (1986).

within an area (Levin et al., 2001; Rex et al., 2005; Smith et al., 2008a; Rex and Etter, 2010). In most cases, differences between adjacent provinces are likely to be influenced more by POC input (i.e., food availability) than by other environmental parameters such as temperature (e.g., Carney, 2005), unless oxygen levels decline below 1 ml l^{-1} . In the bathyal, POC flux is highest at moderately high latitudes and under upwelling zones (e.g. eastern Pacific, North Pacific, SE Atlantic) and within an area might vary by a factor of 2 depending on seafloor depth (Fig. 17). The effect of upwelling zones and water mass convergences on POC flux to the seafloor can be seen clearly at abyssal depths (Fig. 18). Highest flux values are seen in the eastern equatorial Pacific, North Pacific and North Atlantic, and in the Indian and Atlantic Oceans in the region of the formation of Antarctic Intermediate Water. At abyssal depths, the benthic provinces are likely to be structured primarily by POC flux in these highly food limited environments (Smith et al., 2008a; Ebbe et al., 2010).

4.2. Benthic biological data

As is well known, sampling in the deep-sea is limited by equipment and funds for ship time, and compiling the existing taxonomic data from large numbers of disparate sources is difficult and time consuming. Nevertheless, there are some compiled species-level data that can be used to test some of the boundaries proposed here. This is most easily done for the abyssal basins of the Atlantic, where data are available for some faunal components over most of the ocean. In contrast, the bathyal, while more easily reached and in some areas sampled extensively, contains more complex bottom conditions and so some features such as seamount and island slopes, mid-ocean ridges, and canyon walls that

harbor large megafaunal populations are still mostly unsampled on large regional or global scales.

4.2.1. Bathyal faunas

There are few extensive studies of the bathyal fauna that cross our proposed biogeographic boundaries. The boundary between the Nazca Plate and SE Pacific Ridges provinces was proposed by Parin et al. (1997). They suggested that the fauna of the seamounts of the Sala y Gomez Ridge and transitional Sala y Gomez/Nazca ridge zone westward of $83\text{--}84^\circ\text{W}$ should be considered to be a separate Nazcaplatensis Province belonging to the Indo-West Pacific region. This unit we have named SE Pacific Ridges Province and extended its proposed boundaries north and south. The remainder of the Nazca Ridge to the east was considered either as an impoverished portion of the Nazcaplatensis province or as part of the eastern Pacific subcontinental region, largely under the influence of a strong and deep oxygen minimum zone. We have proposed it as a separate Nazca Plate Province, expecting that as the deeper parts of the bathyal below the oxygen minimum zone are sampled, a distinct fauna will appear.

O'Hara et al. (2011) analyzed the ophiuroid fauna in the region around New Zealand and Australia and found a bathyal boundary between tropical and temperate zones to exist at about 28°S , with another boundary between temperate and polar groups at $58\text{--}60^\circ\text{S}$. Some bathyal species, however, extended well to the south, as far as 50 or 60°S , and some (fewer) southern species extended well into the lower latitudes. They also noted that these latitudinal bands extended into the Indian Ocean, suggesting a similar biogeographic pattern, perhaps related to water masses that extend most of the way around the southern hemisphere.

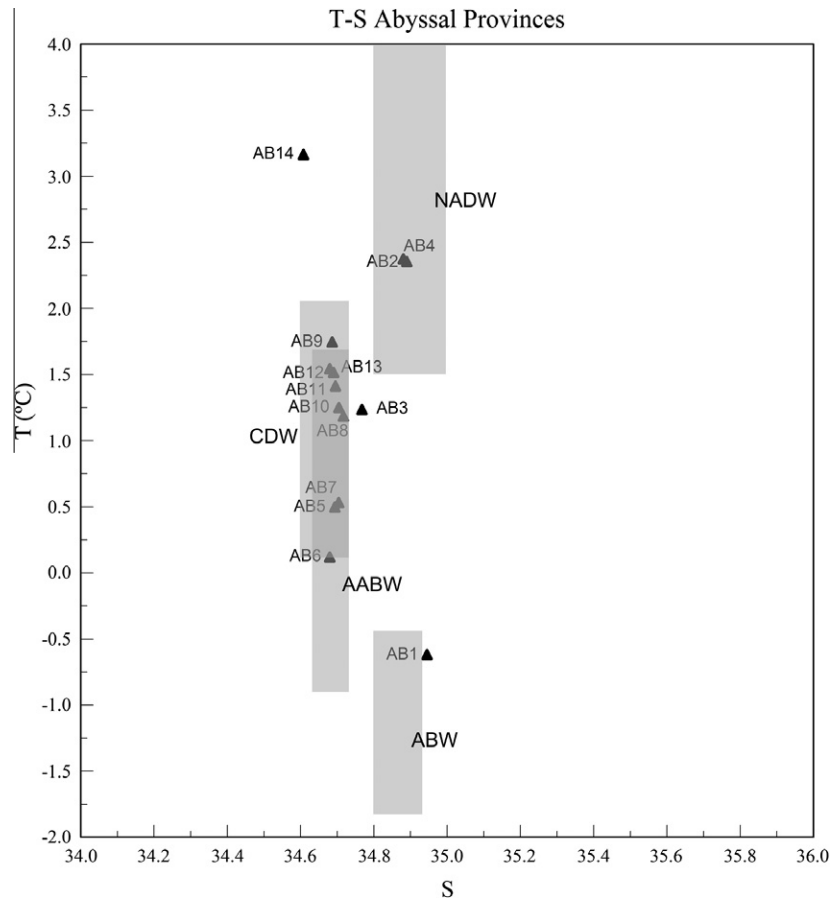


Fig. 23. Plot of mean temperature vs. mean salinity for each abyssal province. Abyssal water mass data (shaded areas) from Emery and Meincke (1986).

Seamounts and ridges provide areas of lower bathyal depth in offshore areas dominated by abyssal plains. These elevated topographic features can have a different fauna from the surrounding deep seafloor because they are “islands” of shallower habitat providing a wide range of depths for different communities. Benthic invertebrate communities on seamounts may often be populated from a regional species pool, and be similar to other habitats at corresponding depths (see review in Rowden et al., 2010), and hence they may conform to the more general benthic provinces identified in this paper. However, the importance of depth changes affecting community structure is illustrated on seamounts by McClain et al. (2010) and seamounts may “sample” only a subset of regional fauna; hence there may be considerable variation between seamounts within a province.

Seamounts have often been associated with reports of high endemism, with values as high as 50–60% (see review by Stocks and Hart, 2007). However, most published records are much lower than this, and an increase in seamount sampling in recent years through the Census of Marine Life has highlighted that estimates of endemism can be artefacts of limited sampling, selectivity of the gear used, and the consistency of taxonomic identification (e.g., Rowden et al., 2010; Clark et al., 2012). These issues are not unique to seamounts, but apply equally to biodiversity data in bathyal and abyssal environments. Hence, although endemism could be an important criterion of biogeographic differences, we cannot prescribe any particular level of endemism as indicative of provincial separation.

The lower bathyal zones are acknowledged to be very broad. In some oceanic regions, the depth range could warrant further subdivision where there may be marked changes in species

composition or diversity (e.g., Carney, 2005). In the South Pacific, for example, demersal fish communities change with depth, and lower continental slope faunas dominated by species such as orange roughy and oreos decline below about 1200 m (Koslow et al., 1994; Francis et al., 2002). Deep-sea corals (Order Scleractinia) are abundant at depths of 600–1400 m where they can form extensive reef-type habitat on seamounts and ridge peaks (e.g., Clark et al., 2010a; Tracey et al., 2011). However, this dominant coral group is rare below 2000 m (Rogers et al., 2007; Tittensor et al., 2009; Davies and Guinotte, 2011). On seamounts off Tasmania, Thresher et al. (2011) noted a change below about 1800 m from scleractinian coral dominance to high densities of barnacles, anemones, and bamboo corals. Differences in benthic community structure between transects at selected depths were found by McClain et al. (2010) on Davidson seamount, with relative abundance of taxa changing between summit and upper flanks (depths to about 1770 m), and the deeper flanks between 2500 and 3300 m. Genetic studies of the population structure of deep-sea bivalves also show changes with depth, with genetic distance varying for several species at around 2000 m (Etter et al., 2005). Hence, there is some evidence for a finer subdivision of the wide bathyal range, based on the characteristics of particular regions and taxa. A seamount classification developed by Clark et al. (2011) applied the lower bathyal divisions used here but added a subdivision to the depth band in the Southwest Indian Ocean at 1500 m because reef-forming scleractinian corals were less abundant below that depth.

Demersal fishes at bathyal depths in ocean areas also show some conformity with the broad provinces described here, although high mobility and extensive larval dispersal means many fish species can have very wide distributions. In the Southwest

Pacific there are marked changes in the seamount fish communities along the Norfolk Ridge between New Zealand and New Caledonia (Clark and Roberts, 2008; Zintzen et al., 2011). Clark et al. (2010b) examined seamount fish communities from a number of global regions, at depths between about 500 and 1000 m, and noted similarities between components of the fauna at ocean basin scale levels driven by water mass characteristics at depth. Connectivity within Antarctic Intermediate Water and North Atlantic Deep Water masses were thought to be key environmental drivers of this distribution, especially for some widespread fish species such as orange roughy. Nevertheless, detailed species composition varied between areas, and separation of communities revealed by multivariate analyses were generally consistent with the bathyal provinces.

Reducing environments were not considered in this study, but hydrothermal vents were included in the GOODS report (UNESCO, 2009). Data have recently been analyzed by Bachraty et al. (2009) to define six global biogeographic provinces for vent fauna: Mid-Atlantic Ridge (MAR, in the North Atlantic), Southwest Pacific (SW, covering the mid-central and southwest Pacific Ocean, and southern Indian Ocean), Northwest Pacific (NW), and three provinces dividing the eastern Pacific Ocean (Northeast (NE), northern East Pacific Rise (NEPR), southern East Pacific Rise (SEPR)). These hydrothermal provinces correspond reasonably well with the general bathyal provinces we propose. The MAR hydrothermal province maps well to BY4, SEPR to BY5, NE to BY3, and NEPR to BY7. The very large SW is covered by several generic provinces, BY6, BY10 and BY12. The NW province is part of BY12. Recent vent surveys off New Zealand suggest further subdivision of the SW province (NIWA, unpublished data), which will improve the match to BY6 and BY12.

4.2.2. Abyssal basin faunas

At abyssal depths in the Atlantic, Monniot (1979) found tunicates of the Cape and Angola Basins in the SE to have relatively high affinity with the Europe and Labrador Basins in the north. The basins of the western Atlantic, especially Surinam, Brazil, and Argentina, had weak affinities with any other basin.

Allen and Sanders (1996) summarized the distributions of protobranch bivalves sampled from all of the basins in the Atlantic Ocean. Using cluster analysis on a subset of stations, they noted that depth was a dominant factor in the classification. One major

cluster contained most of the stations sampled between 1000 and 3000 m, while the deeper clusters often grouped stations from more than one basin. We re-analyzed the entire >3000 m sample set using Primer 6 (Clark and Gorley, 2006) to see whether a basin-based pattern could be discerned (Fig. 24). The results are complicated by the fact that some basins are heavily sampled and others much less so. Nevertheless, samples from the Argentine (cluster A), West European (G) Brazil (I), and Angola Basins (J) are mainly found within single clusters, suggesting the basins have distinct protobranch faunas. Samples from the North American and Guyana Basins, on the other hand are found in two or more clusters.

Watling (2009) took a similar approach with cumacean sample data compiled for most of the deep basins in the Atlantic. He found all basins to have distinguishable faunas except in the North Atlantic where the eastern (European) and western (North American) basin faunas seemed to intermingle.

Gheerardyn and Veit-Köhler (2009) found that paramesochrid harpacticoid copepods from SE Atlantic abyssal basins showed little biogeographic distinction among the basins, but the fauna of the Angola and Guinea basins differed significantly from that of the Scotia Sea and the Weddell Sea.

Faunal studies have also been conducted across the postulated transition zone between the Equatorial and North Central Pacific provinces, i.e., traversing a gradient from moderate to very large POC flux to the seafloor. Substantial changes in dominant species, and levels of species diversity, were observed across the postulated transition zone for the nodule dwelling fauna, for macrofaunal polychaetes, and for sediment dwelling foraminiferans (Mullineaux, 1987; Glover et al., 2002; Nozawa et al., 2006; Veillette et al., 2007; Smith et al., 2008b; Ebbe et al., 2010). These changes are consistent with the strong role we postulate for POC flux and consequent food availability as a driver of biogeographic patterns at abyssal depths (Smith et al., 2008a).

4.2.3. Hadal faunas

Hadal (ultra-abyssal) biogeography has not been extensively reviewed or revised since the schema of Belyaev (1989) and Vinogradova (1997). These were the basis of the GOODS classification and are presented here. They treated most trenches around the world as separate biogeographic units, based on limited sampling that had revealed an apparently high degree of endemism (e.g., Wolff,

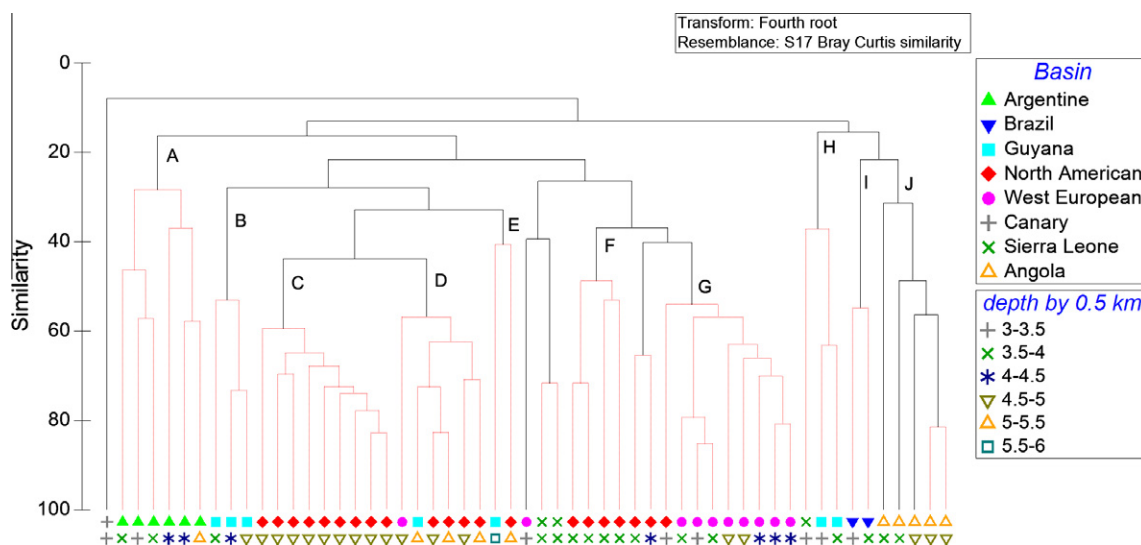


Fig. 24. Re-analysis of the protobranch data of Allen and Sanders (1996) for stations deeper than 3000 m. Station identifiers have been replaced by symbols for Atlantic basins (upper row) and depth intervals of 0.5 km from 3 to 6 km (lower row).

1970; Belyaev, 1989). Detailed knowledge of trench fauna remains patchy, although in recent years there has been a dramatic increase in trench research with deployment of deep baited-landers and fish traps, especially in the Pacific Ocean (e.g., Fujii et al., 2010; Jamieson et al., 2011). These studies are revealing considerable variation in physical characteristics and faunal community composition within and between trenches (e.g., Jamieson et al., 2010) and also indicate that trench communities are distinct from adjacent abyssal plains (Jamieson et al., 2011), providing support for a separate hadal biogeography. In their review of hadal ecology, Blankenship-Williams and Levin (2009) summarize some of the key issues of hadal biogeography, and note that for the hadal zone depth is a key physiological driver, with the abyssal zone sharing few fauna with trench communities at 8000–9000 m, but more at depths of 6500–7000 m. This is consistent with our earlier conclusion that geographical and depth gradients are likely to yield transitional zones, rather than sharp boundaries between deep-sea biogeographic provinces.

4.3. Management implications

Biogeographic classifications can be used with other management tools and quantitative analyses (e.g., predictive habitat modeling) to help balance exploitation and conservation in the deep sea. Seafloor ecosystems are widely impacted by human activities, but while impacts of marine industries like bottom fishing and oil drilling are well known, other activities in the deep sea such as waste disposal and seafloor mining are of increasing concern (e.g., Davies et al., 2007; Smith et al., 2008b; Ramirez-Llodra et al., 2011; Sutherland et al., 2011). These activities can be highly destructive to seafloor ecosystems in the deep sea and hence there is a need for large-scale management for conservation of biodiversity and preservation of ecosystem function (e.g. Roberts, 2002; Probert et al., 2007).

An important component to achieve the necessary ecosystem approach to management is the use of networks of marine protected areas designed to preserve representative and unique marine habitats as well as ecosystem structure and function (e.g., Airame et al., 2003; Johnston and Santillo, 2004; PISCO, 2007). Several global initiatives have been developed to perform this work. The Convention on Biological Diversity has agreed to develop representative networks of MPAs (CBD, 2010) with a 2020 target of 10% of “coastal and marine areas”, while 20–30% of each marine habitat was recommended by the World Parks Congress in 2003 (Anon, 2003). The CBD has initiated a programme to identify ecologically and biologically significant areas (EBSAs), and adopted scientific criteria (CBD, 2009). Identifying EBSAs and areas for inclusion in high seas MPA networks is the main objective of the Global Ocean Biodiversity Initiative (GOBI; GOBI, 2010). Benthic habitat protection is also an increasing issue for fisheries management. FAO Guidelines on High Seas Deep-Sea Fishing (FAO, 2009) specifically refers to identification and protection of “vulnerable marine ecosystems” and this has been a central point also of United Nations General Assembly Resolutions 61/105 and 64/72.

Part of the process for representative habitat conservation is to identify areas that contain, or are likely to contain, distinct habitats or communities. Biogeographic and ecological classification approaches are among the most common methods used (Carpenter et al., 1999). Clark et al. (2011) applied the 2008 bathyal GOODS biogeographic province arrangement as part of a classification of global deep-sea seamounts and demonstrated how it could be used to give a geographical basis to aid the determination of protected areas. Dunstan et al. (2011) selected a region spanning two bathyal provinces in their work to select priority EBSA seamount regions. The GOODS system was also used as input to a CBD-sponsored workshop to facilitate description of EBSAs in the Western South

Pacific (CBD, 2012). These efforts demonstrate the utility of biogeographic classifications to provide a structure to management planning for conservation of areas in the deep sea and an impetus to both utilize the work described in this paper, which updates the GOODS classification, and to further improve data analyses in order to refine or confirm the biogeographic province boundaries.

Acknowledgements

The impetus for this paper came from the meeting held in Mexico City in January, 2007, from which the GOODS report was produced. Since that meeting, the four of us have spent considerable amounts of our personal or professional time re-working some of the boundaries, conducting additional analyses, and generally reconsidering much of what was produced in Mexico. We owe a huge debt of gratitude to our colleagues who participated in the GOODS meeting for pushing us to accomplish something not previously attempted, and for sharing their knowledge of deep-sea systems with us. K. Scanlon, USGS Woods Hole was instrumental in helping us get started by providing us with our first GIS bathymetry and hydrography files. We would like to thank our employers in Mānoa, MCI, and NIWA who let us explore these ideas further as part of our working days. J.G. and L.W. also completed the GIS analysis of this project while at sea on a cruise funded by the Hawaii Undersea Research Lab. We would especially like to thank C. Kelly for the invitation to participate in the cruise and the opportunity to collect deep-sea gorgonians. The Census of Diversity of Abyssal Marine Life project (part of the Census of Marine Life), partially supported CS's efforts on this paper. This is UH Dept. of Biology Publication number 2013-001 and SOEST Publication number 8815.

References

- Anon, 2003. Other marine outcomes from the World Parks Congress. MPA News 5 (4), 3.
- Airame, S., Dugan, J.E., Lafferty, K.D., Leslie, H., McArdle, D.A., Warner, R.R., 2003. Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. *Ecological Applications* 13, 170–184.
- Allen, J.A., Sanders, H.L., 1996. The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: the epilogue. *Progress in Oceanography* 38, 95–153.
- Anderson, T.R., Rice, T., 2006. Deserts on the sea floor: Edward Forbes and his azoic hypothesis for a lifeless deep ocean. *Endeavour* 30, 131–137.
- Bachraty, C., Legendre, P., Desbruyeres, D., 2009. Biogeographical relationships among deep-sea hydrothermal vent faunas at global scale. *Deep-Sea Research I* 56, 1371–1378.
- Becker, J.J., Sandwell, D.T., Smith, W.H.F., Braud, J., Binder, B., Depner, J., Fabre, D., Factor, J., Ingalls, S., Kim, S.-H., Ladner, R., Marks, K., Nelson, S., Pharaoh, A., Trimmer, R., von Rosenberg, J., Wallace, G., Weatherall, P., 2009. Global bathymetry and elevation data at 30 arc-seconds resolution: SRTM30 PLUS. *Marine Geodesy* 32, 355–371.
- Belyaev, G.M., 1974. On the age of deep-sea fauna of the ocean and ultra-abyssal fauna of trenches. *Otdel biologicheskij* 79, 94–112, in Russian.
- Belyaev, G.M., 1989. Deep Sea Ocean Trenches and their Fauna. Nauka, Moscow, 255p (in Russian, translation courtesy of Scripps Institution of Oceanography Library).
- Blankenship-Williams, L.E., Levin, L.A., 2009. Living deep: a synopsis of hadal trench ecology. *Marine Technology Society Journal* 43, 137–143.
- Bouchet, P., Héros, V., Lozouet, P., Maestrati, P., 2008. A quarter century of deep-sea malacological exploration in the South and West Pacific: where do we stand? How far to go? *Mémoires du Muséum national d'Histoire naturelle* 196, 9–40.
- Briggs, J.C., 1974. *Marine Zoogeography*. McGraw-Hill, New York.
- Briggs, J.C., 1995. *Global Biogeography*. Elsevier, Amsterdam.
- Briggs, J.C., Bowen, B.R., 2011. A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*. <http://dx.doi.org/10.1111/j.1365-2699.2011.02613.x>.
- Bruun, A.F., 1957. Deep sea and abyssal depths. In: Hedgpeth, J.S. (Ed.), *Treatise on Marine Ecology and Paleocology*, vol. 67. Geological Society of America Memoir, pp. 641–672.
- Cairns, S., Chapman, R., 2001. Biogeographic affinities of the North Atlantic deep-water Scleractinia. In: Willison, J.H.M., Hall, J., Gass, S.E., Kenchington, E.L.R., Butler, M., Doherty, P. (Eds.), *Proceedings of the First International Symposium on Deep-Sea Corals*. Ecology Action Centre, Halifax, pp. 30–57.
- Carney, R.S., 2005. Zonation of deep biota on continental margins. *Oceanography and Marine Biology: An Annual Review* 43, 211–278.

- Carpenter, C.A., Busch, W.-D., Cleland, D.T., Gallegos, J., Harris, R., Holm, R., Topik, C., Williamson, A., 1999. The use of ecological classification in management. In: Szaro, R.C. (Ed.), *Ecological Stewardship: A Common Reference for Ecosystem Management*, vol. 2, pp. 395–430.
- CBD, 2009. Azores Scientific Criteria and Guidance for Identifying Ecologically or Biologically Significant Marine Areas and Designing Representative Networks of Marine Protected Areas in Open Ocean Waters and Deep Sea Habitats. CBD, Canada, p. 11.
- CBD, <http://www.cbd.int/doc/decisions/cop-10/cop-10-dec-02-en.pdf>, 2010. Decision adopted by the Conference of the Parties to the Convention on Biological Diversity at its Tenth Meeting. X/2. Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets.
- CBD, 2012. Report on the Western South Pacific Workshop to Facilitate Description of Ecologically and Biologically Significant Areas, Nadi, Fiji, November 2011.
- Clark, M.R., 2009. Deep-sea seamount fisheries: a review of global status and future prospects. *Latin American Journal of Aquatic Resources* 37, 501–512.
- Clark, K.R., Gorley, R.N., 2006. PRIMER v6. Plymouth Marine Laboratory.
- Clark, M.R., Roberts, C.D., 2008. Fish and Invertebrate Biodiversity on the Norfolk Ridge and Lord Howe Rise, Tasman Sea (NORFANZ voyage, 2003). *Aquatic Environment and Biodiversity Report No. 28*, 131 p.
- Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K.I., Rogers, A.D., O'Hara, T.D., White, M., Shank, T.M., Hall-Spencer, J., 2010a. The ecology of seamounts: structure, function, and human impacts. *Annual Review of Marine Science* 2, 253–278.
- Clark, M.R., Althaus, F., Williams, A., Niklitschek, E., Menezes, G., Hareide, N.-R., Sutton, P., O'Donnell, C., 2010b. Are deep-sea fish assemblages globally homogenous? Insights from seamounts. *Marine Ecology* 31 (suppl. 1), 39–51.
- Clark, M.R., Watling, L., Rowden, A.A., Guinotte, J.M., Smith, C.R., 2010a. A global seamount classification to aid the scientific design of marine protected area networks. *Journal of Ocean and Coastal Management* 54, 19–36.
- Clark, M.R., Schlacher, T.A., Rowden, A.A., Stocks, K.I., Consalvey, M., 2012. Science priorities for seamounts: research links to conservation and management. *PLoS ONE* 7 (1), e29232. <http://dx.doi.org/10.1371/journal.pone.0029232>.
- Collins, M.A., Bailey, D.M., Ruxton, G.D., Priede, I.G., 2005. Trends in body size across an environmental gradient: a differential response in scavenging and non-scavenging demersal deep-sea fish. *Proceedings of the Royal Society, B* 272, 2051–2057.
- Davies, A., Guinotte, J.M., 2011. Global habitat suitability for framework-forming cold-water corals. *PLoS ONE* 6 (4), e18483. <http://dx.doi.org/10.1371/journal.pone.0018483>.
- Davies, A., Roberts, J.M., Hall-Spencer, J.M., 2007. Preserving deep-sea natural heritage: emerging issues in offshore conservation and management. *Biological Conservation* 138, 299–312.
- Dunstan, P.K., Clark, M.R., Guinotte, J., O'Hara, T., Niklitschek, E., Rowden, A.A., Schlacher, T., Tsuchida, S., Watling, L., Williams, A., 2011. Identifying Ecologically and Biologically Significant Areas on Seamounts. IUCN, Gland, Switzerland, 14 pp.
- Ebbe, B., Billett, D., Brandt, A., Ellingsen, K., Glover, A., Keller, S., Malyutina, M., Martinez Arbizu, P., Molodtsov, T., Rex, R., Smith, C., Tselepidis, A., 2010. Diversity of Abyssal Marine Life. In: *Life in the World's Oceans*. Blackwell, pp. 139–160.
- Ekman, S., 1953. *Zoogeography of the Sea*. Sidgwick and Jackson, London.
- Emery, W.J., Meincke, J., 1986. Global water masses: summary and review. *Oceanologica Acta* 9, 383–391.
- Etter, R.J., Rex, M.A., Chase, M.R., Quattro, J.M., 2005. Population differentiation decreases with depth in deep-sea bivalves. *Evolution* 59, 1479–1491.
- FAO, 2009. *International Guidelines for the Management of Deep-sea Fisheries in the High Seas*. FAO, Rome, 73 p.
- Forbes, E., Godwin-Austen, R., 1859. *The Natural History of the European Seas. Outlines of the Natural History of Europe*. John Van Voorst, London (reprinted 1977).
- Francis, M.P., Hurst, R.J., McArdle, B.H., Bagley, N.W., Anderson, O.F., 2002. New Zealand demersal fish assemblages. *Environmental Biology of Fishes* 65, 215–234.
- Fujii, T., Jamieson, A.J., Solan, M., Bagley, P.M., Priede, I.G., 2010. A large aggregation of liparids at 7703 m depth and a reappraisal of the abundance and diversity of hadal fish. *Bioscience* 60, 506–515.
- Gage, J.D., Tyler, P.A., 1991. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, Cambridge, UK.
- Gheerardyn, H., Veit-Köhler, G., 2009. Diversity and large-scale biogeography of Paramesochridae (Copepoda, Harpacticoida) in South Atlantic abyssal plains and the deep Southern Ocean. *Deep-Sea Research I* 56, 1804–1815.
- Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L., Shearer, M., 2002. Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. *Marine Ecology Progress Series* 240, 157–170.
- GOBI, www.gobi.org, 2010. Global Ocean Biodiversity Initiative: Working Towards High Seas Conservation. IUCN, BFE, 21 p.
- Grassle, J.F., Sanders, H.L., 1973. Life histories and the role of disturbance. *Deep-Sea Research* 20, 643–659.
- Grigg, R.W., Hey, R., 1992. Palaeoceanography of the tropical eastern Pacific Ocean. *Science* 255, 172–178.
- Hansell, D.A., Whitledge, T.E., Goering, J.J., 1993. Patterns of nitrate utilization and new production over the Bering–Chukchi shelf. *Continental Shelf Research* 13, 601–627.
- Harris, P.T., Whiteway, T., 2009. High seas marine protected areas: benthic environmental conservation priorities from a GIS analysis of global ocean biophysical data. *Ocean and Coastal Management* 52, 22–38.
- Jamieson, A.J., Fujii, T., Mayor, D.J., Solan, M., Priede, I.G., 2010. Hadal trenches: the ecology of the deepest places on Earth. *Trends in Ecology and Evolution* 25, 190–197.
- Jamieson, A.J., Kilgallen, N.M., Rowden, A.A., Fujii, T., Horton, T., Loerz, A.-N., Kitazawa, K., Priede, I.G., 2011. Bait-attending fauna of the Kermadec Trench, SW Pacific Ocean: evidence for an ecotone across the abyssal-hadal transition zone. *Deep-Sea Research I* 58, 49–62.
- Johnston, P.A., Santillo, D., 2004. Conservation of seamount ecosystems: application of a marine protected areas concept. *Archives of Fishery and Marine Research* 51, 305–319.
- Kirkegaard, J.B., 1995. Bathyal and abyssal Polychaeta (errant species). *Galathea Report* 17, 7–56.
- Knudson, J., 1970. The systematics and biology of the abyssal and hadal Bivalvia. *Galathea Report* 11, 7–236.
- Koslow, T., 2007. *The Silent Deep, the Discovery, Ecology and Conservation of the Deep Sea*. University of Chicago Press, Chicago.
- Koslow, J.A., Bulman, C.M., Lyle, J.M., 1994. The mid-slope demersal fish community off south-eastern Australia. *Deep-Sea Research I* 41, 113–141.
- Krylova, E.M., 2006. Bivalves of seamounts of the northeastern Atlantic. Part I. In: Mironov, A.N., Gebruk, A.V., Southward, A.J. (Eds.), *Biogeography of the North Atlantic Seamounts*. KMK Scientific Press, Ltd., Moscow, pp. 76–95.
- Kussakin, O.G., 1973. Peculiarities of the geographical and vertical distribution of marine isopods and the problem of deep sea fauna origin. *Marine Biology* 23, 19–34.
- Lampitt, R.S., Antia, A.N., 1997. Particle flux in deep seas: regional characteristics and temporal variability. *Deep-Sea Research I* 44, 1377–1403.
- Levin, L.A., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanography and Marine Biology Annual Review* 41, 1–45.
- Levin, L.A., 2005. Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. *Oceanography and Marine Biology: An Annual Review* 43, 1–46.
- Levin, L.A., Sibuet, M., 2012. Understanding continental margin biodiversity: a new imperative. *Annual Review of Marine Science* 4, 79–112.
- Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics* 32, 51–93.
- Linse, K., Huw, J.G., David, K.A., Barnes, A.C., 2006. Biodiversity and biogeography of Antarctic and sub-Antarctic Mollusca. *Deep sea Research II* 53, 985–1008.
- Lomolino, M.V., Riddle, B.R., Whittaker, R.J., Brown, J.H., 2010. *Biogeography*, fourth ed. Sinauer Associates, Inc.
- Longhurst, A., 2007. *The Ecological Geography of the Sea*, second ed. Elsevier.
- Lutz, M.J., Caldeira, K., Dunbar, R.B., Behrenfeld, M.J., 2007. Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. *Journal of Geophysical Research* 112, C10011. <http://dx.doi.org/10.1029/2006JC003706>.
- McClain, C.R., Lundsten, L., Barry, J., DeVogelaere, A., 2010. Bathymetric patterns in diversity, abundance and assemblage structure on a northeast Pacific seamount. *Marine Ecology* 31 (Suppl. 1), 14–25.
- Menzies, R.J., George, R.Y., Rowe, G.T., 1973. *Abyssal Environment and Ecology of the World Oceans*. John Wiley and Sons, New York.
- Mironov, A.N., Gebruk, A.V., 2006. Biogeography of the Reykjanes Ridge, the northern Atlantic. In: Mironov, A.N., Gebruk, A.V., Southward, A.J. (Eds.), *Biogeography of the North Atlantic Seamounts*. KMK Scientific Press, Ltd., Moscow, pp. 6–21.
- Mironov, A.N., Gebruk, A.V., Southward, A.J. (Eds.), 2006. *Biogeography of the North Atlantic Seamounts*. KMK Scientific Press, Ltd., Moscow.
- Molodtsova, T., 2006. Black corals (Antipatharia: Anthozoa: Cnidaria) of the northeastern Atlantic. In: Mironov, A.N., Gebruk, A.V., Southward, A.J. (Eds.), *Biogeography of the North Atlantic Seamounts*. KMK Scientific Press, Ltd., Moscow, pp. 141–151.
- Monniot, F., 1979. Faunal affinities among abyssal Atlantic basins. *Sarsia* 64, 93–95.
- Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. *Deep-Sea Research* 34, 165–184.
- Murray, J., Hjort, J., 1912. *The Depths of the Ocean*. Macmillan, London.
- Nozawa, F., Kitazato, H., Tsuchiya, M., Gooday, A.J., 2006. 'Live' benthic foraminifera at an abyssal site in the equatorial Pacific nodule province: abundance, diversity and taxonomic composition. *Deep-Sea Research I* 53, 1406–1422.
- O'Driscoll, K.T.A., Kamenkovich, V., 2009. Dynamics of the Indonesian seas circulation. Part I. the influence of bottom topography on temperature and salinity distributions. *Journal of Marine Research* 67, 119–157.
- O'Hara, T.D., Rowden, A.A., Bax, N.J., 2011. A southern hemisphere bathyal fauna is distributed in latitudinal bands. *Current Biology* 21, 226–230.
- Parin, N.V., Mironov, A.N., Nesin, K.N., 1997. Biology of the Nazca and Sala y Gomez submarine ridges, an outpost of the Indo-West Pacific fauna in the eastern Pacific Ocean: composition and distribution of the fauna, its communities and history. *Advances in Marine Biology* 32, 145–242.
- PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans), www.piscoweb.org, 2007. *The Science of Marine Reserves*, second ed. International version, 22 p.
- Probert, P.K., Christiansen, B., Gjerde, K.M., Gubbay, S., Santos, R.S., 2007. Management and conservation of seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), *Seamounts: Ecology, Fisheries, and Conservation*. Blackwell Fisheries and Aquatic Resources Series, vol. 12. Blackwell Publishing, Oxford, pp. 442–475.

- Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.-A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R., Van Dover, C.L., 2011. Man and the last great wilderness: human impact on the deep sea. *PLoS ONE* 6 (7), e22588. <http://dx.doi.org/10.1371/journal.pone.0022588>.
- Rex, M.A., Etter, R.J., 2010. Deep-Sea Biodiversity: Pattern and Scale. Harvard University Press.
- Rex, M.A., McClain, C.R., Johnson, N.A., Etter, R.J., Allen, J.A., Bouchet, P.A., Warén, A., 2005. A source-sink hypothesis for abyssal biodiversity. *American Naturalist* 165, 163–178.
- Roberts, C.M., 2002. Deep impact: the rising toll of fishing in the deep sea. *Trends in Ecology and Evolution* 17, 242–245.
- Roff, J.C., Taylor, M.E., Laughren, J., 2003. Geophysical approaches to the classification, delineation and monitoring of marine habitats and their communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13, 77–90.
- Rogers, A.D., Baco, A., Griffiths, H., Hart, T., Hall-Spencer, J.M., 2007. Corals on seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), *Seamounts: Ecology, Fisheries, and Conservation*. Blackwell Fisheries and Aquatic Resources Series, vol. 12. Blackwell Publishing, Oxford, UK, pp. 141–169.
- Rowden, A.A., Dower, J.F., Schlacher, T.A., Consalvey, M., Clark, M.R., 2010. Paradigms in seamount ecology: fact, fiction, and future. *Marine Ecology* 31 (Suppl. 1), 226–239.
- Ruhl, H.A., Ellena, J.A., Smith, K.L., 2008. Connections between climate, food limitation, and carbon cycling in abyssal sediment communities. *Proceedings of the National Academy of Sciences* 105, 17006–17011.
- Sibuet, M., 1979. Distribution and diversity of asteroids in Atlantic abyssal basins. *Sarsia* 64, 85–91.
- Sibuet, M., Olu, K., 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Research II* 45, 517–567.
- Smith, C.R., Rabouille, C., 2002. What controls the mixed-layer depth in deep-sea sediments? The importance of POC flux. *Limnology and Oceanography* 47, 418–426.
- Smith, W.H.F., Sandwell, D.T., 1997. Global sea floor topography from satellite altimetry and ship depth soundings. *Science* 277 (5334), 1956–1962.
- Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Martinez Arbizu, P., 2008a. Abyssal food limitation, ecosystem structure and climate change. *Trends in Ecology and Evolution* 23, 518–528.
- Smith, C.R., Levin, L.A., Koslow, A., Tyler, P.A., Glover, A.G., 2008b. The near future of the deep-sea floor ecosystems. In: Polunin, N.V.C. (Ed.), *Aquatic Ecosystems: Trends and Global Prospects*. Cambridge University Press, New York, pp. 334–352.
- Springer, A.M., McRoy, C.P., Flint, M.V., 1996. The Bering Sea green belt: shelf-edge processes and ecosystem production. *Fisheries Oceanography* 5, 205–233.
- Stocks, K.I., Hart, P.J.B., 2007. Biogeography and biodiversity of seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), *Seamounts: Ecology, Fisheries, and Conservation*. Blackwell Fisheries and Aquatic Resources Series, vol. 12. Blackwell Publishing, Oxford, UK, pp. 255–281.
- Stramma, L., Schmidtke, S., Levin, L.A., Johnson, G.C., 2010. Ocean oxygen minima expansions and their biological impacts. *Deep Sea Research I* 57, 587–595.
- Sutherland, W.J., Aveling, R., Bennun, L., Chapman, E., Clout, M., Cote, I.M., Depledge, M.H., et al., 2011. A horizon scan of global conservation issues for 2011. *Trends in Ecology and Evolution* 26, 10–16.
- Thresher, R.E., Adkins, J., Fallon, S.J., Gowllett-Holmes, K., Althaus, F., Williams, A., 2011. Extraordinarily high biomass benthic community on Southern Ocean seamounts. *Nature Scientific Reports* 119, 1–5. <http://dx.doi.org/10.1038/srep00119>.
- Tittensor, D.P., Baco-Taylor, A.R., Brewin, P., Clark, M.R., Consalvey, M., Hall-Spencer, J., Rowden, A.A., Schlacher, T., Stocks, K., Rogers, A.D., 2009. Predicting global habitat suitability for stony corals on seamounts. *Journal of Biogeography* 36, 1111–1128.
- Tomczak, M., Godfrey, J.S., 1994. *Regional Oceanography: An Introduction*. Pergamon, Oxford.
- Tracey, D.M., Rowden, A.A., Mackay, K.A., Compton, T., 2011. Habitat-forming cold-water corals show affinity for seamounts in the New Zealand region. *Marine Ecology Progress Series* 430, 1–22.
- UNESCO, 2009. Global Open Oceans and Deep Seabed (GOODS) – Biogeographic Classification. Paris, UNESCO, IOC Technical Series No. 84.
- Valentine, J.W., 1973. *Evolutionary Paleogeology of the Marine Biosphere*. Prentice-Hall.
- Van Dover, C.L., 2000. *The Ecology of Deep-sea Hydrothermal Vents*. Princeton University Press, Princeton.
- Vaquar-Sunyer, R., Duarte, C.M., 2009. Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences (USA)* 105 (40), 15452–15457.
- Veilleux, J., Sarrazin, J., Gooday, A.J., Galeron, J., Caprais, J.-C., Vangriesheim, A., Etoubleau, J., Christand, J.R., Juniper, S.K., 2007. Ferromanganese nodule fauna in the Tropical North Pacific Ocean: species richness, faunal cover and spatial distribution. *Deep-Sea Research I* 54, 1912–1935.
- Vinogradova, N.G., 1979. The geographical distribution of the abyssal and hadal (ultra-abyssal) fauna in relation to the vertical zonation of the ocean. *Sarsia* 64, 41–49.
- Vinogradova, N.G., 1997. Zoogeography of the abyssal and hadal zones. *Advances in Marine Biology* 32, 325–387.
- Watling, L., 2009. Biogeographic provinces in the Atlantic deep sea determined from cumacean distribution patterns. *Deep-Sea Research II* 56, 1747–1753.
- Wolff, T., 1962. The systematics and biology of the bathyal and abyssal Isopoda Asellota. *Galathea Report* 6, 1–320.
- Wolff, T., 1970. The concept of the hadal or ultra-abyssal fauna. *Deep-Sea Research* 17, 983–1003.
- Yool, A., Martin, A.P., Fernandez, C., Clark, D.R., 2007. The significance of nitrification for oceanic new production. *Nature* 447, 999–1002.
- You, Y., 2003. The pathway and circulation of North Pacific Intermediate Water. *Geophysical Research Letters* 30 (24), 2291. <http://dx.doi.org/10.1029/2003GL018561>.
- You, Y., 2010. Frontal densification and displacement: a scenario of North Pacific Intermediate Water formation. *Deep-Sea Research II* 57, 1171–1176.
- Zezina, O.N., 1973. Biogeographical division of the benthic area of the ocean by brachiopods. In: *Proceedings of the All-Union Research Institute of Marine Fisheries and Oceanography (Trudy VNIRO)*, vol. 84, pp. 166–180 (in Russian, English abstract).
- Zezina, O.N., 1997. Biogeography of the bathyal zone. *Advances in Marine Biology* 32, 389–426.
- Zintzen, V., Roberts, C.D., Clark, M.R., Williams, A., Althaus, F., Last, P.R., 2011. Composition, distribution and regional affinities of the deepwater ichthyofauna of the Lord Howe Rise and Norfolk Ridge, southwest Pacific Ocean. *Deep-Sea Research II* 58, 933–947.