Upper Bathyal Pacific Ocean biogeographic provinces from octocoral distributions

Natalie Summers [a,b,*], Les Watling [a]

[a] *University of Hawaii at Mānoa, Department of Biology, 2538 McCarthy Mall, Honolulu, HI 96822, United States*
[b] *Norwegian University of Science and Technology (NTNU), Department of Biology, Trondheim, Norway*

ABSTRACT

Biogeographical classification schemes such as the Marine Ecoregions of the World (MEOW) have been developed for continental shelf depths. The lack of faunal data in the deep sea has led to the development of biogeographical units based on oceanographic characteristics. The aim of this study was to propose biogeographical schemes for the Upper Bathyal (200–1000 m) across the Pacific Ocean using octocoral distributions. We retrieved over 200 000 octocoral data records from the Deep Sea Coral Data Portal (DSCDP), Ocean Biogeographic Information System (OBIS), Tropical Deep-Sea Benthos program (French National Museum of Natural History), Queensland Museum from the CIDARIS expeditions, and records retrieved from the Siboga expedition reports. We used cluster analysis to examine octocoral distributions against four different biogeographical classification schemes. The classification schemes produced mostly concordant patterns with three major faunal distribution barriers: the North Pacific Current isolates the subarctic units by creating a steep temperature gradient; the Subantarctic Front separates the Subantarctic from the rest of the Pacific; and the East Pacific Barrier separates the East Pacific from the Central and West Pacific. Two other smaller but distinct provinces are the Indo-Pacific where Lower Bathyal genera are found in the Upper Bathyal, and Torres Strait/Coral Sea characterised by mesophotic genera. We propose 12 biogeographic provinces across the Pacific Ocean Upper Bathyal region from 200 to 1000 m depth based on octocoral distributions. The main driver for these units seems to be temperature, a defining feature of water masses. These units could potentially be subdivided into smaller regions based on habitat. Additionally, the clustering of Ecological Marine Units (EMUs) provides evidence that the Upper Bathyal should in certain regions be divided vertically into two depth zones based on water masses.

1. Introduction

Biogeographic classification schemes have been developed to help manage the oceans. For example Large Marine Ecosystems (LME) are based on bathymetry, hydrography, productivity, and trophically connected populations (Sherman et al., 1990), whereas major fisheries areas defined by the Fisheries and Agricultural Organization (FAO) considers the distribution of commercially important organisms. In contrast, the concept of biogeographical provinces or other units often take into account the shared history of organisms living in the same area (Valentine 1973), as well as a certain level of endemism, generally >10%, as proposed by Briggs (1974). Based on the latter approach, Spalding et al. (2007) developed Marine Ecoregions of the World (MEOW) for coastal

and shelf regions with 232 ecoregions nested in 62 provinces within 12 realms. The smallest spatial unit in the system was defined as being distinct from adjacent units by having relatively homogeneous internal species composition. This scheme is limited to the shelf and coastal areas with the suggested lower boundary being the 200 m isobath, which is a widely used demarcation of the shelf edge and start of the Bathyal Zone.

Few attempts have been made to define biogeographic regions for the deeper seabed. The Bathyal Zone, extending from approximately 200–3500 m, occupies 26% of the world's ocean and is where species richness of megafauna reaches its maximum at least in some areas (Rex and Etter, 2010; Watling et al., 2013; Zezina, 1997). One of the first attempts at developing a biogeographic scheme for this zone used data on brachiopods, resulting in a total of 19 geographic units from the shelf
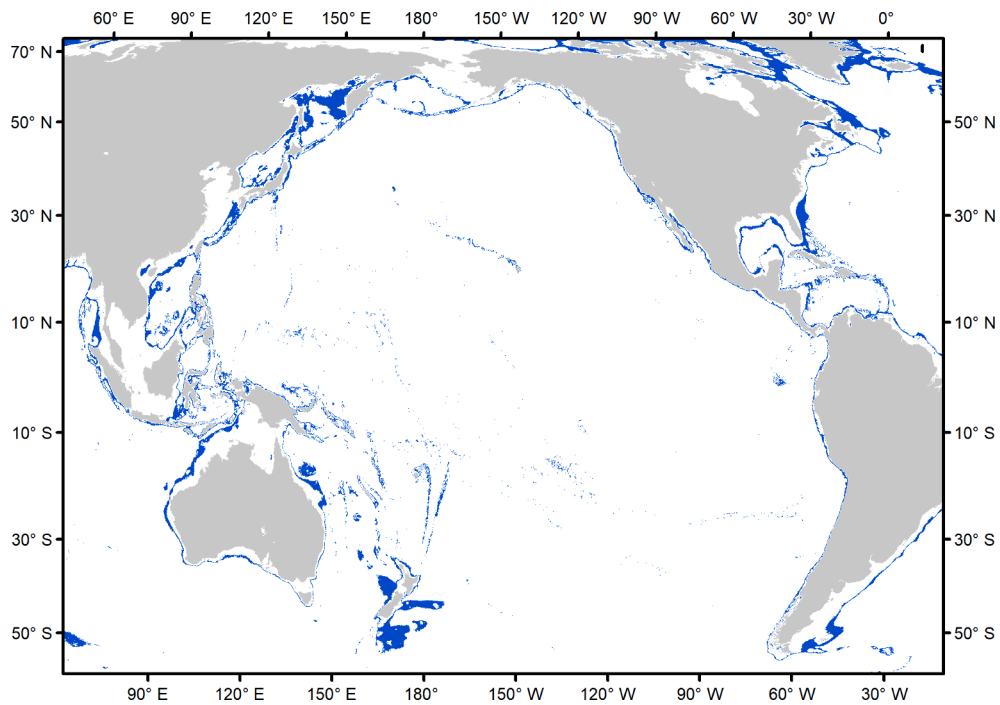

Fig. 1. Bathymetry of the Pacific Ocean showing the spatial extent of the Upper Bathyal (200–1000 m) in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
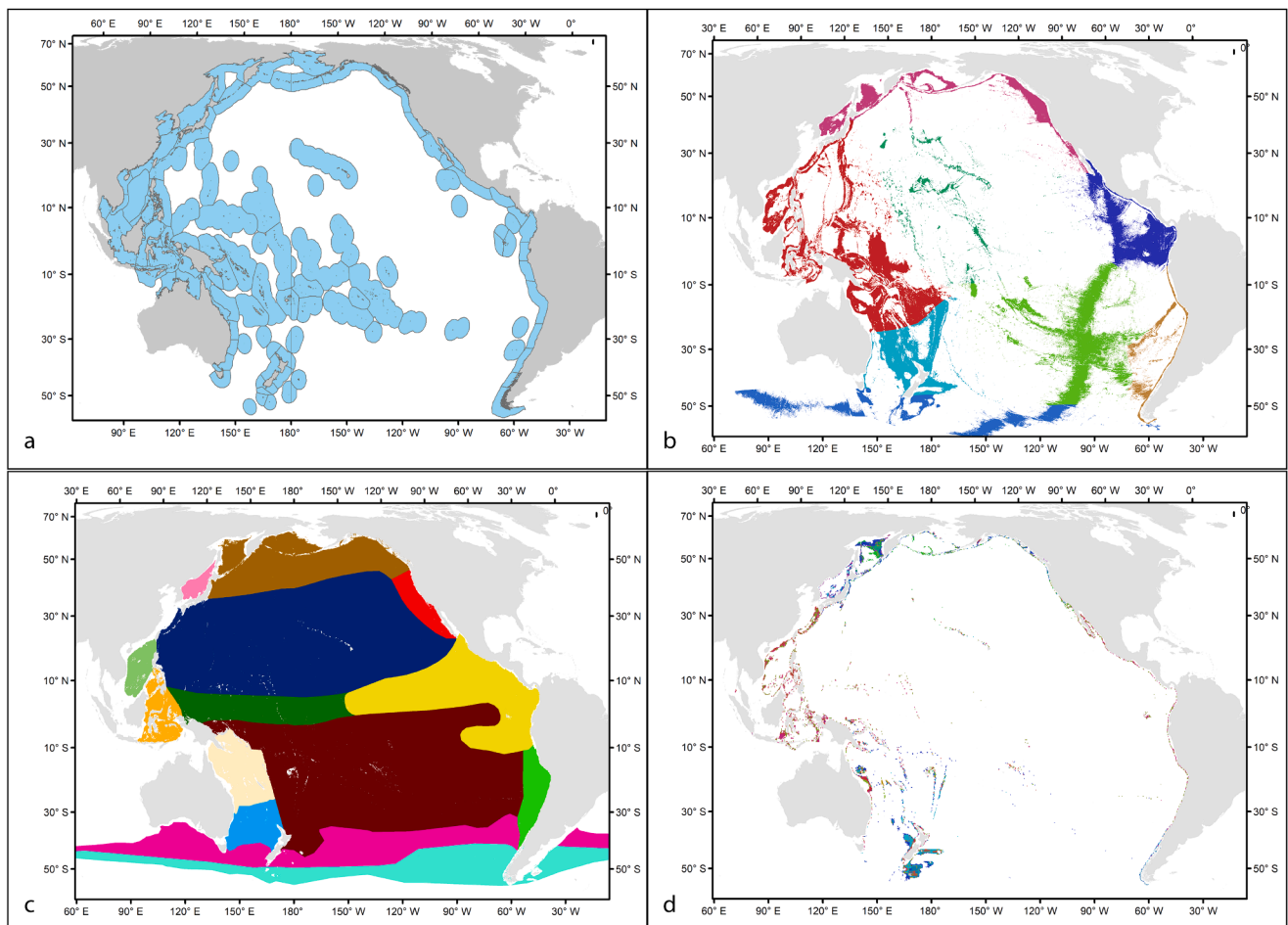

Fig. 2. a) Map of the main MEOW eco-regions in the Pacific (from Spalding et al., 2007); b) Proposed Lower Bathyal (801–3500 m) provinces of Watling et al. (2013); c) Mesopelagic ecoregions in the Pacific (Sutton et al., 2017); d) Upper Bathyal Ecological Marine Units (Sayre et al., 2017).
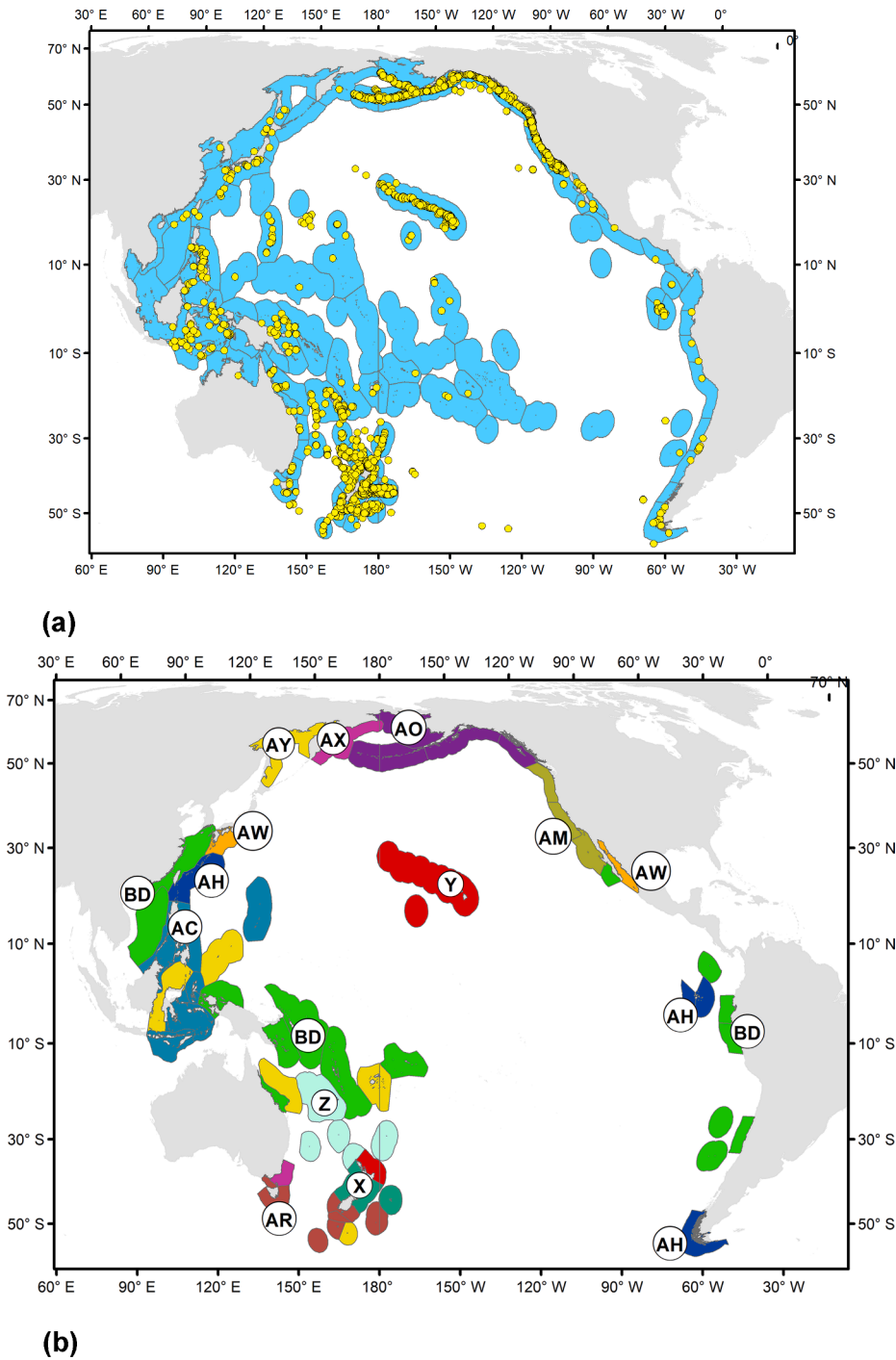
(a)

(b)

Fig. 3. a) Distribution of Upper Bathyal octocoral records plotted over the MEOW ecoregions. b) The location of the resulting groups. c) Hierarchical clustering of the MEOW Ecoregions using Sorensen's index of similarity based on genera of octocorals from the Upper Bathyal. Green lines represent significant region clusters where non-significant clusters have been collapsed (see supplemental, Figure S7 for un-collapsed dendrogram). Abbreviated groups contain more than one region. MEOW cluster groups are as follows: **BD**:*Vanuatu + Central and Southern Great Barrier Reef + Guayaquil + Magdalena Transition + Juan Fernandez and Desventuradas + Southern China + Cocos Islands + South China Sea Oceanic Islands + Solomon Sea + Solomon Archipelago + Papua + Samoa Islands + East China Sea + Central Peru + Central Chile* **AY**:*Campbell Island + Sea of Okhotsk + Sulawesi Sea/Makassar Strait + Coral Sea + Fiji Islands + West Caroline Islands* **AX**: *Cape Howe + Kamchatka Shelf and Coast* **AW**:*Central Kuroshio Current + Cortezian* **AR**:*Auckland Island + Bounty and Antipodes Islands + South New Zealand + Snares Island + Bassian + Macquarie Island* **AO**:*Gulf of Alaska + North American Pacific Fijordland + Eastern Bering Sea + Aleutian Islands* **AM**:*Oregon, Washington, Vancouver Coast and Shelf + Southern California Bight + Northern California* **AH**:*Channels and Fjords of Southern Chile + South Kuroshio + Western Galapagos Islands + Eastern Galapagos Islands* **AC**:*Lesser Sunda + Mariana Islands + Palawan/North Borneo + Halmahera + Banda Sea + Eastern Philippines* **Z**:*Kermadec Island + New Caledonia + Lord Howe and Norfolk Islands + Three Kings-North Cape* **Y**:*Northeastern New Zealand + Hawaii* **X**:*Central New Zealand + Chatham Island.* (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
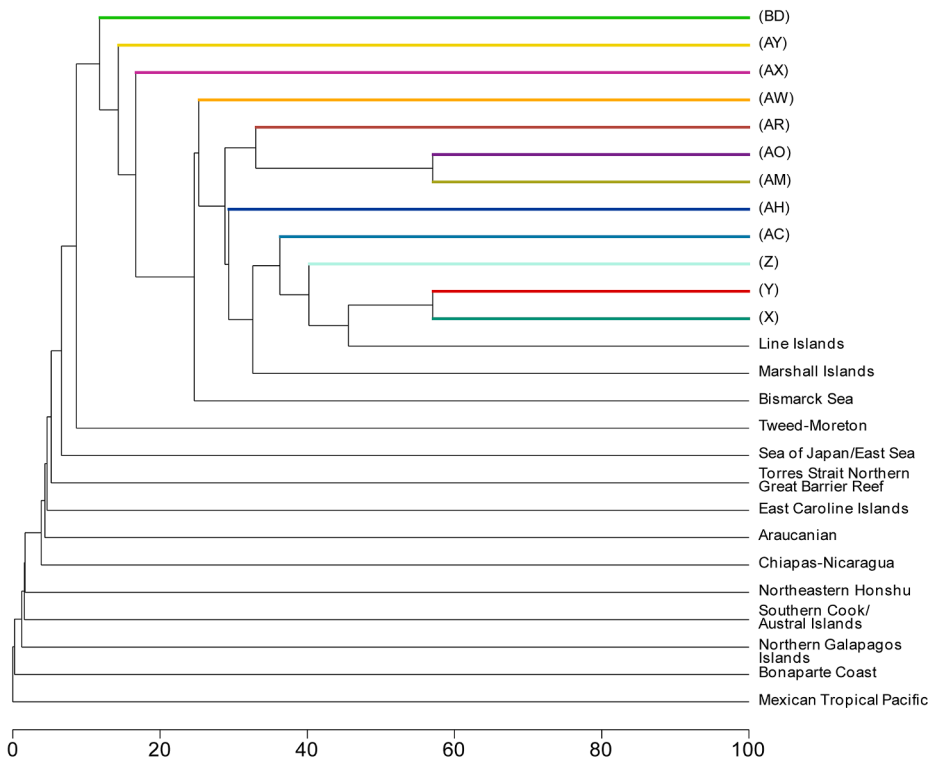
Fig. 3. (*continued*).

edge and upper parts of the slope (Zezina, 1997). Bathyal ophiuroid distributions in the South West Pacific (O'Hara et al., 2011) showed concordance with the brachiopod partitions suggested by Zezina (1997) providing evidence for the division of the Bathyal Zone into upper and lower units as noted by Watling et al. (2013), however, the latter authors did not analyse data from the Upper Bathyal. These proposed biogeographic schemes reveal that bio-units increase in area while decreasing in number with increasing depth (Watling et al., 2013; Zezina, 1997). More recently, Costello et al. (2017) conducted a global analysis using all taxa downloaded from OBIS to defined 30 provinces, however, they were not subdivided by depth. The resulting provinces were similar to the 33 mesopelagic regions proposed by Sutton et al. (2017) and were therefore likely driven by mesopelagic fauna.

Watling et al.'s (2013) approach to defining provinces was to define areas based on oceanographic characteristics assumed to be important for faunal distributions. For Lower Bathyal habitats from 800 to 3500 m, 14 provinces were proposed based on temperature, salinity, dissolved oxygen, and particulate organic carbon flux from surface waters. These variables were chosen because they were thought to have physiological effects on deep sea organisms thus limiting their distribution (Watling et al., 2013). Temperature is hypothesized to be important in setting the upper and lower depth limits of a species due to a combination of thermal and hydrostatic pressure thresholds (Somero et al. 2017), while particulate organic carbon (POC) flux is expected to limit distributions of deep-sea species as it controls food availability (Carney, 2005). The ocean floor at these depths is considered food limited, variation in POC flux is correlated with species turnover (Glover et al., 2002) and limits of distribution, while low POC flux has been found to set the lower depth limit of many deep-sea species (Carney, 2005). In addition, temperature-salinity combinations are used to characterise different water masses which is important when determining connectivity of species and their patterns of dispersal (Carney, 2005). Using a similar approach but with the additional variables of nitrate, phosphate and silicate, a three-dimensional Ecological Marine Units (EMU) scheme was proposed comprising 37 global units (Sayre et al., 2017). Both schemes propose

that these oceanographic characteristics will influence faunal distributions, however, this hypothesis needs to be tested. For example, in the mesopelagic, Reygondeau et al. (2018) defined 13 biogeochemical provinces. However, when faunal data was included in the analysis, (Sutton et al., 2017) 33 provinces were defined. Discrete areas within each biogeochemical province were often separated geographically limiting the faunal connectivity.

Technological advances in the past half-century, such as the development of ROVs and manned submersibles, are allowing scientists to explore even the most rugged terrain in the deep sea where samples were previously unattainable. High-definition video and other imagery is available for the Pacific from along the Aleutian Ridge, Tasmania, New Zealand, Hawaiian Ridge, and Indo-Pacific (Indonesia) in addition to trawl and dredge samples from New Caledonia, Louisville Ridge (Southwest Pacific), and areas around Japan (some of which are summarised in Watling et al. 2011). Thus, we now have a more extensive dataset of deep-sea octocoral distributions, Octocorals make ideal subjects for biogeographic work that relies predominantly on imagery. They are large enough to image easily, have characters that can be seen using relatively modern imaging technology so that identification to genus level is possible in most cases, and live attached or anchored in the substrate for long periods of time, often on the order of hundreds of years (Etnoyer et al., 2006; Watling et al., 2011). Octocorals can also have an important ecological role as their structure enhances habitat complexity that benefits other deep-sea species. Black corals and sponges can also be used in this way, but our knowledge of the taxonomy of those groups is not as detailed as it is for octocorals. Despite these advances, there is still insufficient data to do a full biogeographical analysis for the deep-sea (such as that done by Spalding et al. 2007 for the shelf areas). However, the available data can be used to test current proposed biogeographical schemes and compare emerging patterns.

Delimitation of the Upper Bathyal varies among studies and is likely to change regionally based on topography and hydrographic conditions. Depth limits based on major changes in species composition have been recorded in several studies (Gage and Tyler, 1991; Carney, 2005; Yeh
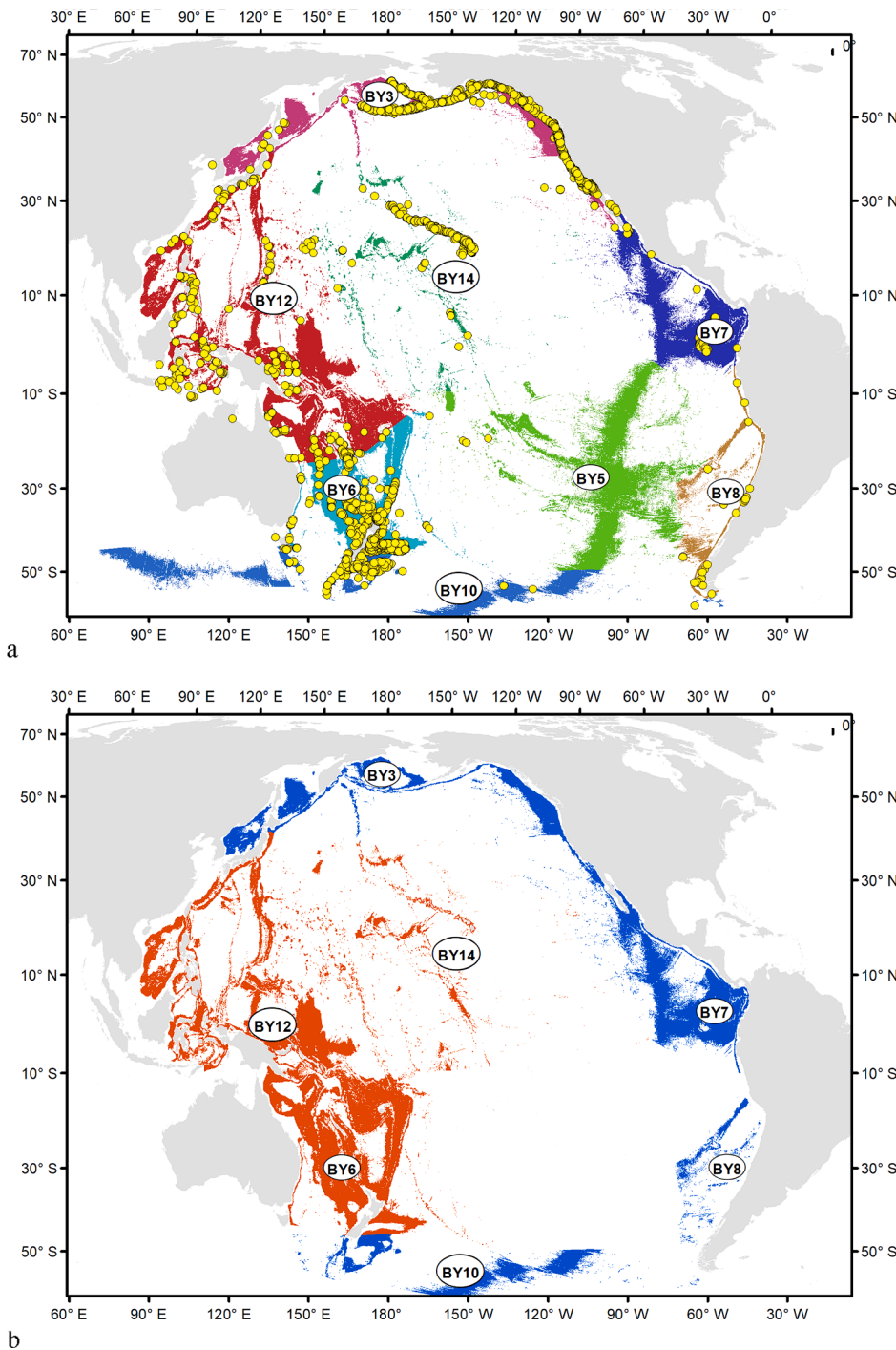
Fig. 4. a) Octocoral records plotted over proposed Lower Bathyal provinces from Watling et al. (2013); b) distribution of Upper Bathyal octocorals over the Lower Bathyal Provinces from; c) hierarchical clustering of the Lower Bathyal provinces using Sorensen's index of similarity based on genera of Upper Bathyal octocorals. Dashed red lines on tree represent non-significant clustering and solid lines represent significant clusters (SIMPROF test with 5% significance). A significant division is seen separating the East Pacific group (orange): 3 – North Pacific; 7- Cocos Plate; 8-Nazca Plate; 10- Subantarctic and The West Pacific (blue): 6- New Zealand-Kermadec; 12- West Pacific; 14-North Pacific. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and Drazen, 2009). Analysis of demersal scavenging communities of the Hawaiian Islands show faunal transitions at depths of 250–500 m, 1000 m and between 1500 and 3000 m (Yeh and Drazen, 2009). The MEOW scheme uses 200 m depth contour to define the lower shelf limit for ecoregions, provinces and realms (Spalding et al., 2007). In Watling et al (2013) the Lower Bathyal is defined as the region between 800 and 3500 m depth.

In this study, hierarchical cluster analysis of octocoral genera location data were used to test how well four different classification schemes represent the distributions of octocorals of the Upper Bathyal, which was not included in the analysis of Watling et al. (2013). We chose to use the MEOW (Spalding et al., 2007) and Lower Bathyal (Watling et al., 2013)

classifications as they represent the layers immediately above and below the Upper Bathyal. The Mesopelagic classification (Sutton et al., 2017) and EMU (Sayre et al., 2017) schemes both overlap with the Upper Bathyal and will give us information about the strength of benthic-pelagic coupling and whether the Upper Bathyal should be considered as a uniform layer. Some EMUs are distributed widely over the Pacific resulting in discrete areas being geographically separated with potentially few connections for faunal communities and little regard to water masses (Supplemental Figure S1). From these analyses we will propose a classification of the Upper Bathyal into some number of Provinces. We hypothesize that the Upper Bathyal provinces will be clusters of MEOW ecoregions that closely resemble the Lower Bathyal, perhaps showing
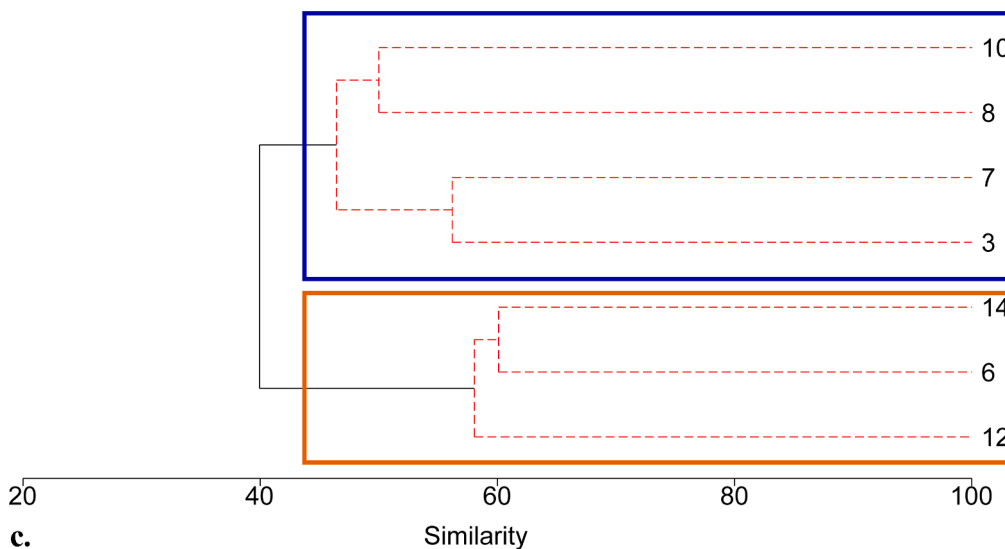
c.

connections that are evident in the Mesopelagic classification. We hypothesize that the EMUs will not be useful in defining biogeographical units based on faunal distributions.

2. Methods

2.1. Study area

The area of study covers the Pacific Ocean from the Aleutians in the north to south of New Zealand, and from 200 m to 1000 m depth (Fig. 1). The 200 m isobath has often been used as a proxy for the shelf edge (Spalding et al., 2007) and is used as the upper limit in this study. We chose to use 1000 m as the lower limit of the Upper Bathyal as there is a species composition shift around this depth (Carney, 2005; Quattrini et al., 2013, 2017). We acknowledge, however, that this lower depth limit may vary with latitude (Carney 2005).

2.2. Sources of octocoral data

Genera level data from online marine biological databases were retrieved and consolidated. The largest data sources were the Deep Sea Coral Data Portal (DSCDP) (NOAA) and OBIS (Ocean Biogeographic Information System, (OBIS, 2018) which provide information about diversity, distribution, and abundance of all marine organisms as well as physical and chemical environmental information. See Supplemental Table S2 for a complete list of datasets used and Supplemental Table S3 for the number of records for each genus. Some datasets were found in both OBIS and DSCDP. In such cases duplicates were removed from the OBIS dataset and kept in the DSCDP dataset. These were supplemented with data culled from the Siboga Expedition reports from 1899 to 1900 with 34 stations between 200 and 1000 m, records provided by the Queensland Museum from the CIDARIS expeditions as well as the Muséum national d'histoire naturelle (MNHN) in Paris (https://expeditions.mnhn.fr/) data from ten different dredging expeditions (BIO-PAPUA, EXBODI, KANACONO, KANADEEP, KAVIENG, MADEEP, PAPUA NIUGINI, TARASOC, TERRASSES and Zhongsha). In the latter case, all specimens were examined and generic designations tentatively assigned by us or colleagues. The scientific names were checked using the Taxize package 0.9.4 (Chamberlain et al., 2018) in R (R Team 2017) which compares lists of scientific names to accepted taxonomic names from the World Register of Marine Species (WoRMS). In the end, however, we have to acknowledge that even though most of the genera were assigned to specimens by us or other highly qualified octocoral taxonomists, some genera assignments might not be correct since many specimens were identified from images and others, such as those from the MNHN have not been examined in detail. Discrepancies stemming from errors in the databases themselves (such as mistakes in the latitude and longitude) when found did not affect our results. We are therefore confident that any remaining errors of this type are inconsequential.

2.3. Biogeographical classification schemes

Octocoral distributions were compared with four different biogeographical classification schemes. The MEOW classification in the Pacific (Spalding et al. 2007) from the coast to 200 m depth (immediately above the Upper Bathyal), consisted of 72 ecoregions (Fig. 2a) containing at least one octocoral genus (Supplemental Table S4). Watling et al. (2013) defined eight Lower Bathyal Provinces from 800 to 3500 m in the Pacific (Fig. 2b). The Southeast Pacific Ridge (BY5) was removed from our analysis as most of the ridges in that province are too deep resulting in only 2 genera at Upper Bathyal depths. Sutton et al. (2017) defined 14 Mesopelagic Provinces in the Pacific (Fig. 2c) based on daytime mesopelagic faunal communities as well as environmental proxies derived from the MEOW ecoregions (Sutton et al., 2017). The three-dimensional EMU classification was based on temperature, salinity, dissolved oxygen, nitrate, phosphate, and silicate data obtained from the 2013 World Ocean Atlas. An ocean point mesh at ¼° × ¼° horizontally and 102 depth zones from 5 m to 5500 m was created then clustered together resulting in 37 EMUs. This is the only scheme that divides the Upper Bathyal into several depth zones (Sayre et al., 2017). The Ecological Marine Units V1. Pacific Ocean was downloaded from ESRI website. From this dataset, we selected all points labelled as "bottom" or "both" in Special Class column which allowed us to get only the bottom layer of units. We then selected units that were in the upper bathyal depth range (200–1000 m) by removing all those whose "top" depth were deeper than 1000 m and those whose "bottom" depth were above 200 m. Overlaying the selected EMUs with the ETOPO-1 Bathymetry confirmed that our selection was correct. We then created a square "buffer" around each point of 0.125 decimal degrees (to get the 1/4-degree polygons as described by Sayre et al. 2017). Thus, we found seventeen bottom EMUs in the Pacific Upper Bathyal (200 m-100 m deep). EMUs 3, 13, 36 and 37 are described as bathypelagic, and EMUS 8, 10, 11, 14, 19, 21, 24, 25, 26, 30, 31, 33 and 35 are described as epipelagic.
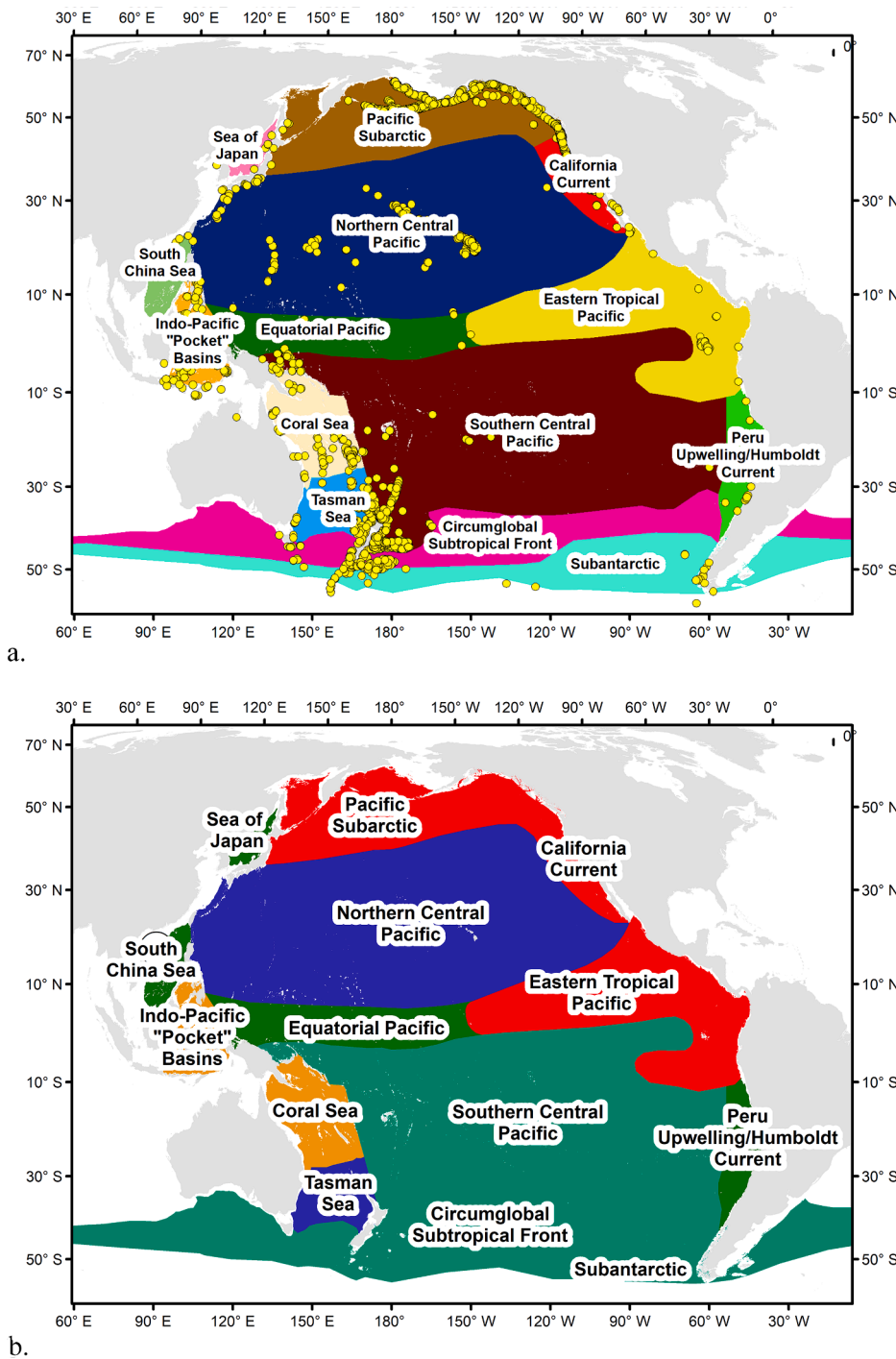
Fig. 5. a) Proposed mesopelagic biogeographic units from Sutton et al. (2017) with octocoral record locations plotted in yellow; b) classification of octocoral records plotted by Mesopelagic provinces from cluster analysis in c), the hierarchical clustering of the mesopelagic provinces using Sorensen's index of similarity based on genera of octocorals. Dashed red lines on tree represent non-significant clustering and solid lines represent significant clusters (SIMPROF test with 5% significance). Two green boxes represent the clusters with the fewest octocoral occurrences (South China Sea, Equatorial Pacific, Sea of Japan and Peru Upwelling/Humboldt Current). These clusters are plotted in green in b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. Analysis

Octocoral occurrences for the Upper Bathyal were plotted over the biogeographic units for each scheme using Arc Map. For each scheme, units with no occurrences (see Supplemental 4 for tables of the number of genera found within each unit) were removed from the analysis. Octocorals were assigned to the units they were within for the analysis of MEOW (59 out of 72 ecoregions), and EMU (14 out of 17 units). For the Lower Bathyal (7 out of 8 provinces) and Mesopelagic classification scheme (14 units), octocorals were assigned to the units to which they were closest. Octocoral occurrences were transformed to "presence-absence" in Primer 6 to account for differences in sampling methods and

effort. Similarity of octocoral composition between different geographic units was computed using Sorensen's index, which compares taxon composition based on presence and gives more weight to shared taxa and to differences between genus-poor areas.

$$S_{jk} = 100[2a/(2a + b + c)]$$

S_{jk} = Sorensen's index comparing community composition in regions j and k

a = the number of taxa which are present in both j and k;

b = the number of taxa present only in j;

c = the number of taxa present only in k;

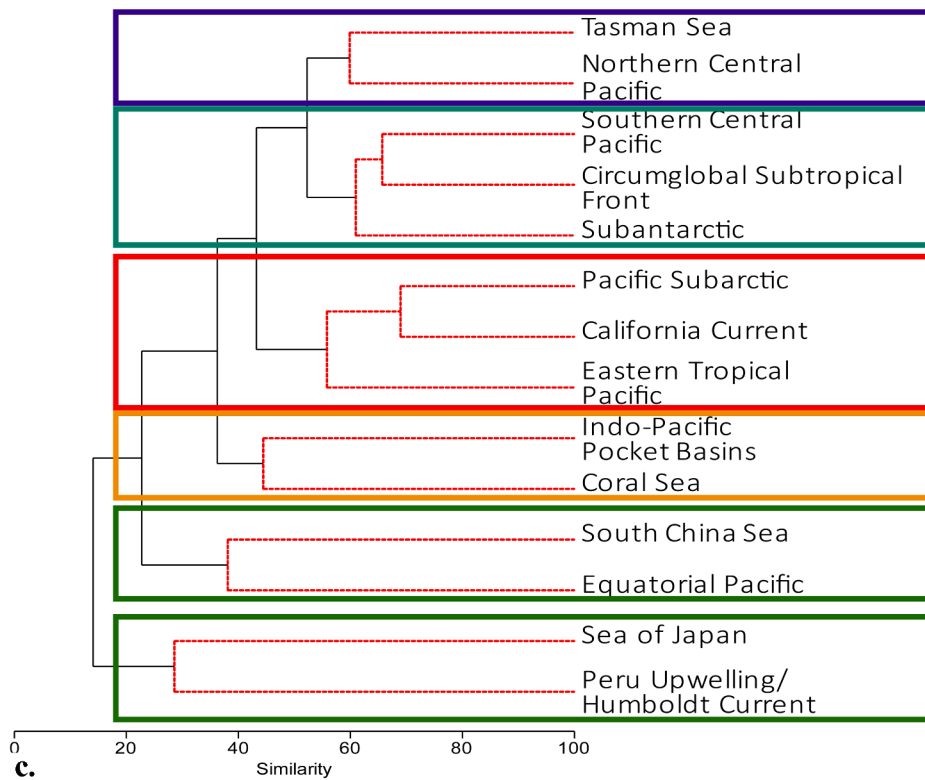A dendrogram was then constructed based on hierarchical clustering

to group similar units followed by a SIMPROF test to determine which clusters were significantly different from one another (Clarke & Gorley, 2006; Clarke & Warwick, 2001). Results from the four different classification scheme analyses were then compared to each other.

3. Results

Together, all data sources comprised over 200 000 records from 197 genera in the Pacific (Supplemental Table S2). The median depth of the total number of records was 629 m with 20 000–30 000 records within each 100 m depth interval except for 800–900 m which had about 48 000 octocoral records (Supplemental Figure S5). Data-poor areas were mostly in the North-West Pacific along the continental slopes of China and Japan and the South East Pacific Ocean along the South America slope. Out of the 207 genera found for the 200–1 000 m layer, the ten most common overall were *Heteropolypus, Funiculina, Swiftia, Umbellula, Paragorgia, Anthomastus, Halipteris, Corallium, Narella,* and *Plumarella.* These are all widely distributed genera (Supplemental Figure S6).

3.1. MEOW

Octocoral records clustered according to MEOW ecoregions formed 12 significant geographical groups (Fig. 3) b). In the North Pacific, two main groups appear with the most northern cluster including the Gulf of Alaska, North American Pacific Fjordland, Eastern Bering Sea and Aleutian Islands regions (designated as cluster AO) and a group along the North American slope off Oregon, Washington, Vancouver Coast and Shelf, Southern California Bight and Northern California (designated as cluster AM). In the West Pacific, the Central Kuroshio Current forms a cluster with the Cortezian region of the East Pacific (designated as cluster AW). Similarly, Lesser Sunda, Mariana Islands, Palawan/North Borneo, Halmahera Banda Sea, Eastern Philippines, (designated as cluster AC) forms a distinct Indo-Pacific group. In the South Pacific, Central New Zealand and Chatham Island (designated as cluster X) were

closely linked with a group consisting of Northeastern New Zealand and Hawaii (designated as cluster Y) as well as group Z consisting of Kermadec Island, New Caledonia, Lord Howe and Norfolk Islands, and Three Kings-North Cape. However, it differs from the South New Zealand group of Auckland Island, Bounty and Antipodes Islands, South New Zealand, Snares Island, and Bassian, Macquarie Island (designated as cluster AR). Other groups (such as cluster BD and individual units with little similarity to any others) represent the units with few widely distributed genera (Fig. 3).

3.2. Lower Bathyal provinces

Clustering of octocoral records from the Pacific by Lower Bathyal benthic provinces produced two distinct geographical groups. The East Pacific group combined North Pacific (BY 3), Cocos Plate (BY 7), Nazca Plate (BY 8), and Subantarctic provinces (BY 10) (Fig. 4). The West Pacific group combines West Pacific Province (BY 12) with the New Zealand-Kermadec province (BY 6).

3.3. Mesopelagic provinces

Clustering of octocoral records according to boundaries of the mesopelagic units produced four major groups. The North Pacific unit consisted of Pacific Subarctic, California Current, and Eastern Tropical Pacific. The Northern Central Pacific clustered with Tasman Sea. The southern Pacific group consisted of the Southern Central Pacific, Subantarctic and Circumglobal Subtropical Front. Both the Indo-Pacific Pocket Basin and the Coral Sea are distinct from all other regions. The South China Sea, Equatorial Pacific and Peru Upwelling/Humboldt Current had the least number octocoral genera (Fig. 5).

3.4. EMU

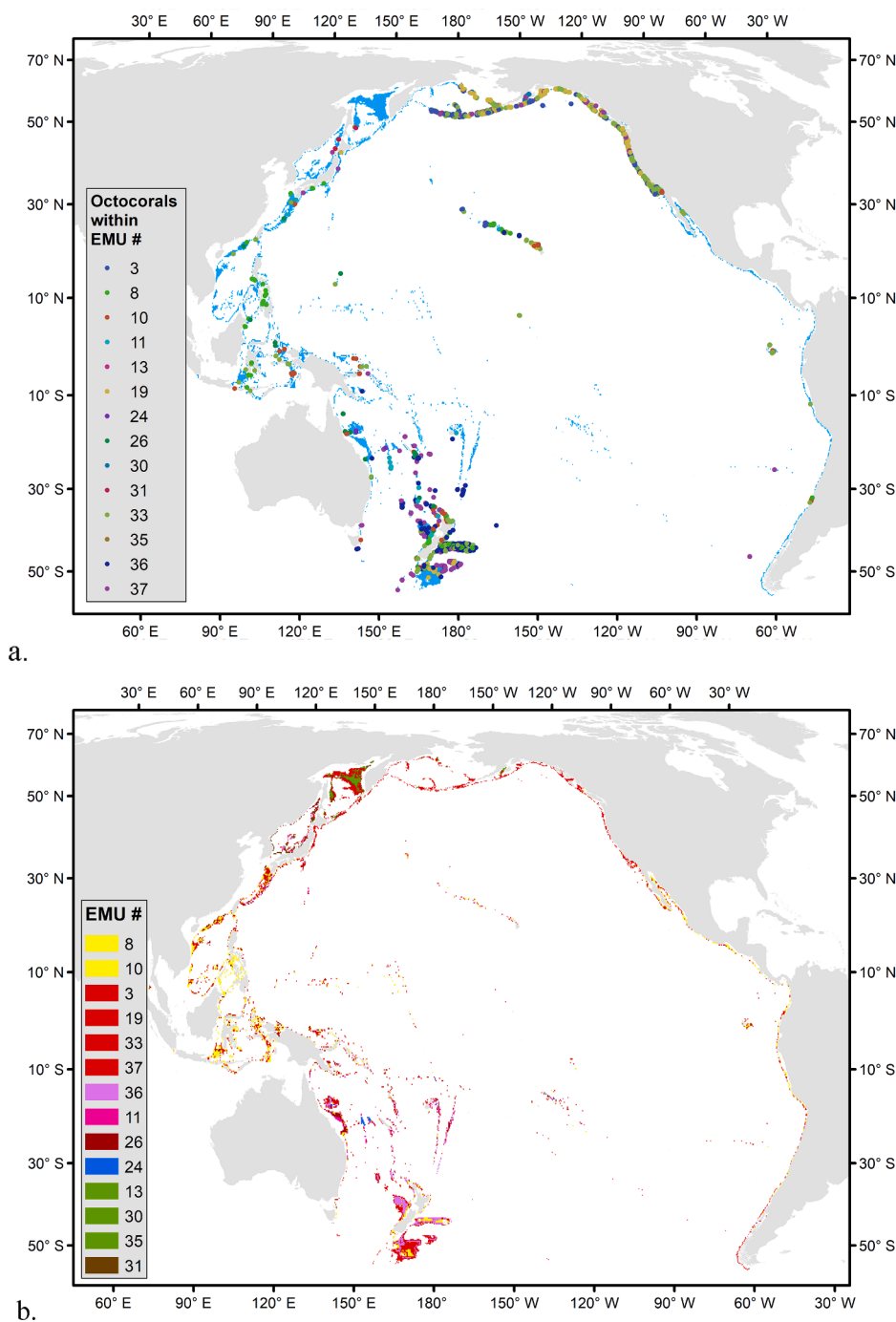Clustering of octocoral records according to the boundaries of the

Fig. 6. a) Distribution of Upper Bathyal octocoral records plotted over the spatial extent of EMUs. b) EMUs coloured by clusters from c), the hierarchical clustering of octocoral records according to the EMU in which they were found using Sorensen's index of similarity. Dashed red lines on tree represent non-significant clustering and solid lines represent significant clusters (SIMPROF test with 5% significance). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

EMUs resulted in five major geographic groups that are nested within individual EMUs (Fig. 6) EMUs 8 and 10 formed the first group located in the Central and South Pacific. EMUs, 3, 19, 33 and 37 formed the second group located across the Pacific. These two groups seem to be clustered within EMU 36, 11, and 26. The fourth group consists of units 13, 30 and 35 located in the North Pacific all of which have 6 or fewer genera. EMU 24 forms a unit by itself in the south Pacific as does EMU 31 in the West North Pacific; however both of these EMUs have only 3 genus records (Fig. 6).

4. Discussion

4.1. Taxonomic resolution

Octocoral taxonomy is largely based on the shape and contractility of the polyps, the shape and positioning of sclerites in the polyps, and characters of the colony axis. However, deep sea octocoral data is often based on imagery rather than collected specimens. As a result, genus level identification was thought to be more appropriate, and likely more accurate than trying to discern species. There are many unsolved issues with the taxonomy of octocorals, as evidenced by the recent splitting of certain taxonomic groups based on molecular genetic information. For example, the old *Anthomastus* now is subdivided into *Pseudoanthomastus*
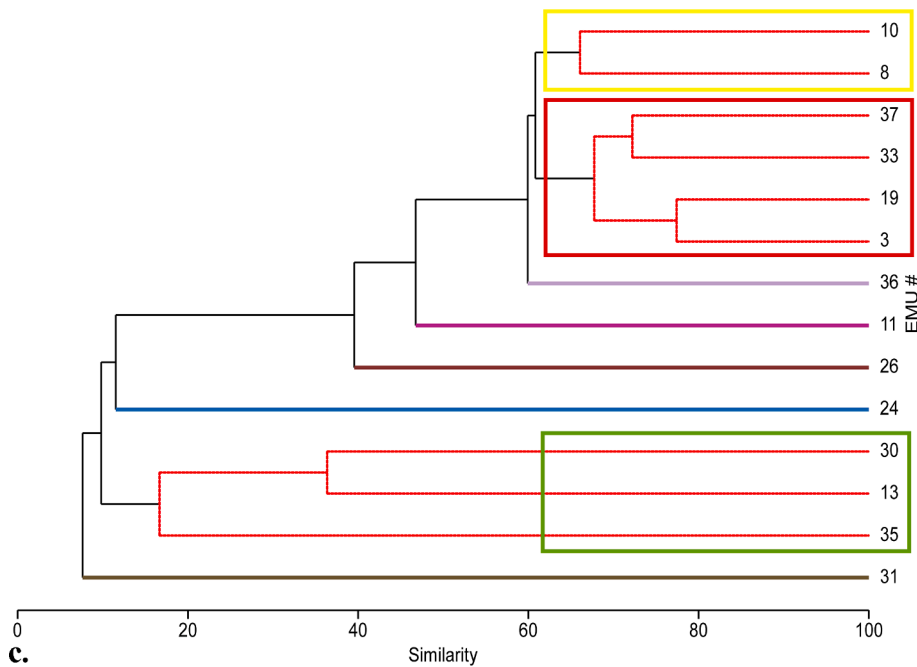
Fig. 6. (*continued*).

and *Heteropolypus* as well as *Anthomastus*. Some of the data we used was collected before changes were made and the reported records have not been revised. In addition, the taxonomy for some of the octocoral groups is currently being revised but has not yet been published (this is the case of bamboo corals, for example, but since that is work being done by us and our colleagues we used clade names based on characters that we have established from the genetic analyses). With updated taxonomy, we expect either the same result or clearer boundaries. We would also expect better resolution with more boundaries at species level. However, Costello et al. (2017) found provinces defined using genus level data were similar to those defined using species level information (Costello et al., 2017).

4.2. East/West division

The clustering of octocoral locations according to the Lower Bathyal provinces showed a large East/West division with the East Pacific group including the most northern and southern areas of the basin. This division is validated in three different classification schemes. The classification based on the MEOW eco-regions showed the eastern groups to be mostly different from the western group with a unique northern cluster in the Aleutians and Gulf of Alaska. The mesopelagic-based units show a difference between East and West coastal groups separated by larger central units. This East/West distinction was seen in the brachiopod distribution data of Zezina (1997) (Fig. 7) with the Indo-West Pacific unit being similar to that based on the Lower Bathyal provinces BY6, BY12 and BY14. These patterns suggest that the East Pacific Barrier seen in shallow water (Bowen et al., 2016) extends downward to the Upper Bathyal (Fig. 8a).

The Line Islands MEOW-based ecoregion group, located at the border between Eastern Tropical and Equatorial Mesopelagic Provinces, were grouped with the Eastern Galapagos MEOW-based ecoregion, which also clustered with Hawaii and New Zealand highlighting a connection of oceanic islands at the genus level. These regions are possibly being grouped by genera found in the deeper part of the Upper Bathyal where temperatures don't vary as much as in the shallower Upper Bathyal (Fig. 8). We hypothesize that upwelling around oceanic islands would result in a shallower boundary between the Upper Bathyal and Lower

Bathyal thus driving this pattern. However, we currently do not have supporting data for this proposed mechanism. A species level analysis is likely to differentiate these regions.

4.3. North Pacific

Groups based on the Mesopelagic provinces differed from the MEOW-based units in the North Pacific. The division between the California Coast MEOW group and Alaska MEOW group was strong. In contrast, there was no division of the groups based on the mesopelagic classification scheme potentially because the mesopelagic regions are larger overall and was based on mobile pelagic fauna as opposed to sessile benthic fauna. The North East Pacific is a very dynamic system with the California Undercurrent flowing northwards in the Upper Bathyal (opposite to the direction of the California current). The core depth of this undercurrent is 250 m reaching deeper than 1000 m in some places. In addition, the North Pacific current includes the eastward flow of the subpolar and subtropical gyres. The flow from the subpolar gyre then turns northwards as it gets closer to the coast whereas the flow from the subtropical gyre veers southwards (MacDonald et al., 2009; You, 2010; Talley et al., 2011, Fig. 9). The mixing of these currents likely results in the California slope being a transitional zone with high species richness where different units overlap. This pattern was also reported in brachiopods where all four distributional limits occur along this continental slope (Zezina, 1997; Fig. 7b).

The North Pacific Current also creates a temperature barrier isolating Alaska and the Aleutians from Hawaii and the rest of the Pacific (Fig. 8a). The mixing of the subpolar gyre and the subtropical gyre in the North Pacific current creates 4 °C temperature barrier isolating the Subarctic units (Alaska, Aleutians, Kamchatka Shelf, Sea of Okhotsk) from the rest of the Pacific (Fig. 8a). Lack of octocoral data in the Sea of Okhotsk and Kamchatka shelf MEOW-based regions most likely explains their separate clustering. Additional octocoral data would likely group them with the Subarctic Mesopelagic Province group in accordance with the brachiopod distributions (Zezina, 1997). Other MEOW-based unit clusters in the North Pacific include Marianna Island (clustered with New Caledonia & Kermadec Island), and central Kuroshio Current (clustered with Cortezian) which also have too few records from which
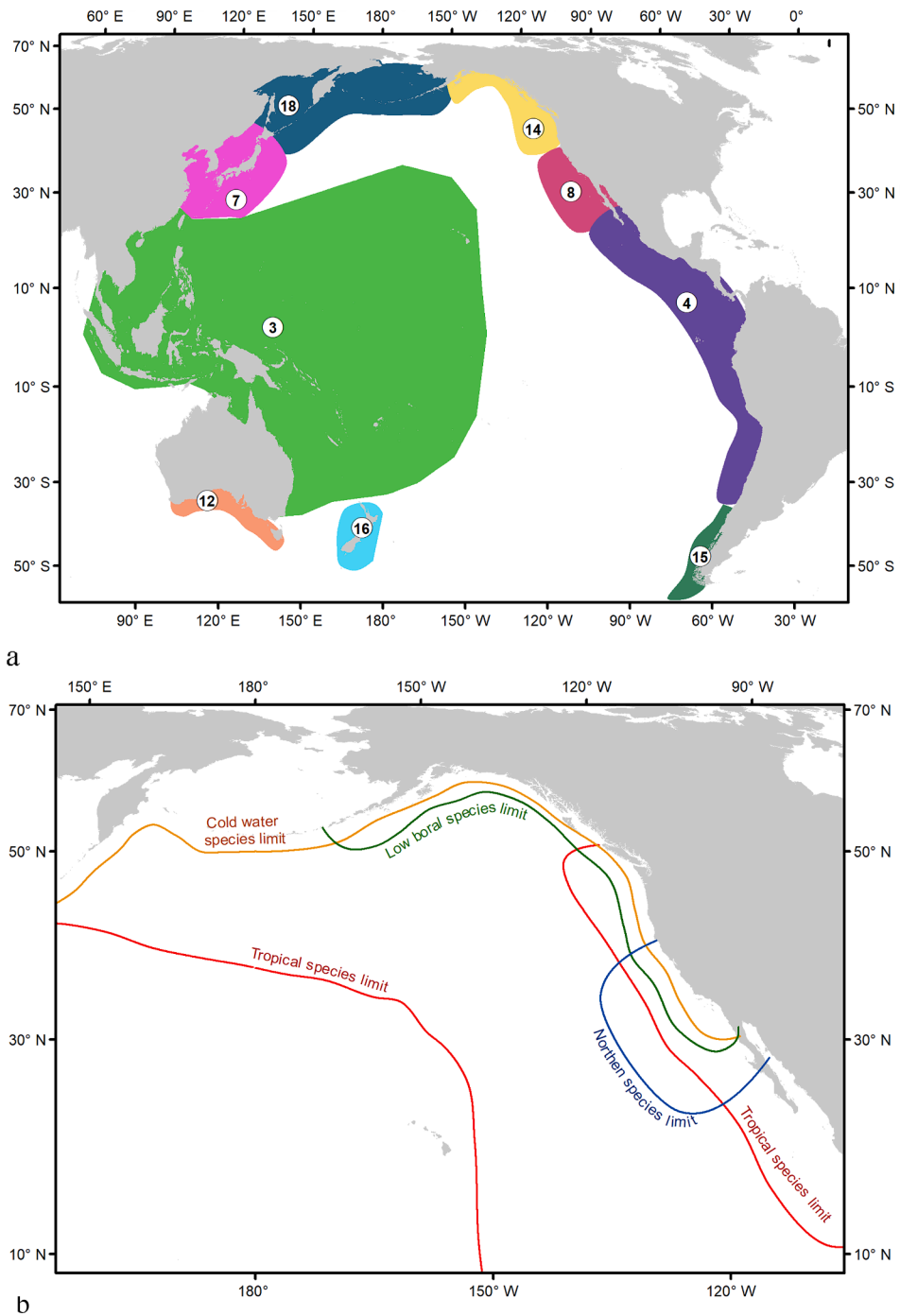
Fig. 7. a) Geographic units based on brachiopod distribution; geographic units shown are: 3, Indo-West Pacific; 4, East Pacific; 7, Japanese; 8, California; 12, South Australian; 14, Oregonian; 15, South American; 16, New Zealandian; North Pacific (drawn from Zezina 1997). b) Brachiopod distribution limits in the North Pacific, modified from Zezina (1997).
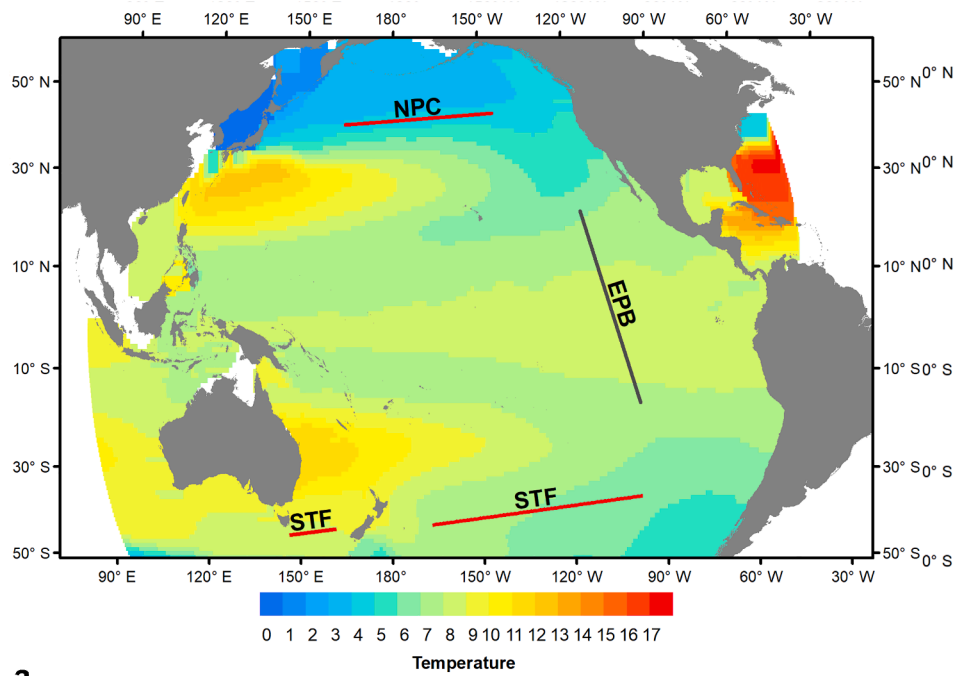
Fig. 8. a) Mean decadal temperature (2005–2012) at 500 m depth showing the three Upper Bathyal barriers. The temperature barriers (red) are the North Pacific Current (NPC) and the Subtropical Front (STF). East Pacific Barrier (EPB) is a distance barrier (grey). b) Temperature at 800 m. (Locarnini et al. 2018, data downloaded from NODC database 03/2019 (Boyer et al., 2013)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
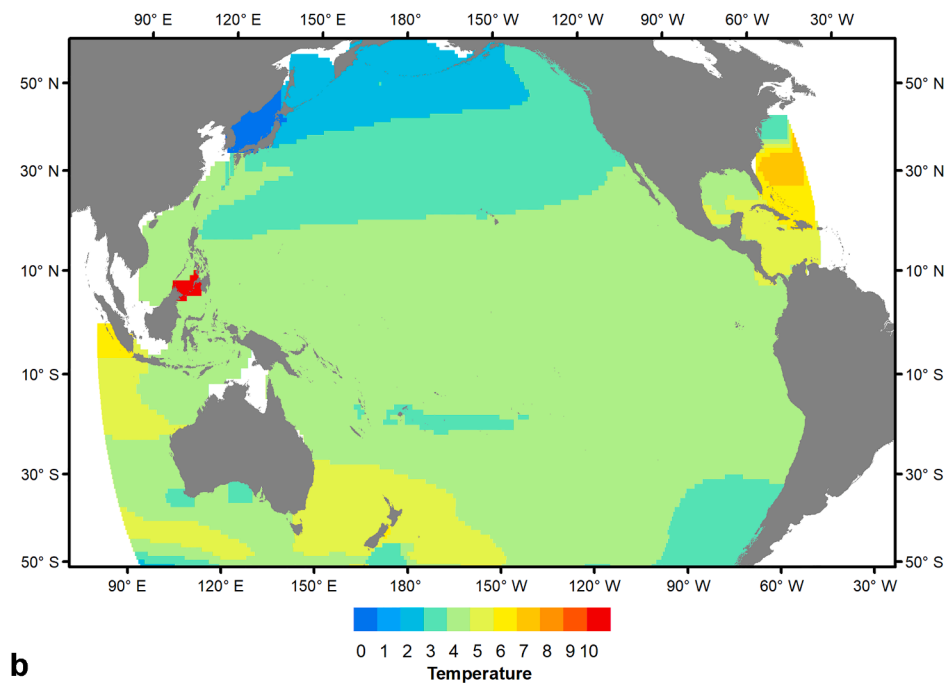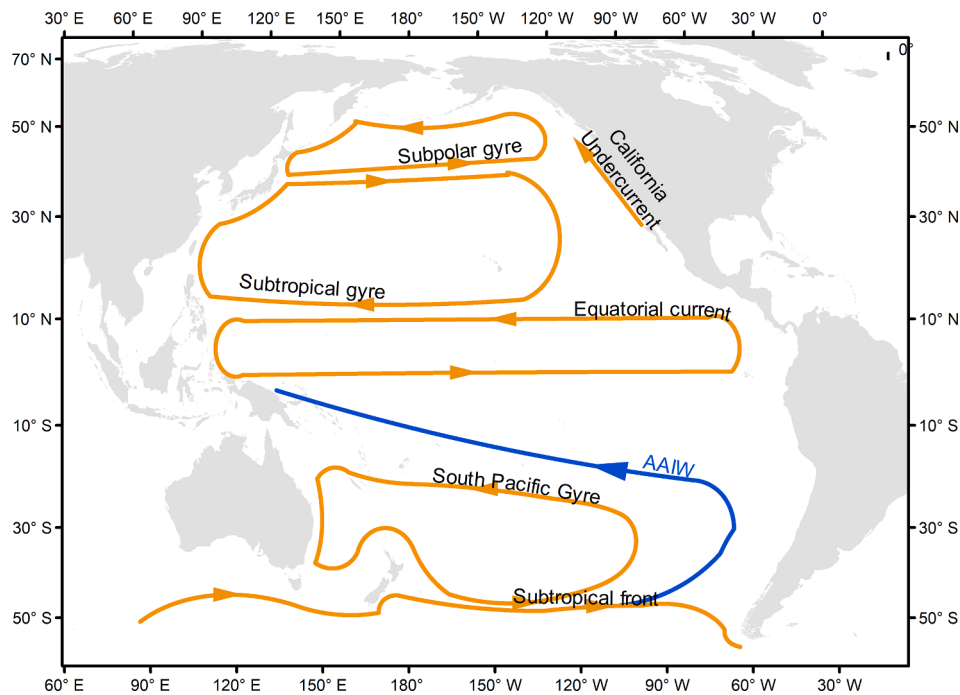
Fig. 9. Pacific Ocean circulation for the Upper Bathyal (from Kawabe and Fujio, 2010; MacDonald et al., 2009; Talley et al., 2011).

to draw conclusions.

4.4. Indo-Pacific

Mesopelagic, MEOW and EMU-based units all show a unique Indo-Pacific group around the Coral Triangle. This group is defined by coral clusters that are found deeper elsewhere in the Pacific. Although sampling in this area is not as extensive as in the North Pacific, the coral cluster is unique to this area and is characterised by octocorals usually found in the Lower Bathyal. The size of this group and how far it extends into the Indian Ocean differs between the pelagic and mesopelagic-based units. Brachiopod distributions suggested a faunal connectivity between the two ocean basins in that region (Zezina, 1997).

4.5. South Pacific

Torres Straight and Coral Sea MEOW-based units were very distinct from all other Pacific Ocean regions and characterised by genera known from mesophotic depths. The division halfway along the east coast of Australia is supported by the mesopelagic scheme and is probably caused by water mass movement from the South Pacific Gyre. The ophiuroid distribution around Australia also supports a division just south of the Coral Sea and provides evidence for a large coral sea region that would include the Kermadec, New Caledonia, Lord Howe and Norfolk Islands and Three Kings North Cape MEOW-based regions (O'Hara et al., 2011)

The North and South New Zealand barrier is seen in the clustering of units based on three of the classification systems (MEOW, Lower Bathyal and Mesopelagic) and can be explained by the presence of the Subtropical Front (Figs. 8 and 9). The north–south New Zealand division was not observed in the ophiuroid distributions (O'Hara et al., 2011). This may be because the brittle star distribution pattern was driven by the Lower Bathyal species which have large latitudinal ranges. When looking at brachiopod distributions, New Zealand was identified as its own region (Fig. 7) but southern New Zealand included northern and southern species not found in the rest of the region (Zezina, 1997).

4.6. The Subantarctic

This unit combines the Macquarie Islands and Channels & Fjords of South Chile MEOW-based regions. Although these areas are on different sides of the South Pacific, they are connected by water mass movement from the Subtropical Front (Kawabe and Fujio, 2010; MacDonald et al., 2009). In the Mesopelagic Province clustering, the Southern Central Pacific clustered with the Subantarctic units, most likely due to the disproportionate distribution of data around New Zealand. There is a mismatch between where the Mesopelagic units divide along the New Zealand Coast and where the Subtropical Front is found.

4.7. Depth boundaries

As predicted, EMUs did not result in any geographical pattern. Only EMUs that were more geographically limited followed a clustering pattern similar to the other 3 analyses. EMU 8 and 10 form a group covering most of the Pacific except the Subarctic regions (Alaska, Aleutians). The core volume of this cluster is found in the upper bathyal depths extending to the mesopelagic. A second cluster consisting of EMU 3, 19, 33 and 37 are spread across the Pacific. Except for EMU 19, the core volume of this group is found from upper bathyal to the lower bathyal depths (Fig. 10). These two groupings suggest that there is a depth break in certain regions of the Upper Bathyal. However, the geographical distribution is a stronger factor than depth. The third major group consists of EMUs 13, 30 and 35 found in the North Pacific. However, these EMUs have too few octocoral genera (1 to 6) to be reliable.

Studies of octocoral distributions on seamounts present evidence of depth zonation within the Upper Bathyal. DuPreez et al. (2016) report distinct depth layer based faunal communities driven by depth as well as slope and rugosity. Braga-Henriques et al. (2013) also showed depth to be an important driver for faunal distributions in the Atlantic with a transition around 600 m. Changes related to depth are associated with other factors such as temperature, pressure, and food availability (Carney 2005, Clark et al. 2010). Among those, temperature and water masses play important roles as shown by Bryan and Metaxas (2006) and
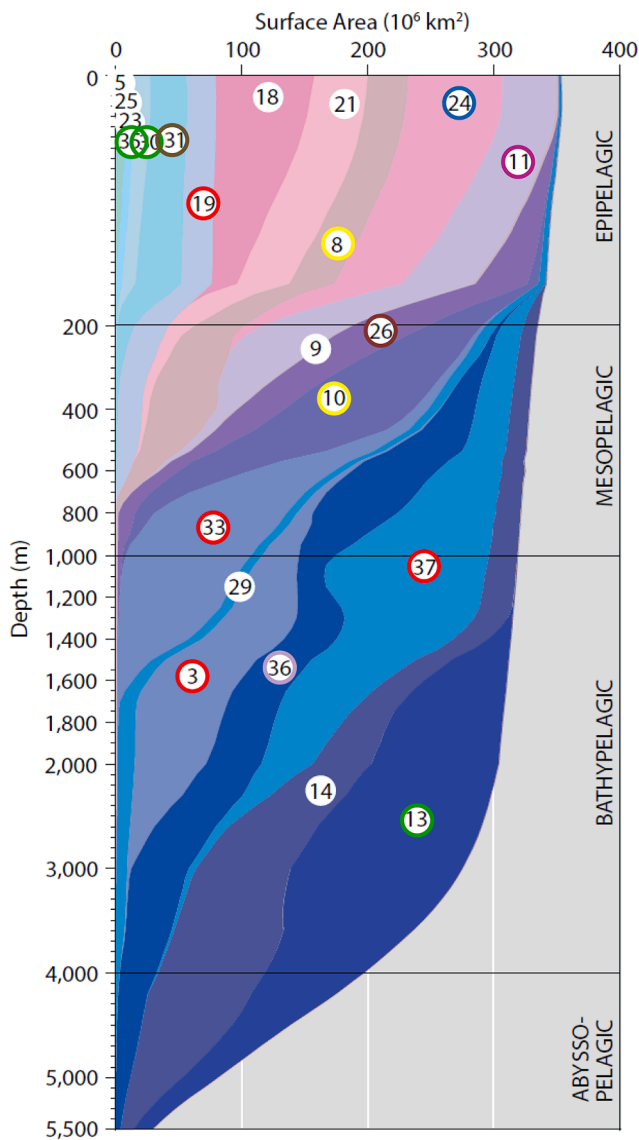
Fig. 10. EMU depth ranges coloured by clusters corresponding to Fig. 6. Modified from Sayre et al., (2017).

Victorero et al. (2018). Depth boundaries can vary by region within the Pacific, for example, the North Pacific and South Pacific gyres are notable features at 500 m where these two gyres create a 3 to 4 °C temperature gradient, but are no longer distinct at 800 m (Fig. 8). Further studies focusing on regional drivers would help define depth-related patterns.

4.8. Conclusion

Based on our analysis, we conclude that the Pacific comprises 10 biogeographical provinces in the Upper Bathyal (Fig. 11). This proposed scheme concurs with the theory that biogeographic provinces become larger with depth. The MEOW classification scheme proposed 29 provinces at shelf depths in the Pacific (Spalding et al., 2007) and the Lower Bathyal classification scheme defined eight provinces (Watling et al., 2013). Observed patterns seem to be driven mostly by temperature, water masses and currents.

MEOW ecoregions were a good starting point for this analysis due to their small size. Many of these units clustered together in the Upper Bathyal forming groups similar to the MEOW Provinces. In contrast, the

Lower Bathyal provinces would need to be subdivided into smaller units to fit the Upper Bathyal octocoral distribution pattern. The validity of the Mesopelagic classification scheme to explain octocoral distributions point towards greater energy and organism exchange than previously suggested by UNESCO (2009). Most deep-sea megafauna are suspension or deposit feeders and thus rely directly on the plankton and nekton production that are used to define the pelagic and mesopelagic provinces. One major difference between these environments is that the benthic units could potentially be further subdivided by habitat type or by analysis at lower taxonomic levels (species). These sub-units would then be nested within the ones described in this study.

Additional support for our proposed Upper Bathyal provinces is provided by further cluster analysis of the province units (Fig. 12) which highlights three major boundaries (NPC, EPB and STF). The North Pacific Current isolates the Subarctic Province by creating a temperature barrier (NPC boundary). Similarly, the Subtropical Front isolates the Subantarctic Province distinguishing the southern tip of New Zealand from North New Zealand and grouping South New Zealand with the southern tip of South America. The East Pacific Barrier (EPB) isolates the Central East Pacific Province from the Western provinces (Fig. 11a). The converging currents in the North Pacific likely make the North East Pacific a transition zone between temperate and tropical slope fauna which is why the Subarctic, North East Pacific and Central East Pacific cluster together. Similarly, the boundaries between the West Pacific, Hawaii and Coral sea are likely transitionary or permeable. The similarity between these three provinces is probably driven by the sub-tropical gyre system. More focused analysis of faunal distribution would help define these boundaries. The Indo-Pacific Province is very distinct from all other provinces. Finally, the South China Sea and the Sea of Japan both lack octocoral data. However, we hypothesize these provinces will remain separate based on the geography of those seas (Fig. 11). Analysis of EMUs lends support to further depth zonation of the Upper Bathyal at least within certain provinces.

With the current and future threats to the deep-sea fauna from mining and fishing, it is important to develop a biogeographical scheme that takes into account taxa distributions. Deep-sea continental shelves, slopes, canyons, and seamounts around the world are home to many species of corals that form hotspots of biodiversity with both scientific and commercial interest (Freiwald et al., 2004). For example, precious black corals (Order Antipatharia) and gold corals (Order Zoanthidea) are harvested for making jewellery. Additionally, these deep sea habitats host commercially important food species such as king crabs (Family Lithodidae), sablefish (*Anoplopoma fimbria*), and orange roughy (*Hoplostethus atlanticus*) with Alaska supporting one of the largest domestic ground fisheries in the U.S. (Hiatt et al., 2007). However, the trawl gear used for these fisheries causes disturbance and damage to benthic organisms that have slow recovery rates (Heifetz et al., 2009). The impact of deep-sea fishing has been documented many times (Fosså and Furevik, 2002; Koslow et al., 2001; Reed et al., 2007) with trawling being one of the most destructive fishing methods. The seafloor between 350 and 700 m depth is the most disturbed and exploited by the fishing industry, at least in some areas (Heifetz et al., 2009). Future exploitation in the form of deep-sea mining may also threaten organisms that live on the sea floor (Niner et al., 2018). Currently the International Seabed Authority (ISA) has leased areas in the Central West Pacific near the Marianna Islands for cobalt rich ferromanganese crust mining exploration (https://www.isa.org.jm) which are at Lower Bathyal depth, and which with recent exploration are producing species new to science (Xu et al., 2020a, 2020b).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
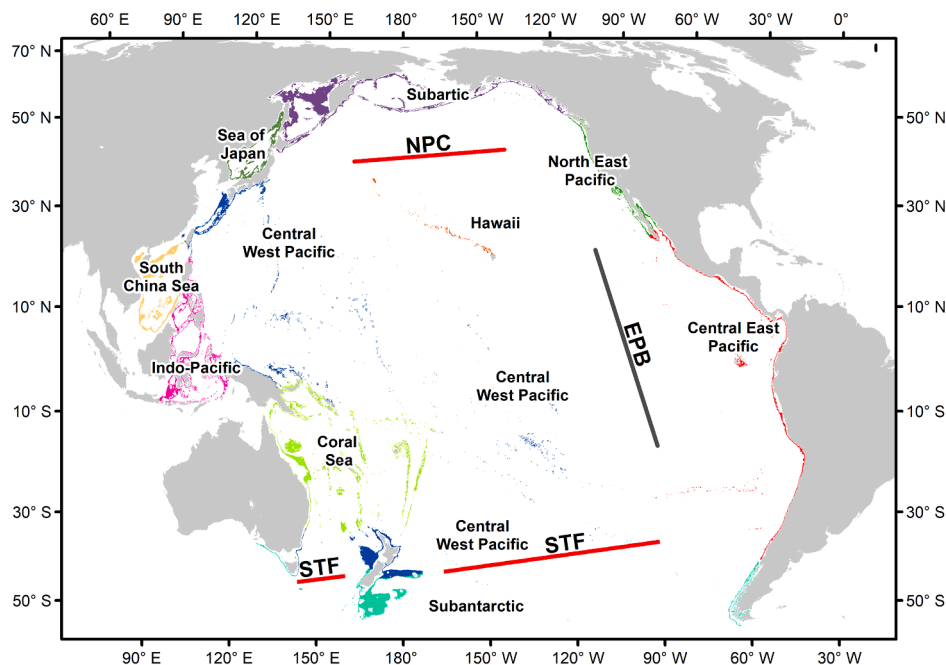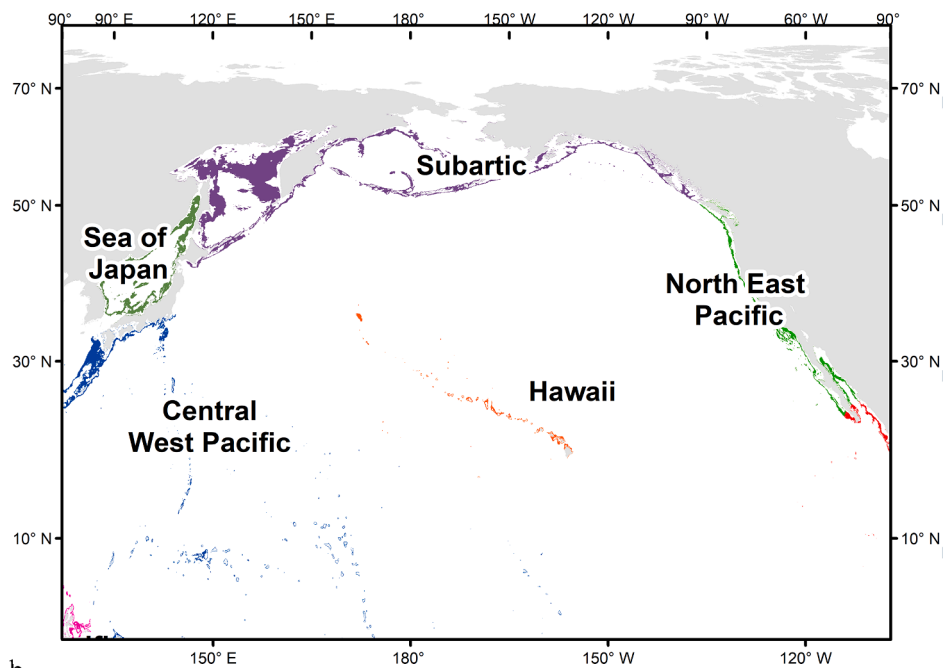
Fig. 11. Proposed Upper Bathyal Provinces for the Pacific Ocean with 3 strong boundaries (a). Close up of North Pacific (b), West Pacific (c), East Pacific (d) and South Pacific (e).
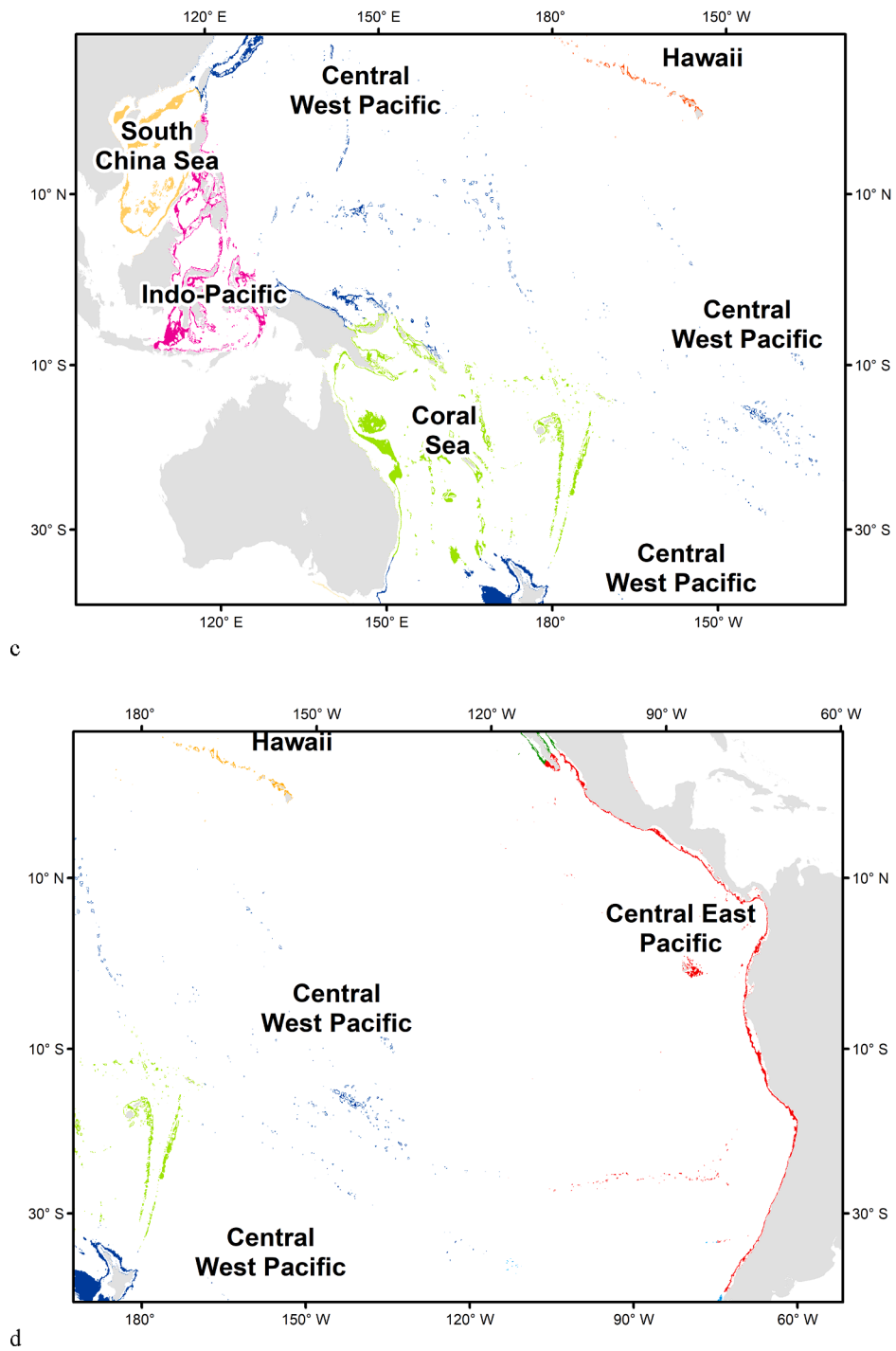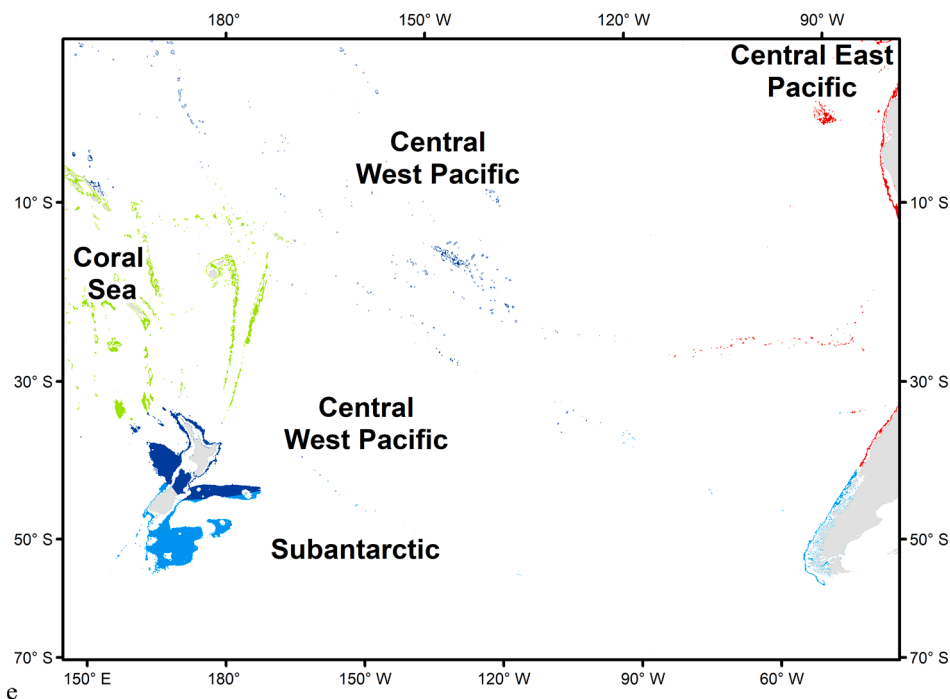
c

d

Fig. 11. (*continued*).
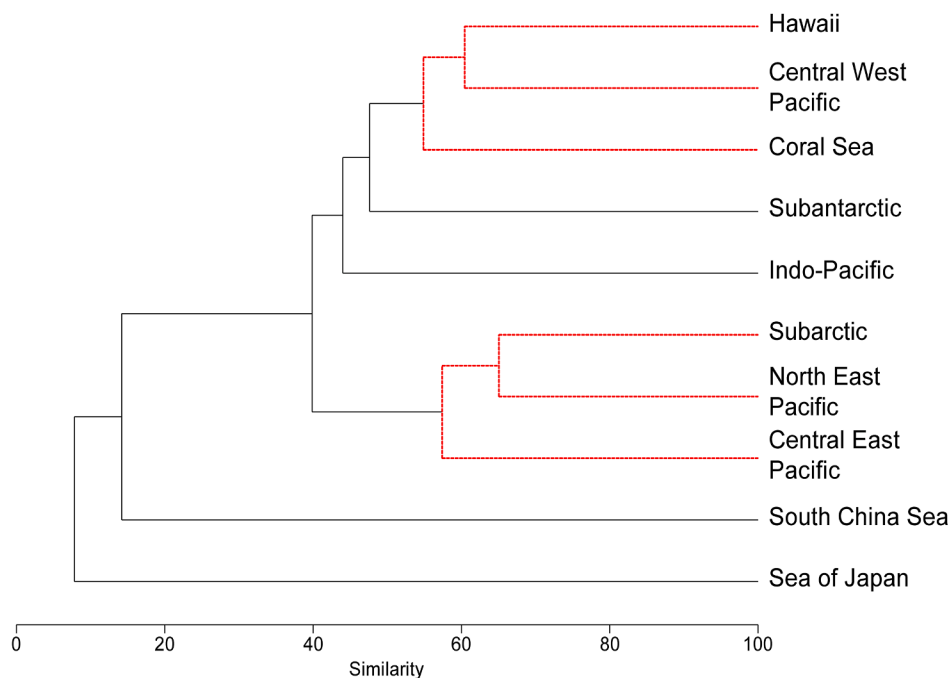
Fig. 11. (*continued*).

Fig. 12. Hierarchical clustering of octocoral records according to Upper Bathyal units in which they were found using Sorensen's index of similarity. Dashed red lines on tree represent non-significant clustering and solid lines represent significant clusters (SIMPROF test with 5% significance). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2020.102509.

References

Braga-Henriques, A., Porteiro, F.M., Ribeiro, P.A., De Matos, V., Sampaio, Í., Ocaña, O., Santos, R.S., 2013. Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic). Biogeosciences 10, 4009–4036. https://doi.org/10.5194/bg-10-4009-2013.

Boyer, T.P., J. I. Antonov, O. K. Baranova, C. Coleman, H. E. Garcia, A. Grodsky, D. R. Johnson, R. A. Locarnini, A. V. Mishonov, T.D. O'Brien, C.R. Paver, J.R. Reagan, D. Seidov, I. V. Smolyar, and M. M. Zweng, 2013: World Ocean Database 2013, NOAA Atlas NESDIS 72, S. Levitus, Ed., A. Mishonov, Technical Ed.; Silver Spring, MD, 209 pp., http://doi.org/10.7289/V5NZ85MT.

Bowen, B.W., Gaither, M.R., DiBattista, J.D., Iacchei, M., Andrews, K.R., Grant, W.S., Toonen, R.J., Briggs, J.C., 2016. Comparative phylogeography of the ocean planet. Proc. Natl. Acad. Sci. 113, 7962–7969. https://doi.org/10.1073/pnas.1602404113.

Briggs, J.C., 1974. Marine Zoogeography. McGraw-Hill, New York.

Bryan, T.L., Metaxas, A., 2006. Distribution of deep-water corals along the North American continental margins: relationships with environmental factors. Deep Res. Part I Oceanogr. Res. Pap. 53, 1865–1879. https://doi.org/10.1016/j.dsr.2006.09.006.

Carney, R.S., 2005. Zonation of deep biota on continental margins. Oceanogr. Mar. Biol. An Annu. Rev. 43, 211–278.

Chamberlain, S., Szoecs, E., Foster, Z., Arendsee, Z., Boettiger, C., Ram, K., Bartomeus, I., Baumgartner, J., O'Donnell, J., Oksanen, J., Tzovaras, B.G., Marchand, P., Vinh, T., 2018. taxize: Taxonomic information from around the web.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

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.M., 2010. The ecology of seamounts: structure, function, and human impacts. Ann. Rev. Mar. Sci. 2, 253–278. https://doi.org/10.1146/annurev-marine-120308-081109.

Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation, Second. ed. PRIMER-E, Plymouth.

Costello, M.J., Tsai, P., Wong, P.S., Cheung, A.K.L., Basher, Z., Chaudhary, C., 2017. Marine biogeographic realms and species endemicity. Nat. Commun. 8, 1057. https://doi.org/10.1038/s41467-017-01121-2.

DuPreez, C., Curtis, J.M.R., Clarke, M.E., 2016. The structure and distribution of benthic communities on a shallow seamount (Cobb Seamount, Northeast Pacific Ocean). PLoS One 11, 1–29. https://doi.org/10.1371/journal.pone.0165513.

Etnoyer, P.J., Cairns, S.D., Sanchez, J.A., Reed, J.K., Lopez, J.V., Schroeder, W.W., Brooke, S.D., Watling, L., Baco-Taylor, A.R., Williams, G.C., Lindner, A., France, S.C., Bruckner, A.W., 2006. Deep-sea coral collection protocols: a synthesis of field experience from deep-sea coral researchers, designed to build our national capacity to document deep-sea coral diversity. NOAA Tech. Memo. NMFS-OPR-28 1–56.

Fosså, H.J., Furevik, D.M., 2002. The deep-water coral Lophelia pertusa in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471, 1–12. https://doi.org/10.1023/A.

Freiwald, A., Helge Fosså, J., Grehan, A., Koslow, T., Roberts, J.M., 2004. Cold-water coral reefs: Out of sight – no longer out of mind. UNEP-WCMC, Cambridge, UK. https://doi.org/10.1016/j.dsr.2008.04.010.

Gage, J.D., Tyler, P.A., 1991. Deep-sea biology: a natural his- tory of organisms at the deep-sea floor. Cambridge University Press, Cambridge, UK.

Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L., Sheader, M., 2002. Polychaete species diversity in the central Pacific abyss: Local and regional patterns, and relationships with productivity. Mar. Ecol. Prog. Ser. 240, 157–170. https://doi.org/10.3354/meps240157.

Heifetz, J., Stone, R.P., Shotwell, S.K., 2009. Damage and disturbance to coral and sponge habitat of the Aleutian archipelago. Mar. Ecol. Prog. Ser. 397, 295–303. https://doi.org/10.3354/meps08304.

Hiatt, T., Felthoven, R., Dalton, M., Garber-Yonts, B., Haynie, A., Herrmann, K., Lew, D., Sepez, J., Seung, C., Sievanen, L., Staff of Northern Economics, 2007. Stock assessment and fishery evaluation report for the groundfish fisheries of the Gulf of Alaska and Bering Sea/Aleutian islands area: economic status of the groundfish fisheries off Alaska, 2006, NPFMC Economic SAFE.

Kawabe, M., Fujio, S., 2010. Pacific ocean circulation based on observation. J. Oceanogr. 66, 389–403. https://doi.org/10.1007/s10872-010-0034-8.

Koslow, J.A., Gowlett-Holmes, K., Lowry, J.K., O'Hara, T., Poore, G.C.B., Williams, A., 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Mar. Ecol. Prog. Ser. 213, 111–125. https://doi.org/10.3354/meps213111.

Locarnini, R.A., Mishonov, A. V., Baranova, O.K., Boyer, T.P., Zweng, M.M., Garcia, H.E., Reagan, J.R., Seidov, D., Weathers, K.W., Paver, C.R., Smolyar, I. V., 2018. World Ocean Atlas 2018. Volume 1 : Temperature. A. Mishonov Technical Ed.; NOAA Atlas NESDIS 81, 52 pp.

MacDonald, A.M., Mecking, S., Robbins, P.E., Toole, J.M., Johnson, G.C., Talley, L., Cook, M., Wijffels, S.E., 2009. The WOCE-era 3-D pacific ocean circulation and heat budget. Prog. Oceanogr. 82, 281–325. https://doi.org/10.1016/j.pocean.2009.08.002.

Niner, H.J., Ardron, J.A., Escobar, E.G., Gianni, M., Jaeckel, A., Jones, D.O.B., Levin, L. A., Smith, C.R., Thiele, T., Turner, P.J., Van Dover, C.L., Watling, L., Gjerde, K.M., 2018. Deep-Sea mining with no net loss of biodiversity—an impossible aim. Front. Mar. Sci. 5 https://doi.org/10.3389/fmars.2018.00195.

NOAA National Database for Deep-Sea Corals and Sponges (version 20180809-N). https://deepseacoraldata.noaa.gov/; NOAA Deep Sea Coral Research & Technology Program.

OBIS, 2018. Distribution records of Octotocorals (Available: Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. https://obis.org/. Accessed: 2018-08-05).

O'Hara, T.D., Rowden, A.A., Bax, N.J., 2011. A Southern Hemisphere bathyal fauna is distributed in latitudinal bands. Curr. Biol. 21, 226–230. https://doi.org/10.1016/j.cub.2011.01.002.

Quattrini, A.M., Georgian, S.E., Byrnes, L., Stevens, A., Falco, R., Cordes, E.E., 2013. Niche divergence by deep-sea octocorals in the genus Callogorgia across the continental slope of the Gulf of Mexico. Mol. Ecol. 22, 4123–4140. https://doi.org/10.1111/mec.12370.

Quattrini, A.M., Gómez, C.E., Cordes, E.E., 2017. Environmental filtering and neutral processes shape octocoral community assembly in the deep sea. Oecologia 183, 221–236. https://doi.org/10.1007/s00442-016-3765-4.

Reed, J.K., Koenig, C.C., Shepard, A.N., 2007. Impacts of bottom trawling on a deep-water Oculina coral ecosystem off Florida. Bull. Mar. Sci. 81, 481–496.

Rex, M.A., Etter, R.J., 2010. Deep-sea biodiversity: Pattern and scale. Harvard University Press, Cambridge, MA.

Reygondeau, G., Guidi, L., Beaugrand, G., Henson, S.A., Koubbi, P., MacKenzie, B.R., Sutton, T.T., Fioroni, M., Maury, O., 2018. Global biogeochemical provinces of the mesopelagic zone. J. Biogeogr. 45, 500–514. https://doi.org/10.1111/jbi.13149.

Sayre, R., Wright, D., Breyer, S., Butler, K., Van Graafeiland, K., Costello, M., Harris, P., Goodin, K., Guinotte, J., Basher, Z., Kavanaugh, M., Halpin, P., Monaco, M., Cressie, N., Aniello, P., Frye, C., Stephens, D., 2017. A three-dimensional mapping of the ocean based on environmental data. Oceanography 30, 90–103. https://doi.org/10.5670/oceanog.2017.116.

Sherman, K., Aquarone, M.C., Adams, S. (Eds.), 1990. Sustaining the World's Large Marine Ecosystems, Science (New York, N.Y.). IUCN, Gland, Switzterland. https://doi.org/10.1126/science.299-b.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M.A.X., Halpern, B.S., Jorge, M.A., Lombana, A.L., Lourie, S.A., Martin, K.D., Manus, M.C., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas 57, 573–583.

Somero, G.N., Lockwood, B.L., Tomanek, L., 2017. Biochemical Adaptation, response to environmental challenges from life's origins to the Anthropocene. Sinauer Associates, Sunderland, MA, USA, p. 572.

Sutton, T.T., Clark, M.R., Dunn, D.C., Halpin, P.N., Rogers, A.D., Guinotte, J., Bograd, S. J., Angel, M.V., Perez, J.A.A., Wishner, K., Haedrich, R.L., Lindsay, D., Drazen, J. C., Vereshchaka, A., Piatkowski, U., Morato, T., Błachowiak-Samołyk, K., Robison, B. H., Gjerde, K.M., Pierrot-Bults, A., Bernal, P., Reygondeau, G., Heino, M., 2017. A global biogeographic classification of the mesopelagic zone. Deep Res. Part I Oceanogr. Res. Pap. 126, 85–102. https://doi.org/10.1016/j.dsr.2017.05.006.

Talley, L.D., Pickard, G.L., Emery, W.J., Swift, J.H., 2011. Pacific Ocean, in: Descriptive Physical Oceanography: An Introduction: Sixth Edition. Elsevier Ltd, London.

Team, R.C., 2017. R: A language and environment for statistical computing.UNESCO, 2009. Global Open Oceans and Deep Seabed (GOODS) - biogeographic classification. IOC Tech. Ser. 84, 84.

Valentine, J.W., 1973. Evolutionary Paleoecology of the Marine Biosphere. Prentice-Hall.

Victorero, L., Robert, K., Robinson, L.F., Taylor, M.L., Huvenne, V.A.I., 2018. Species replacement dominates megabenthos beta diversity in a remote seamount setting. Sci. Rep. 8, 1–11. https://doi.org/10.1038/s41598-018-22296-8.

Watling, L., France, S.C., Pante, E., Simpson, A., 2011. Biology of deep-water octocorals. Adv. Mar. Biol. 60, 41–122. https://doi.org/10.1016/B978-0-12-385529-9.00002-0.

Watling, L., Guinotte, J., Clark, M.R., Smith, C.R., 2013. A proposed biogeography of the deep ocean floor. Prog. Oceanogr. 111, 91–112. https://doi.org/10.1016/j.pocean.2012.11.003.

Xu, Y., Zhan, Z., Li, Y., Xu, K., 2020a. Morphology and phylogenetic analysis of two new species of deep-sea golden gorgonians (Cnidaria: Octocorallia: Chrysogorgiidae) from seamounts in the Western Pacific Ocean. Zootaxa 4731, 249–262.

Xu, Y., Zhan, Z., Xu, K., 2020b. Morphology and molecular phylogeny of three new deep-sea species of Chrysogorgia (Cnidaria, Octocorallia) from seamounts in the tropical Western Pacific Ocean. PeerJ 8, e8832. https://doi.org/10.7717/peerj.8832.

Yeh, J., Drazen, J.C., 2009. Depth zonation and bathymetric trends of deep-sea megafaunal scavengers of the Hawaiian Islands. Deep Res. Part I Oceanogr. Res. Pap. 56, 251–266. https://doi.org/10.1016/j.dsr.2008.08.005.

You, Y., 2010. Frontal densification and displacement: a scenario of North Pacific Intermediate Water formation. Deep Res. Part II Top. Stud. Oceanogr. 57, 1171–1176. https://doi.org/10.1016/j.dsr2.2009.12.006.

Zezina, O.N., 1997. Biogeography of the Bathyal Zone. Adv. Mar. Biol. 32, 389–426, 10.1016/S0065-2881(08)60020-6.