Title: The role of continental shelf bathymetry in shaping marine range shifts in the face of climate change

Running Head: Bathymetric limits on range shifts

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Data accessibility statement: All data used in the following analyses are available publicly. ETOPO2 bathymetric data are available from NOAA, https://www.ngdc.noaa.gov/mgg/global/etopo2.html. Continental shelf delineation is available from Blue Habitats, https://www.bluehabitats.org/?page_id=58. Large Marine Ecosystem shapefiles are available from the USGS https://www.sciencebase.gov/catalog/item/55c77722e4b08400b1fd8244. FAO Major Fishing Areas are available from the FAO, http://www.fao.org/geonetwork/srv/en/main.home?uuid=ac02a460-da52-11dc-9d70-0017f293bd28. Code and aggregated data are available on the public GitHub repository, https://github.com/zoekitchel/shelf_habitat_distribution.

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Abstract

As a consequence of anthropogenic climate change, marine species on continental shelves around the world are rapidly shifting deeper and poleward. However, whether these shifts deeper and poleward will allow species to access more, less, or equivalent amounts of critical habitats remains unclear. By examining the proportion of seabed area at a range of depths for each Large Marine Ecosystem (LME), we found that shelf area declined monotonically for 22% of LMEs examined. However, the majority exhibited a greater proportion of shelf area in mid-depths or across several depth ranges. By comparing continental shelf area within 2˚ latitudinal bands, we found that all coastlines exhibit multiple instances of shelf expansion and contraction, which have the potential to promote or restrict poleward movement of marine species. Along most coastlines, overall shelf habitat increases or exhibits no significant change moving towards the poles. The exception is the Southern West Pacific which experiences overall habitat loss with increasing latitude. These changes in shelf habitat availability are likely to affect the number of species these ecosystems are able to support. These geometric analyses help identify conservation priorities and ecological communities most likely to face attrition or expansion.

Introduction

Many species in terrestrial and aquatic systems are shifting where they live in response to climate change (Lenoir & Svenning, 2015). Marine species are particularly sensitive to temperature changes associated with climate change, in part because they have evolved in the relatively stable thermal conditions characteristic of the ocean (Pinsky et al., 2019). This high sensitivity, coupled with higher dispersal potential and limited biogeographical barriers have led marine species to track isotherms poleward six times faster than their terrestrial counterparts (Lenoir et al., 2020). In addition, there is evidence that marine species are moving deeper to maintain their thermal niche (Dulvy et al., 2012; Perry et al., 2005; Pinsky et al., 2013; Poloczanska et al., 2016).

As species undergo range shifts, they also experience changes in the availability and quality of habitat (Platts et al., 2019). Sufficient habitat area is critical for population viability, and subsequently, for successful range shifts (Opdam & Wascher, 2004). The number of individuals a habitat can support often scales with the size of the habitat (Alzate et al., 2019; Halpern et al., 2005). Larger habitats provide more opportunities for establishment and growth in the case of sessile individuals, and more opportunities for foraging for more mobile individuals (Bender et al., 1998; Griffen & Drake, 2008; MacArthur & Wilson, 1967). Many species rely on metapopulation structure across space in order to maintain populations large enough to avoid inbreeding depression and buffer against the risk of extinction due to demographic stochasticity and disturbances (Hanski et al., 1996; Kuparinen et al., 2014). Larger habitats also tend to support higher overall species richness because of increased habitat heterogeneity and reduced likelihood of extinction (Cornell & Karlson, 2000; MacArthur & Wilson, 1967).

Continental shelves support productive, complex, and economically and culturally important marine ecosystems (Amoroso et al., 2018; Bell, 2009; Buhl-Mortensen et al., 2012; Gomes et al., 2018; Smith & Brown, 2002). These essential habitats exhibit high nutrient availability due to upwelling and freshwater inputs (X. Chen et al., 2000; García-Reyes et al., 2015). The relatively shallow waters (typically less than 200 m) permit light to penetrate the water column to the substrate, promoting primary production in the form of plant and algal growth (Duarte, 1991; Kahng et al., 2019). On the continental shelf, depth and seafloor area are key components of suitable habitat. Unique biogenic and geologic structures that provide habitat and refuge supporting diverse and productive ecosystems are limited to the continental shelf (Buhl-Mortensen et al., 2012; Malatesta & Auster, 1999; Nagelkerken et al., 2000; Townsend et al., 2004). Many marine species are restricted to living on the continental shelf due to metabolic tolerances, and their reliance on the primary production occurring within the photic zone (Brown & Thatje, 2015; Mestre et al., 2013; Smith & Brown, 2002). It is unlikely that marine species will successfully establish off of the continental shelf even as species make range shifts into deeper waters (Dulvy et al., 2012). In support of this limitation on range shifts, studies have revealed distinct shelf, slope, and abyssal plain species assemblages, and even distinctive clustering within these larger ocean zones (Brandt et al., 2007; Fujita et al., 1995; Pearcy et al., 1982; Rocha et al., 2018).

Marine species face heterogeneity in shelf area as they move poleward and deeper to track temperature isotherms. The width of the continental shelf ranges from over 1000 km off the northern coasts of Russia to less than one kilometer off the coast of the southeastern United States (Emery, 1966; Kang et al., 2017). The shelves exhibit high variability in structure across latitudes and depths, often bisected by deep canyons and channels (Heezen et al., 1964; Lastras et al., 2011). How shelf availability will change as species shift due to climate change, however, has yet to be examined. The late Ordovician extinctions provide evidence that lack of shelf habitat due to changes in global climatic conditions can drive global losses in species richness (Finnegan et al., 2016; Sheehan, 2001). Similar barriers are faced by terrestrial species as they shift in latitude and elevation. In some cases, corridors such as latitudinally oriented protected areas can facilitate poleward movement, while in other cases, obstacles such as rivers or human altered landscapes can restrict movement (Beier, 2012; Jha & Kremen, 2013; Thomas, 2010). Shifts of marine species into deeper habitat have been mirrored by terrestrial species shifting to higher elevations (Freeman, Lee-Yaw, et al., 2018; Freeman, Scholer, et al., 2018; Vitasse et al., 2021). Despite the prevailing assumption that montane surface area decreases with elevation and therefore that species will lose habitat as they track temperature upslope, topographic analyses revealed that the relationship between habitat area and elevation differs by mountain range (Elsen & Tingley, 2015). For the majority of mountain ranges, surface area does not decrease monotonically as species move upslope, and in a few select ranges, species will find the largest areas of suitable habitat at the highest elevations (Elsen & Tingley, 2015). However, no comparable analysis has yet been conducted on continental shelf area as a function of ocean depth or latitude. Unlike for terrestrial systems, there is not a dominant expectation in marine ecology for how habitat availability may vary across these axes.

The goal of this study is to assess changes in continental shelf area that species will face as they make range shifts into deeper depths or higher latitudes. We evaluate the regional changes in shelf area availability across depths and latitudes in the Pacific, Atlantic, and Indian Oceans. These bathymetric analyses highlight key areas where populations and communities may be enhanced or constrained by continental shelf area.

Methods

Habitat area by depth within LMEs

First, we assessed how continental shelf availability varies across depth at the scale of Large Marine Ecosystems (LME). Because of their distinct bathymetry, hydrology, productivity, and trophic interactions, LMEs are a useful regional unit to assess the extent and impact of depth shifts (Sherman & Alexander, 1986; Sherman & Duda, 1999). We obtained LME delinitations from the ScienceBase Catalog of the United States Geological Survey (*Large Marine Ecosystem Spatial Features*, 2017). We used the continental shelf definition from the Blue Habitats web portal (Harris et al., 2014a, 2014b), which included all submerged area adjacent to land and islands from the low water mark to the point where the slope increased markedly beyond a slope of 1:2000 and towards ocean depths (IHO, 2008). We note that LMEs contain areas deeper than the continental shelf, which is on average ~200m. Conversely, not all continental shelf regions are included by LMEs. Therefore, the LME shapefiles were trimmed to the continental shelf area to focus on continental shelf habitat within LMEs for the depth analyses. Continental shelf areas excluded from LME designation are left out of the depth analyses.

We used the ETOPO2 two arc-minute global digital elevation model (DEM) dataset to extract bathymetry for the continental shelf regions within LMEs (NOAA National Geophysical Data Center., 2006). The Blue Habitat shelf delineation primarily includes shallow shelf regions, but we excluded any areas with depths below 2000 meters to eliminate any misclassifications (0.01% of grid cells). We characterized the distribution of shelf area at depth by plotting hypsometric curves for each LME. Because of the deep bathymetry of the Central Arctic (LME 64) and the unique isolation of the Antarctic (LME 61), both polar LMEs were excluded from the analyses. Area in km^2 at each one meter depth bin was calculated using the area function of the raster package implemented in R (Hijmans, 2020; R Core Team, 2021). We verified that calculating area from projected polygons did not meaningfully change results (comparison in Supplementary Information).

We classified the depth distribution of LMEs into five categories based on the skew, modality, and uniformity of the hypsometric curve: Shallow-Dominant, Mid-Dominant, Deep-Dominant, Uniform, and Multimodal (Figure 1). Curves for which we were unable to reject the null hypothesis of a uniform distribution using the Kolmogorov–Smirnov test (p-value > 0.05) were classified as uniform (Kolmogorov, 1933; Smirnov, 1939). When uniformity was rejected, Hartigan's Dip Test was implemented in R to assess modality (Hartigan & Hartigan, 1985; Michaeler, 2016). Curves with a Dip Test statistic greater than 0.01 and p-value < 0.05 were categorized as Multimodal. All curves that did not meet the criteria for Multimodal or Uniform were categorized based on skew. Curves with skew values less than -1 were assigned to Deep Dominant, between -1 and 1 to Mid-Dominant, and greater than 1 to Shallow-Dominant.

Habitat area across latitude

To analyze the changes in seafloor area experienced by species shifting poleward, we joined together the continental shelf components of LMEs along each continental boundary. We analyzed changes in habitat availability from low to high latitudes for the West Pacific, East Pacific, West Atlantic, East Atlantic, West Indian, and East Indian continental shelves. For coastlines not contained within LMEs (i.e., southern coast of Sumatra and Papua New Guinea), we supplemented the LME-restricted ETOPO2 bathymetric rasters with ETOPO2 bathymetric rasters trimmed to continental shelf areas within FAO major marine fishing areas (FAO, 2019; Area 57 assigned to East Indian and Area 71 assigned to West Pacific). Large islands were kept in the analysis if they were a part of a mainland LME (e.g. Madagascar), but excluded if they were an individual LME (e.g. New Zealand). For reasons described in the previous section, the Central Arctic and Antarctic LMEs were again excluded from these analyses. Again, we used the Blue Habitat shelf delineation to restrict analyses to the continental shelf. We calculated area in km^2 of the continental shelf for 2° latitudinal bins using the area function of the raster package implemented in R (Hijmans, 2020; R Core Team, 2021). We again verified that calculating area from projected polygons did not meaningfully change results (comparison in Supplementary Information). Additionally, we calculated the percent change in seafloor area from each bin to the next poleward bin. The 2˚ latitudinal bin size is representative of the average range shift for marine species over a forty year period (Lenoir 2020). The International Union for the Conservation of Nature classifies species that have experienced a 50% loss in habitat or population as Vulnerable to Extinction (IUCN Standards and Petitions Committee, 2019), therefore we identified locations where there was either doubling (Expansion) or halving (Contraction) in seafloor area from one 2˚ latitudinal bin to the next poleward bin. Finally, to assess the overall pattern in habitat availability over latitude, we regressed the continental shelf areas of each bin against the bin mid-latitudes and extracted the slope and the p-value of the resulting linear model.

Estimating changes in species richness using species area curves

To calculate the potential change in species richness associated with a given change in continental shelf area, we used the species area relationship (SAR) developed for fishes along the Northeast Pacific coast: $S = 16.18 * A^{0.226}$ (Levin et al., 2009). Assuming all species underwent a latitudinal shift of 2˚ (the approximate expected latitudinal shift over four decades; Lenoir et al., 2020) or a depth shift of 15 meters (the approximate expected depth shift over four decades; Dulvy et al., 2012), we calculated the anticipated the change in species richness communities will experience as they move into the neighboring poleward latitudinal bin or the next depth bin in each LME.

Results

Available habitat across depth within LMEs

Overall, 22% of LMEs were classified as Shallow-Dominant, 9% were classified as Mid-Dominant, and 69% were classified as Multimodal (Figure 1, Figure 2). No LMEs were classified as Deep-Dominant or Uniform. In response to a 15 m shift deeper, individual assemblages (defined as 15 m depth bins) experience a change in shelf area ranging from an increase of 114,000 km^2 within the East Siberian Sea (LME 56) to a decrease of 240,000 km^2 within the Northern Bering - Chukchi Seas (LME 54; Supplementary Figure 2).

Available habitat across latitude

Continental shelf availability varied with latitude across all six contiguous coastlines (Figures 3-5). Each coastline exhibited multiple instances of contraction (halving of shelf area) and expansion (doubling of shelf area) associated with 2˚ poleward shifts (Figures 3-5). Contractions were proportionally most common along the Southern East Indian coastline (29% of poleward shifts), and least common in the Northern West Indian coastline (no contractions; Figure 6). Expansions were proportionally most common along the Northern West Indian coastline (36% of poleward shifts), and least common along the Northern West Atlantic coastline (2.4% of poleward shifts; Table 1 and Figure 6).

Most regions exhibited significant relationships between continental shelf area and latitude (Table 1; Figs. 3-5). On average, shelf area decreased towards the poles along the coastline of the Southern West Pacific. In contrast, shelf area increased towards the poles along coastlines of the Northern West Pacific, the Northern East Pacific, the Southern West Atlantic, the Northern West Indian, the Northern East Atlantic, the Northern West Atlantic, and the Southern East Atlantic. No significant relationship between latitude and continental shelf area was found along the coastlines of the Southern West Indian, Southern East Indian, Northern East Indian, or Southern East Pacific (Table 1).

Expected change in species richness

Defining an assemblage as the species within a 2˚ latitudinal band that then shifts 2˚ poleward, species area relationships predicted changes ranging from a gain of 91 in part of the Southern East Indian to a loss of 116 in part of the Northern East Pacific (Figs. 3 & 5). Proportionally, part of the Southern West Pacific experienced the largest decline in richness (54% loss) and part of the Northern East Pacific experienced the largest increase in richness (67% gain) (Fig. 3). On average across all ocean coastlines, communities gained one species with the change in area expected with a 2 latitudinal shift (Figs. 3-5).

Defining an assemblage as the species within a 15m depth band that then shifts 15 deeper, species area relationships predicted changes ranging from a gain of 67 in a depth band of the East China Sea (LME 47) to a loss of 89 in a depth band of the Yellow Sea (LME 48) (Supplementary Figure 3). Proportionally, part of the Scotian Shelf (LME 8) experienced the largest decline in richness (57% loss), and part of the Somali Coastal Current (LME 31) experienced the largest increase in richness (69% gain) (Supplementary Figure 3). On average across all ocean coastlines, communities within 15 m depth bins lost three species with a 15 m deeper depth shift (Figure 1, Supplementary Figure 3).

Discussion

Continental shelf area is a limiting resource for a diverse array of marine organisms that depend on shallow and structured zones with high productivity and biodiversity (Buhl-Mortensen et al., 2012; García-Reyes et al., 2015; Townsend et al., 2004). As species shift deeper and poleward in response to climate change, we expect the continental shelf available to them to change depending on local bathymetry. Shelf area serves as a first degree constraint on successful range shifts, but to our knowledge, this is the first assessment of continental shelf area variation by depth and latitude. Similar to terrestrial mountain ranges (Elsen & Tingley, 2015), the majority of marine ecosystems do not exhibit a monotonic decrease in continental shelf area as species move deeper. Additionally, there is tremendous variation in how shelf habitat availability varies by latitude. Whether range shifts across and down the continental shelf will lead to an opportunity for growth or decline at the level of the species and the community depends on regional bathymetry.

Habitat availability across depths and latitudes

Movement deeper onto the continental shelf does not always coincide with a loss in shelf area. For most LMEs, shelf area is either most abundant at moderate depths or there are multiple depths at which shelf area is most readily available. As a result, the change in habitat availability as species shift deeper will be regionally specific due to differing geomorphology. Similar results were found to be true when assessing how continental shelf area will change with projected sea level rise (Holland, 2012). This pattern of regional variability also matches those for habitat at elevation across terrestrial mountain ranges

(Elsen & Tingley, 2015). The lack of LME's exhibiting Deep Dominant distributions reveals that while regions exhibiting monotonic decreases in habitat with depth are uncommon, regions exhibiting monotonic increases in habitat with depth are nonexistent. In some regions, species shifting deeper will experience increased shelf availability, but if species are forced to move past a certain depth threshold, shelf availability will decline precipitously.

Across latitudes, species are likely to encounter substantially different changes in habitat availability, including expansions in the Northern West Indian Ocean and contractions along the Southern East Indian Ocean. Larger shelf areas have the potential to support larger population sizes of individual species, in addition to higher overall species richness (Chisholm et al., 2018; MacArthur & Wilson, 1967; Melbourne & Hastings, 2008; Shaffer, 1981). The most notable contrast between continental shelf distribution in the Northern versus the Southern Hemisphere is apparent in the transition from temperate to polar regions. For species in the Northern Hemisphere, nearly continuous shelf habitat between the equator and the poles serves as a corridor for species to move into the continental shelf habitats of the Arctic Ocean. In contrast, species in the Southern Hemisphere face 100s of kilometers of deep ocean between the most southern points of Oceania, Africa, and South America and the deep and narrow shelves of Antarctica. Habitat continuity for species in the southern hemisphere is truncated at 55˚S, while the complementary pathway for species in the northern hemisphere to latitudes above 80˚N. This break in habitat continuity, in tandem with the Antarctic Polar Front and the Antarctic Circumpolar Current, has limited poleward range expansion of species through evolutionary time (Rogers, 2007; Wilson et al., 2016). However, evidence is accumulating for some dispersal of plant and invertebrate species across the Antarctic Polar Front through rafting and rare long distance dispersal events which may facilitate some range shifts of a diverse array of species despite the lack of contiguous continental shelf area (Bernardes Batista et al., 2018; Fraser et al., 2017).

Shifts in climate regime through the geologic record and subsequent changes in species distributions and richness provide context for the role of continental shelf area in shaping modern range shifts in the ocean. The Late Ordovician greenhouse–icehouse transition led to a mass extinction of an estimated 85% of marine species (Sheehan, 2001). Similar greenhouse-icehouse transitions occurred later in the Cenozoic, but did not lead to the same magnitude of loss in species globally. This inconsistency can be partially explained by differences in the continental configurations. The Late Ordovician planet was characterized by isolated island continents which would have limited the capacity for species to shift their ranges into more suitable habitat. In contrast, the latitudinally oriented coastlines present today were also largely formed by the Cenozoic, allowing for poleward shifts in distributions and therefore reducing overall extinction risk (Finnegan et al., 2016).

Impacts of shelf habitat availability on populations and species richness

Population sizes vary with habitat availability (Alzate et al., 2019; Halpern et al., 2005). Larger habitats provide more resources for individuals, supporting a larger population. Small populations run the risk of stochastic extinction and restricted growth due to Allee effects (Aalto et al., 2019; Hanski et al., 1996; Kuparinen et al., 2014; Opdam & Wascher, 2004; White et al., 2021). Range shifts into depths or latitudes of reduced shelf habitat availability may lead to local extinction or the inability to establish. In contrast, shifts into depths or latitudes of increased shelf habitat may lead to increased population growth rates as individuals of a species take advantage of increased space and foraging opportunities.

Given that species area relationships suggest that the number of species scales with habitat size, we expect latitudes and depths of greater continental shelf area to support a larger number of species as niche space, resource availability, and likelihood of species arrival increase (Chisholm et al., 2018; MacArthur & Wilson, 1967; Rosenzweig, 1995). Shifts in latitude and depths have the potential to impact regional species richness as the number of species able to successfully shift is limited by continental shelf area. The anticipated changes in species richness due to variations in shelf area are tightly linked to geographic features at the local and regional scale. For one, because of the non-linearity in species area relationships, we predict much more dramatic shifts in richness across latitudes and depths in areas of overall limited shelf habitat in comparison to areas defined by wide continental shelves. For example, changes in species richness as a result of equatorward shifts along the tropical and temperate regions of the East Pacific will reflect changes from a baseline narrow shelf area. In contrast, changes in richness along the Northern Atlantic coasts will likely be muted due to the wide shelf habitats in these regions. Using species area curves ignores the complexities of endemic versus cosmopolitan distributions and assumes species are randomly distributed (He & Hubbell, 2011) and our calculations must therefore be viewed cautiously. However, our analyses identify regions at a higher risk of species loss and regions that may serve as biodiversity refuges.

Other barriers to successful range shifts

Availability of continental shelf habitat acts as a first-order constraint on movement poleward and deeper. However, other constraints will likely be important for particular species, including availability of biogenic habitat, prey, or mutualists (Brooker et al., 2007; Urban et al., 2019) and the presence of predators or competitors (Bates et al., 2014; Gilman et al., 2010; McIntosh et al., 2018; Spence & Tingley, 2020). Changes in habitat area offers a proxy for expected trends in richness and population sizes, but these patterns can be complicated by species interactions. Movement into depths or latitudes with more shelf habitat may actually lead to a decline in population growth for some low trophic species due to an increased risk of predation (McIntosh et al., 2018). In the case of depth shifts, many species of plants and algae that form the foundation for many types of marine structures only grow in the photic zone. The intensity of light decreases exponentially with depth and can restrict the productivity of photosynthetic organisms like seagrasses and coral symbionts (Duarte, 1991; Kahng et al., 2019; Lesser et al., 2021). Light can also constrain latitudinal shifts because highly seasonal diel cycles lead to reduced nutrient availability and limited opportunities for visual foraging in the winter (G. Chen & Wang, 2016; Last et al., 2020; Ljungström et al., 2021).

Range shifts are also limited by abiotic habitat. The distribution of abiotic habitat is determined by geologic history, and therefore stationary in ecological time (Ford & HilleRisLambers, 2020; Spence & Tingley, 2020). Marine species highly dependent on a particular substrate, rugosity, or geologic feature will be limited in their ability to track temperature isotherms poleward or deeper (Champion & Coleman, 2021; Harman et al., 2003; McHenry et al., 2019), similar to plant communities limited by soils (Carteron et al., 2020; Smithers & North, 2020). The potential for marine species to occupy thermally suitable continental shelf habitat may also be limited by water characteristics as ideal temperature conditions do not guarantee tolerable pressure, oxygen, or pH conditions. A number of LMEs, including the California Current , Benguela Current, the Arabian Sea, and the Bay of Bengal have Oxygen Minimum Zones (OMZ) that span from roughly 200m to 1000m in depth (Al Azhar et al., 2017; Bograd et al., 2008; Zettler et al., 2009). Marine ectotherms have specific oxygen requirements to maintain effective metabolism, and therefore most are limited to depths above the OMZ (Stramma et al., 2012). Latitudinal variation in pH can also limit successful poleward range shifts. Because of the tilt of the earth on its axis and circulation patterns in the ocean, the most acidic waters are found in polar regions. These same regions are also experiencing the fastest rates of ocean acidification, posing a challenge for growth and reproduction for a wide array of marine ectotherms, most notably calcifying species (Fabry et al., 2009; Qi et al., 2017; Yara et al., 2012). Even when continental shelf habitat is available, range shifts may be restricted due to both biotic and abiotic factors.

Regions of opportunity, and regions of concern

We have highlighted areas with reductions in continental shelf habitat where shifting species may face challenges. These areas include Shallow-Dominant LMEs and areas of coastline where substantial contractions in continental shelf habitat occur. Species that experience warming and are living in regions with limited shelf area in adjacent regions are most at risk. For example, the Arabian Sea exhibits a Shallow-Dominant shelf bathymetry and its semi-enclosed basin limits latitudinal movement (Ben-Hasan

& Christensen, 2019). Warming, coupled with declining oxygen concentrations has already led to a rise in Harmful Algal Blooms and resultant fish kills in this relatively understudied region (Al Azhar et al., 2017; Ben-Hasan & Christensen, 2019; Harrison et al., 2017). Other regions pose risks to resident species due to less conspicuous latitudinal restrictions. One example is the East Japan Sea, which has experienced consistent warming of up to 0.5˚C since the 1960s and shoaling of the OMZ (Kim et al., 2001). On top of rising temperatures and declining access to oxygenated waters, continental shelf habitat in this region is limited. Shelf area contracts 77% as species shift from 38˚ to 40˚ N, and remains limited until 56˚ N when the wide shelf of the Bering Sea becomes accessible.

We have also highlighted regions where species may benefit from continental shelf expansions as a result of tracking temperature isotherms deeper and poleward. LMEs across the globe exhibit opportunities for range expansion into deeper continental shelf habitat, if light and other factors are not limiting. The rapidly warming North Sea's (LME 22) Multimodal depth distribution may partially explain why many species have successfully shifted deeper in this region (Dulvy et al., 2012). Additionally, species moving poleward along each coastline will have opportunities to take advantage of expansions in shelf area. For example, species shifting from Brazil south towards the coasts of Uruguay and Argentina will gain access to wider continental shelves. Similarly, species shifting poleward along the eastern coast of Australia will gain access to more shelf habitat as they move with the Leeuwin Current into the Great Australian Bight along the continent's southern coast.

This information can be used to prioritize conservation efforts at a broad scale, focusing on regions where species will experience the greatest reductions in seafloor area following predicted range shifts. Designation of protected areas that include latitudinal corridors and implementation of climate-ready management in high risk regions to limit habitat degradation, pollution, and resource extraction may help facilitate successful range shifts despite limited continental shelf availability (Frazão Santos et al., 2020; Meyer-Gutbrod et al., 2018; Mills et al., 2013).

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Figures and Tables

Table 1. Percent of total 2˚ latitudinal bin shifts that experienced a doubling (expansion) or halving (contraction) in habitat area. Coefficient and p-value of linear model for area versus latitude is also reported for each hemisphere-region combination.

Coastline	Hemisphere	% of 2˚ Shifts Contractions	% of 2˚ Shifts Expansions	Coefficient $km^2/1˚$ Latitude	P-value
West Pacific	Northern	5.0	5.0	5094	0.00038
West Pacific	Southern	17	8.7	-6999	3.4×10^{-6}
East Pacific	Northern	13	16	2327	3.2×10^{5}
East Pacific	Southern	11	25	131	0.19
West Atlantic	Northern	9.8	2.4	1135	0.0059
West Atlantic	Southern	11	7.4	1974	2.8×10^{6}
West Indian	Northern	0.0	36	3768	0.00016
West Indian	Southern	22	33	701	0.10
East Atlantic	Northern	10	13	6586	4.8×10^{-8}
East Atlantic	Southern	11	11	615	0.013
East Indian	Northern	10	10	1238	0.34
East Indian	Southern	29	21	-410	0.49

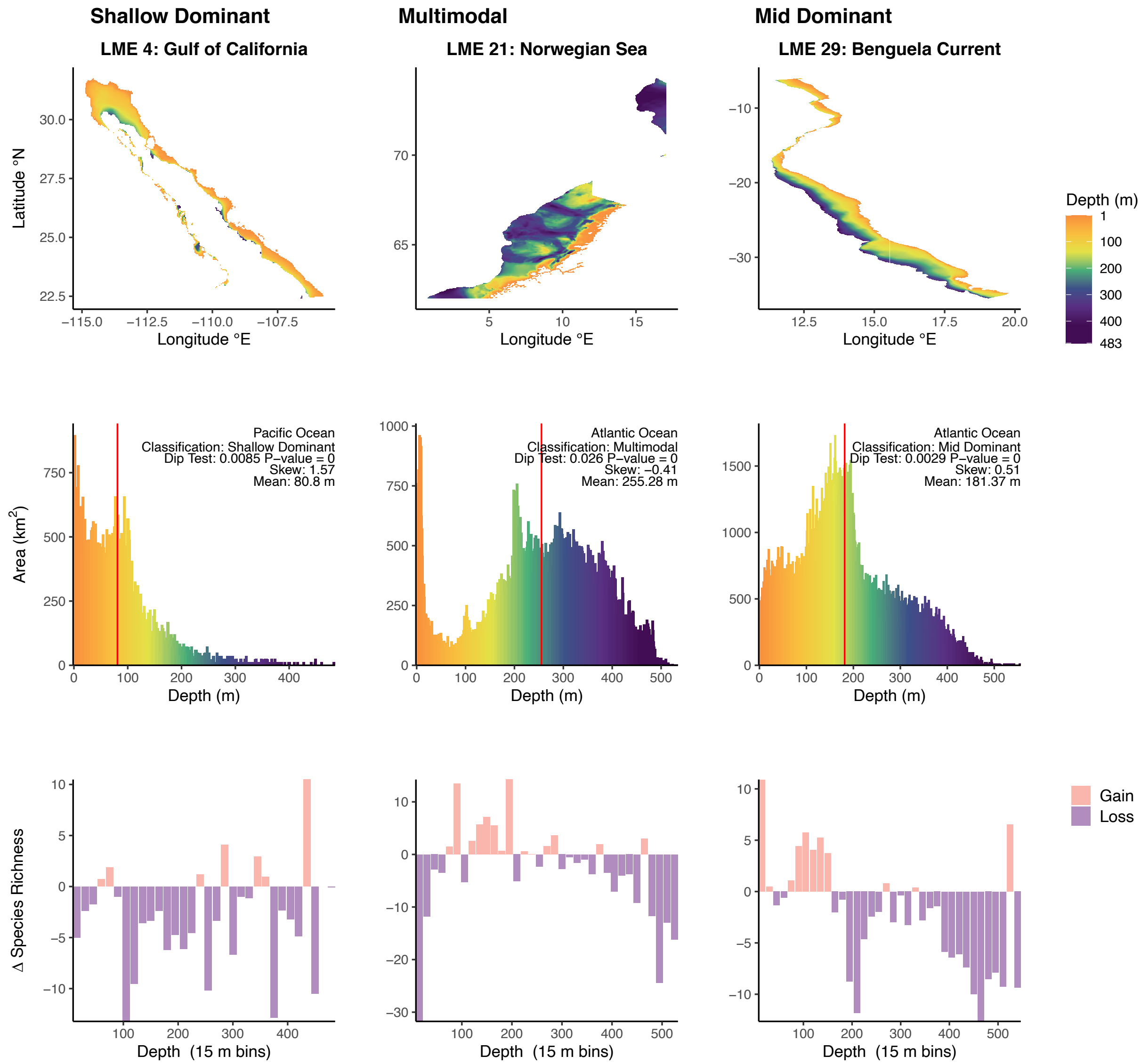

Figure 1. Example classifications for how habitat availability changes with depth within a LME. Depth distribution map (above), hypsometric curve (middle), and species area relationship richness predictions (bottom). Deep Dominant and Uniform are not shown as no LMEs were assigned to these types. Color represents depth (above, middle), and the vertical red bar on the hypsometric curves (middle) indicate mean depth for the LME. Predicted change in species richness was calculated for a 15 meter depth shift using a species area relationship (bottom). See Supplementary Figures 1-3 for depth maps, hypsometric curves and change in species richness for all 64 LMEs.

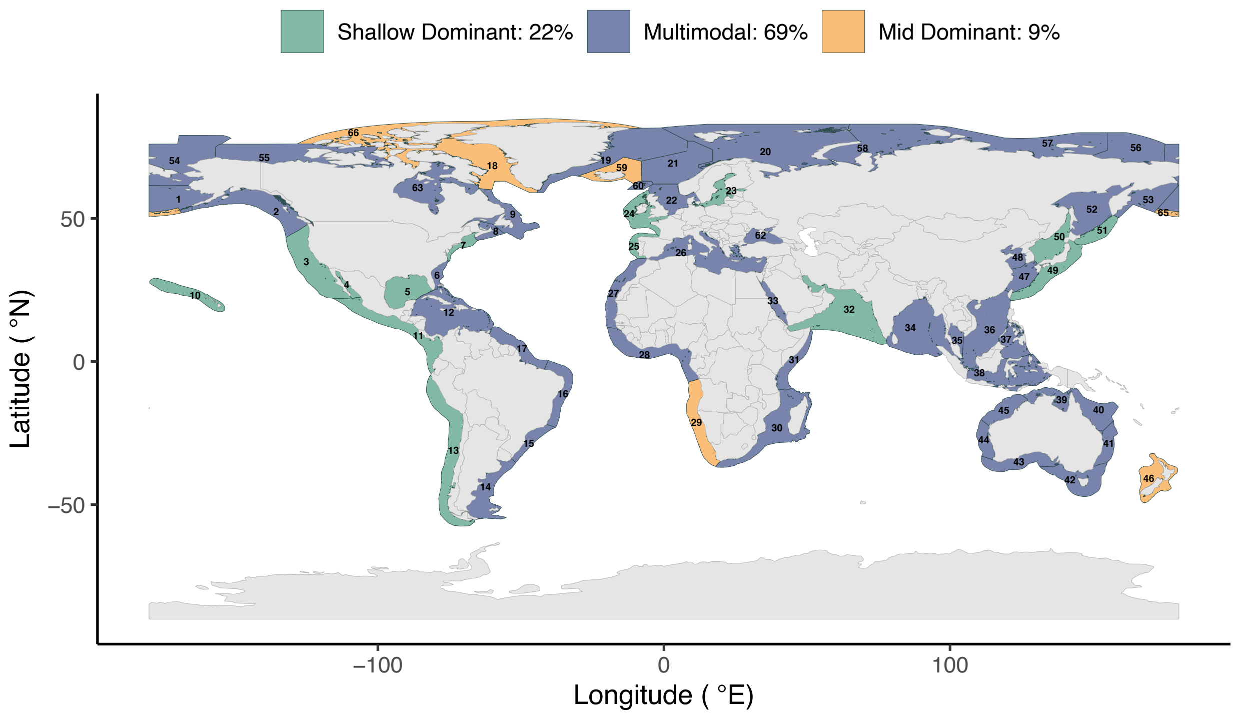

Figure 2. World map with 64 LMEs colored by depth distribution classification. No LMEs were classified as Deep Dominant or Uniform.

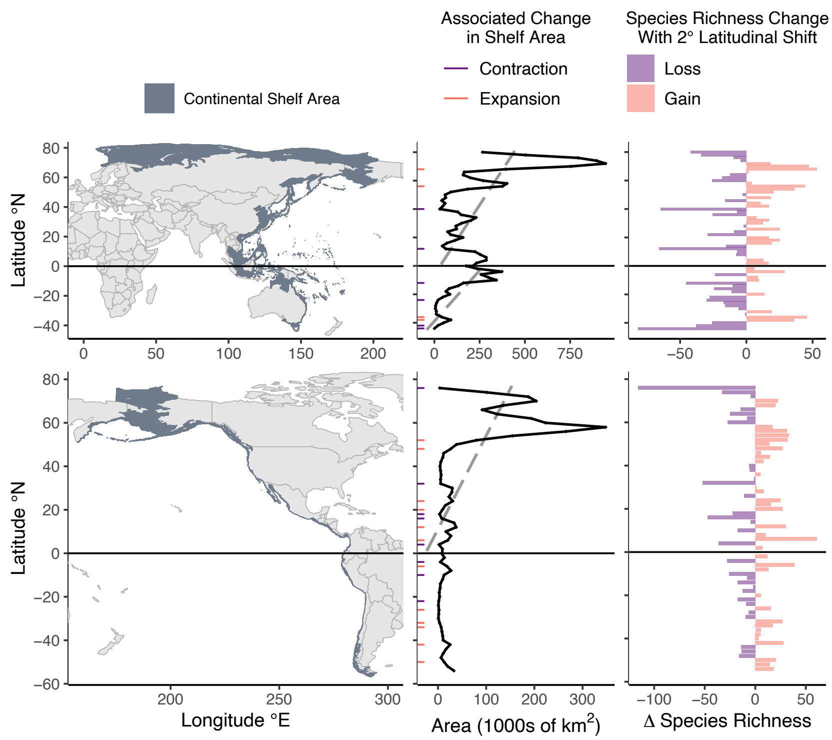

Figure 3. Continental shelf habitat availability by latitude along the western (upper) and eastern (lower) Pacific Ocean basin. Left panels show distribution of shelf habitat along coastlines of the Pacific. Middle panels show shelf habitat availability within 2˚ latitudinal bins in 1000s of km^2. Poleward shifts that involve at least a halving of area (contraction) or a doubling of area (expansion) of continental shelf habitat area are highlighted in purple and orange, respectively. Grey dashed line represents the best fit linear model for area versus latitude where the coefficient is significant ($p < 0.05$). Right panels show the predicted losses (purple) and gains (orange) in species richness from a 2˚ latitudinal shift using a species area relationship.

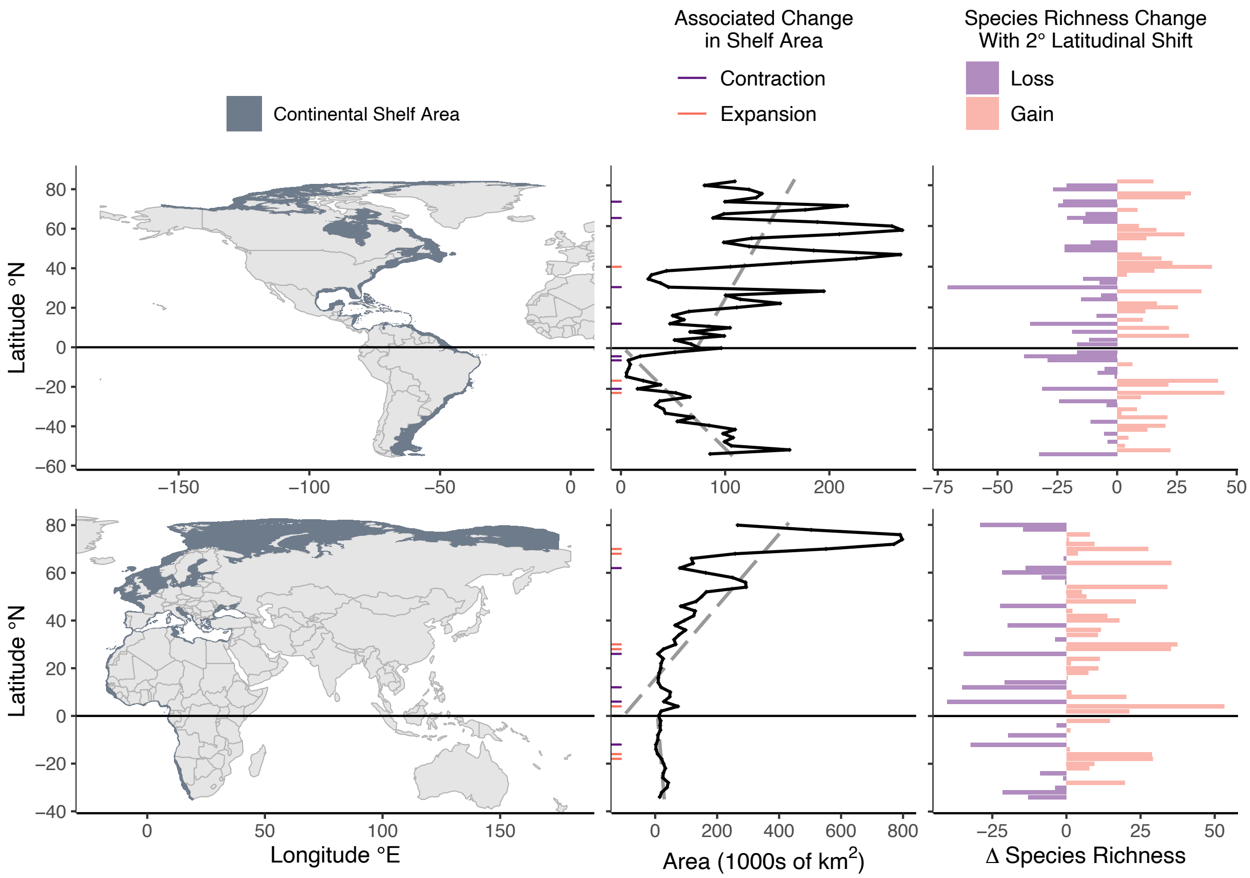

Figure 4. Continental shelf habitat availability by latitude along the western (upper) and eastern (lower) Atlantic Ocean basin. Otherwise, see legend for Fig. 3.

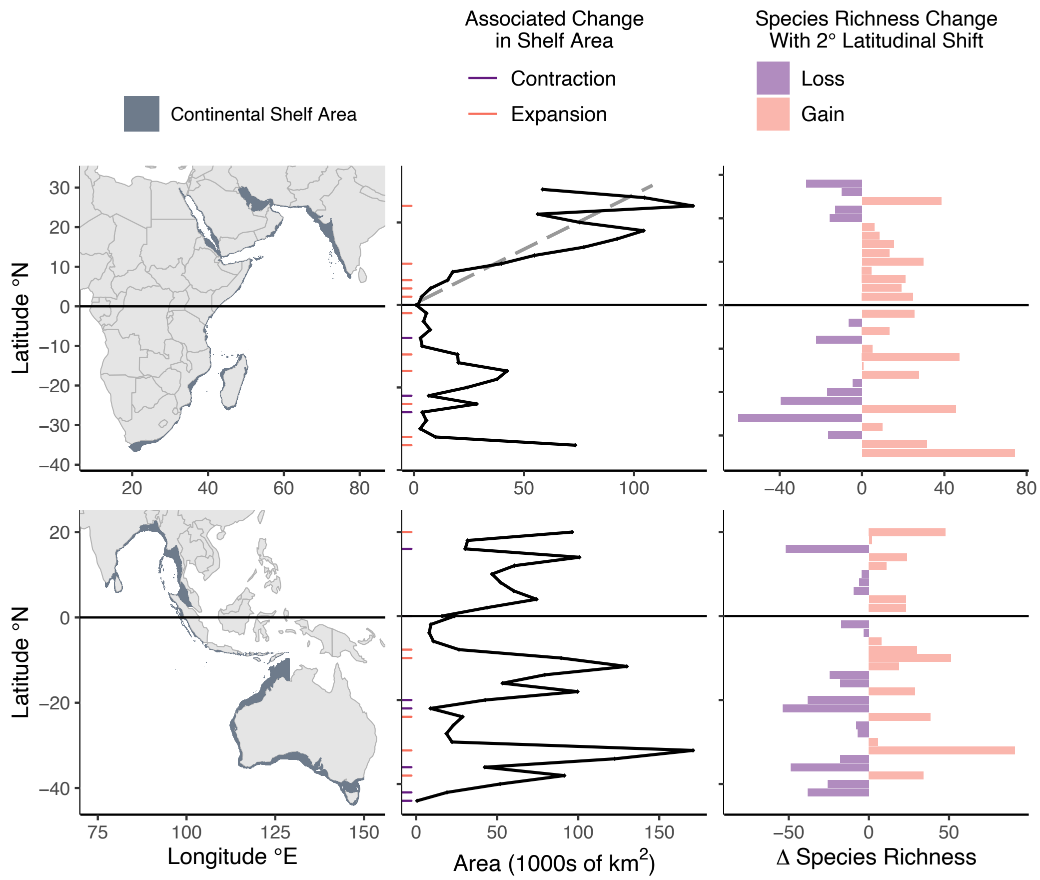

Figure 5. Continental shelf habitat availability by latitude along the western (upper) and eastern (lower) Indian Ocean basin. Otherwise see legend for Fig. 3.

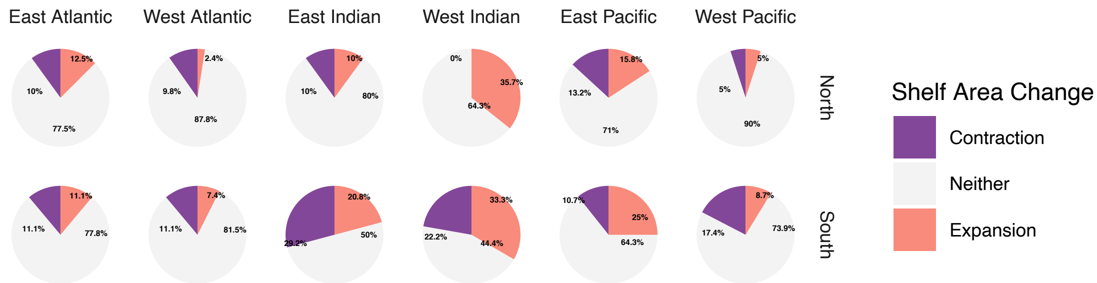

Figure 6. Proportion of 2˚ poleward shifts associated with a substantial contraction (purple) or expansion (orange) of continental shelf habitat for east and west coastlines of the three focal ocean basins. Poleward shifts that would experience between a halving or doubling of area are shown in grey.