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DISTRIBUTION RANGES OF COMMERCIAL FISHES AND INVERTEBRATES[1]

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ABSTRACT

Distribution ranges of commercial fish and invertebrates are required by the *Sea Around Us* Project for mapping of global fisheries catches. However, published ranges exist for only a small fraction of the 1231 taxa, composed of 923 species, 161 genera and 147 higher groups used in the latest version of the mapping process (Version 3.1, representative of catches from 1950 to 2003).

This paper summarizes the methods employed by the *Sea Around Us* Project to reduce potentially global distributions to realistic ranges by identifying key ecological information for each of the 1231 commercial taxa, specifically: (i) presence in FAO area(s); (ii) latitudinal range; (iii) range-limiting polygons; (iv) depth range; and (v) habitat preferences. Furthermore, this paper presents an additional filter that outlines how (ii) and (iv) are used to correct the depth range for the effect of 'equatorial submergence.' Several examples are used to illustrate this process, notably the Florida pompano (*Trachinotus carolinus*) and the Silver hake (*Merluccius bilinearis*).

Throughout this paper, the data sources emphasized include FishBase, other fish and invertebrate databases, and online information where applicable. In addition, simple heuristics are used to replace ecological information that is unavailable or missing.

It should be noted that the *Sea Around Us* Project does not explicitly use temperature and primary production for any of the procedures discussed in this paper. The purpose of this is to allow for subsequent analyses of distribution ranges using these variables.

INTRODUCTION

The *Sea Around Us* Project, hosted at the Fisheries Centre, University of British Columbia, is a research initiative devoted to documenting the effects of fisheries on marine ecosystems worldwide and to propose methods to mitigate these impacts. One of the key elements of this work is mapping of marine fisheries catches onto the ecosystems from which they were extracted. The approach used therein is documented in Watson *et al.* (2004) and its results, regularly updated, are available on the project website (www.seaaroundus.org). This mapping approach depends crucially on the availability of distribution ranges for all taxa (species, genera, etc) reported in marine fisheries catch statistics. Previous mapping of catches relied on distributions constructed from a mixed set of ecological information that resulted in varying degrees of accuracy.

This paper, therefore, documents a major revision of all commercial distribution ranges (totaling 1231 for the time period 1950 – 2003) using a set of rigorously applied filters that markedly improved the accuracy and appearance of the *Sea Around Us* Project maps and other products. These filters include: (i) presence in FAO area(s); (ii) latitudinal range; (iii) range-limiting polygons; (iv) depth range; (v) habitat preferences; and (vi) accounting for the effect of 'equatorial submergence' (Ekman, 1967) Two sample taxa are used to illustrate the results of the filter process, the Florida pompano (*Trachinotus carolinus*) and the Silver hake (*Merluccius bilinearis*), each representing pelagic and demersal species, respectively. Other species are used to illustrate specific aspects of this filter process, and are referred to in the appropriate section.

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The procedures presented here avoid use of temperature and primary production to define or refine distribution ranges for any of the taxa. This was done in order to allow for subsequent analyses of distribution ranges to be legitimately performed using these variables. This differs from previous construction methods of distribution maps that used primary production to distinguish area of low *vs.* high abundance within a taxon's distribution range (Watson *et al.*, 2004).

Material and Methods

The 'filters' used here are listed in the order that they are applied; each filter is documented with a figure and a short description of major sources for the information required at that level.

Prior to the 'filter' approach presented below, the identity and nomenclature of each taxon was verified using FishBase (www.fishbase.org) and other sources, and the English common names and scientific names were updated.

Filter 1: FAO Area

The United Nations Food and Agriculture Organization (FAO) has divided the world's oceans into 18 areas for statistical reporting purposes (Figure 1). Information on the occurrence of commercial taxa within these areas is available primarily through: (a) FAO publications and the FAO website (www.fao.org) and (b) FishBase. Figures 2a and 3a illustrate FAO area occurrence of Silver hake and Florida pompano respectively.

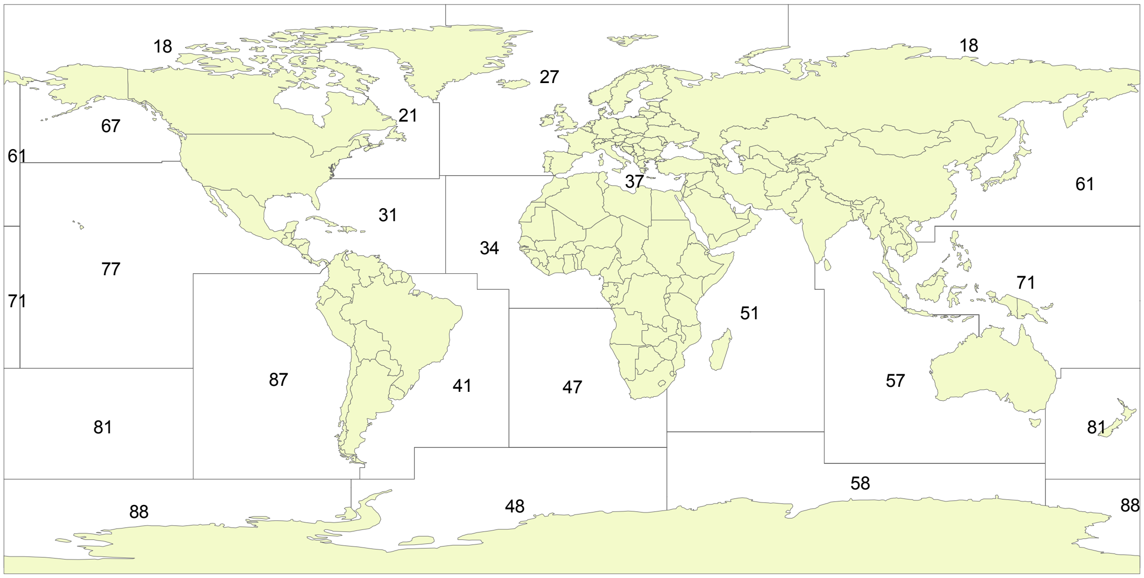
Filter 2: Latitudinal range

The second filter applied in this process is latitudinal ranges. Charles Darwin, after reviewing literature on the distribution of marine organisms, concluded that "latitude is a more important element than longitude" (see Pauly 2004, p. 125, for the sources of this and the quote below).

This does not mean, however, that longitude and other factors do not play a role in determining a taxon's distribution. Still, in the following quote, Darwin illustrates how latitude provides the key to understanding the composition of certain fauna: "Sir J. Richardson says the Fish of the cooler temperate parts of the S. Hemisphere present a much stronger analogy to the fish of the same latitudes in the North, than do the strictly Arctic forms to the Antarctic."

Latitudinal range is defined as a taxon's northernmost and southernmost latitudes of what is considered their 'normal' distribution range and can be found in FishBase for most fishes. For other fishes and invertebrates, latitudes were inferred from the latitudinal range of countries that reported them, and/or from occurrence records in the Ocean Biogeographic Information System website (OBIS; www.iobis.org).

A further refinement of a taxon's latitude range can be defined by its relative occurrence throughout its latitudinal range. From first principles, a taxon can be assumed to be most abundant at the center of its range (McCall, 1990). In cases of distributions confined to either of the two hemispheres, this is approximated by a symmetrical triangular distribution peaking at the mean of the northernmost and southernmost latitudes. For distributions that straddle the equator, it is assumed that a taxon's range can be broken into three parts – the outer two thirds and the inner or middle third. If the equator falls within one of the outer thirds of the latitudinal range, then the abundance is assumed to be the same as above, and thus the symmetrical triangular distribution can be applied. If, however, the equator falls in the middle third of the range, then the abundance distribution is assumed to be flat in the middle third and decreasing to the poles for the remainder of the distributions range. Figures 2b and 3b illustrate the result of the FAO and Latitudinal filter combined. Both the Silver hake and the Florida pompano follow the symmetrical triangular distribution as noted above.



FAO #	FAO Name	FAO #	FAO Name	FAO #	FAO Name
21	Atlantic, North West	48	Antarctic (South Atlantic)	87	Pacific, South East
27	Atlantic, North East	51	Indian, West	18	Arctic Sea
31	Atlantic, West Central	57	Indian, East	61	Pacific, North West
34	Atlantic, East Central	58	Antarctic (South Indian)	71	Pacific, West Central
37	Mediterranean & Black Sea	67	Pacific, North East	81	Pacific, South West
41	Atlantic, South West	77	Pacific, East Central	88	Antarctic (South Pacific)
47	Atlantic, South East				

Figure 1 The 18 areas of the world's oceans that the United Nations Food and Agriculture Organization (FAO) uses for statistical reporting purposes.

Filter 3: Range-limiting polygons

The third filter in the distribution process is the use of range-limiting polygons. Range-limiting polygons help to confine species in areas where they are known to occur and also to prevent occurrence in semi-enclosed seas (e.g., of low salinity) where the taxon does not occur, but which are otherwise located within its FAO areas, latitude and depth ranges.

Polygonal distributions for a vast number of species of commercial fish and invertebrates can be found in various publications, most notably those of FAO (species catalogues, species identification sheets, guides to the commercial species of various countries or regions), and in various online sources.

For taxon without published polygons, the filters described in this paper were used to generate range maps from which polygons were then drawn. In the case of many invertebrates, however, this procedure was reversed, whereby the countries that reported the taxon are used as the taxon's occurrence. In these instances, particular emphasis was given to the FAO statistics, where countries that reported the taxon in their catch were used as occurrence. However this method was not used if the taxon was caught by the country's distant water fleet.

In addition to the above polygonal methods, faunistic works that cover the high-latitude end of continents and/or semi-enclosed coastal seas with depauperate faunas (e.g., Hudson Bay, or the Baltic) were used to avoid, where appropriate, distributions reaching into these extreme habitats. Polygons were then drawn resembling those published for similar species, i.e., at similar distances from coastlines.[2]

All available polygons, whether available from a publication or newly drawn, were digitized used ESRI's ArcGIS and stored in the *Sea Around Us* Project's database, along with the latitude ranges derived from them, which were then used for inferences on equatorial submergence (see below).

Figures 2c and 3c illustrate the result of the combination of the first three filters, i.e., FAO, latitude and range-limiting polygons. These parameters and polygons will be revised periodically, as our knowledge of the species in question increases.

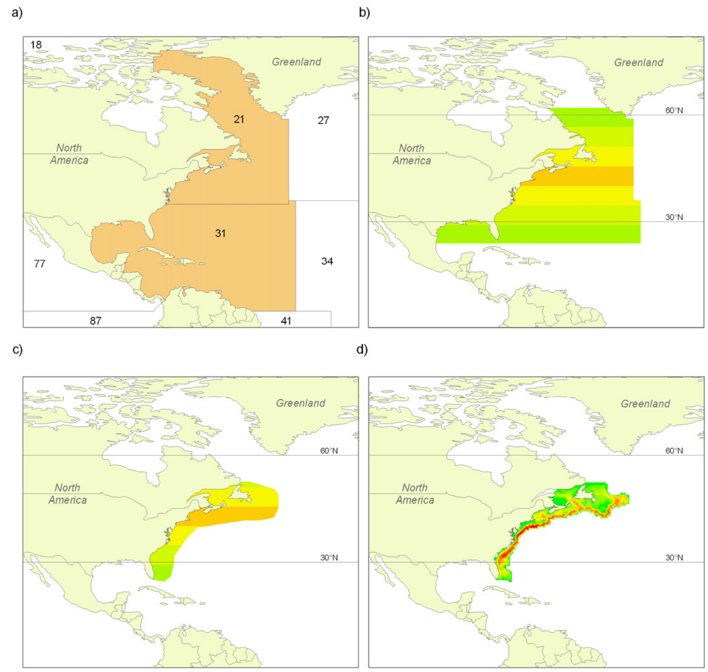


Figure 2 Sequence of filters used for deriving the species distribution range of the Silver hake (*Merluccius bilinearis*): (a) illustrates the Silver hake's presence in FAO areas 21 and 31; (b) illustrates the result of applying the FAO and latitudinal range (24°S to 62°N); (c) shows the result of applying the FAO, latitudinal, and the range-limiting polygon; and (d) illustrates the final result after the application of the four filters.

Habitat parameters for higher taxa

It should be noted that, because the *Sea Around Us* Project mapping process only deals with commercially-caught species, the distribution ranges for higher level taxa (genera, families, etc) were generated using the combination of range polygons from the taxa level below it. Thus, the range polygons for genera were built using the range polygons of the commercial species that fall within them. Similarly, family-level polygons were generated from genus-level polygons, and so on. Latitude ranges, depth ranges and habitat preferences were expanded in the same manner.

While this procedure does not mimic the true distribution of the genera in question, which usually consists of more species than are reported in catch statistics, it is likely that the generic names in the catch statistics refer to the very commercial species that are used to generate the distribution ranges, as these taxa are frequently more abundant.

However, to avoid misunderstandings, the number of species used in generating such generic distribution ranges will be made visible where appropriate, and the maps will be referred to as catch distributions, rather than taxon range distributions.

[2] Some of these polygons were obtained by making our GIS system (see below) 'buffer' the distribution ranges resulting from Filter 1, 2 and 4. This yielded polygons slightly different in appearance from the others, but which met our needs, nevertheless.

Filter 4: Depth range

Similar to the latitudinal range, the 'depth range', i.e., "[t]he depth (in m) reported for juveniles and adults (but not larvae), from the most shallow to the deepest [water]", is available from FishBase for most fish species, along with the common depth, defined as "[t]he depth range (in m) where juveniles and adults are most often found. This range may be calculated as the range within which approximately 95% of the biomass occurs" (Froese *et al.*, 2000).

When the depth range for a taxon was not available, it was obtained from FAO (species catalogues, species identification sheets, and guides to the commercial species of various countries or regions), or online sources. One of these sources was OBIS where, in some cases, the deepest record was taken to estimate a taxon's maximum depth. Where no information was available, the depth range of a similar species was applied.

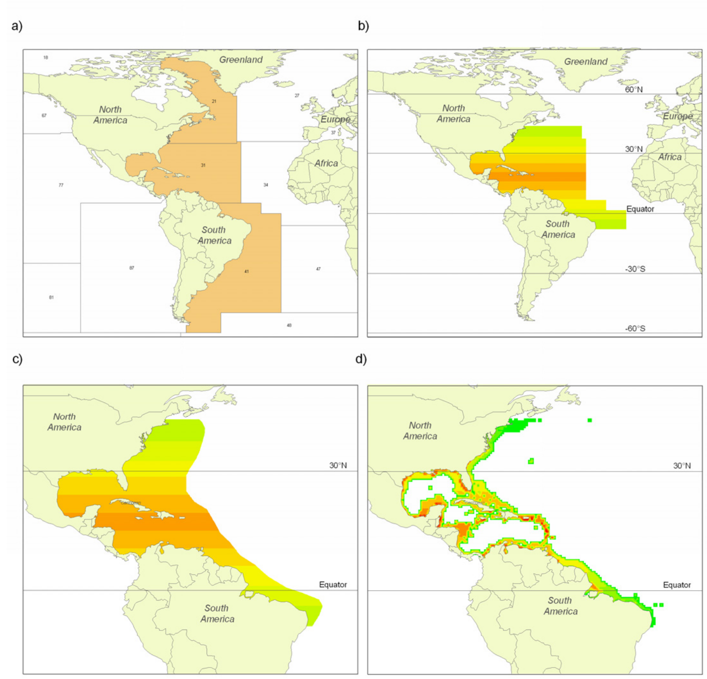


Figure 3 Sequence of filters used for deriving the species distribution range of the Florida pompano (*Trachinotus carolinus*): (a) illustrates the Florida pompano's presence in FAO areas 21, 31, and 41; (b) illustrates the result of applying the FAO and latitudinal range (43°S to -9°N); (c) shows the result of applying the FAO, latitudinal, and the range-limiting polygon; and (d) illustrates the final result after the application of the four filters.

A further refinement of a taxon's depth range is its relative abundance within the water column. Based on Alverson *et al.* (1964), Pauly and Chua (1988), Zeller and Pauly (2001) and other sources, it was assumed that the abundance of a taxon within the water column follows a triangular distribution, whereby a taxon's maximum abundance, approximated by a scalene triangle, occurs in the top one-third of its depth range.

Note that with full implementation of 'equatorial submergence' (described below as 'Filter 6'), the depth of maximum abundance will vary with latitude.

Filter 5: Habitat preference

Habitat preference is an important factor affecting the distribution of marine taxa. Thus the aim of this filter is to enhance the predictions of a taxon's distribution based on its association with different habitats.

In this context, it is assumed that the relative abundance of a taxon in a spatial cell is, in part, determined by the fraction derived from the number of habitats that a taxon associates with in that same cell, and by how far the association effect will extend from that habitat. The latter is assumed to be a function of the taxon's body size (maximum length) and its habitat 'versatility'. Thus a large species that inhabits a wide range of habitats is more likely to occur far from the habitat(s) with which it is associated, than a small species of low habitat versatility (Kramer and Chapman, 1999).

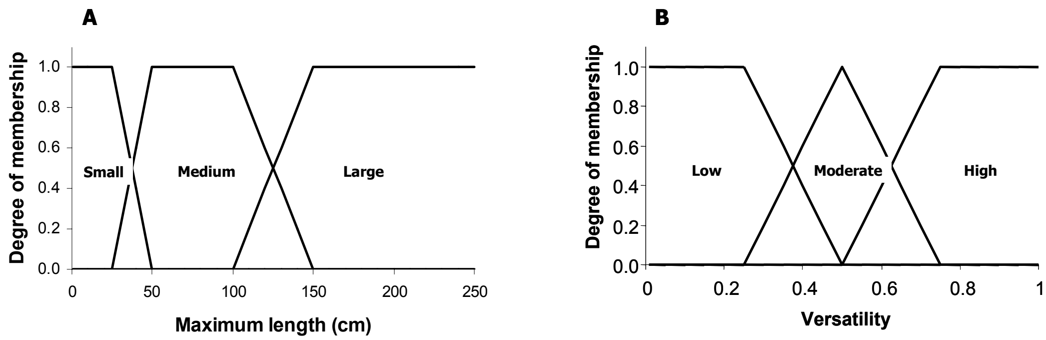


Figure 4 Fuzzy membership functions for the three categories of (**A**) maximum length and (**B**) taxon's versatility. Habitat versatility is defined as ratio of number of habitat types in which a taxon occurs to the total number of defined habitat types.

Table 1 Habitat categories used here, and for which global maps are available in the *Sea Around Us* Project, with some of the terms typically associated with them (in FishBase and other sources).

Categories	Specifications of global map	Terms often used
Estuary	Alder (2003)	Estuaries, mangroves, river mouth
Coral	UNEP World Cons. Monit. Cent. (2005)	Coral reef, coral, atoll, reef slope
Seagrass	Not yet available*	Seagrass bed
Seamounts	Kitchingman and Lai (2004)	Seamounts
Other habitats	–	Muddy/sandy/rocky bottom
Continental shelf	NOAA (2004)	Continental shelf, shelf
Continental slope	NOAA (2004)	Continental slope, upper/lower slope
Abyssal	NOAA (2004)	Away from shelf and slope
Inshore	NOAA (2004)	Shore, inshore, coastal, along shoreline
Offshore	NOAA (2004)	Offshore, oceanic

* The *Sea Around Us* Project is currently developing a global map of seagrass which will be applied when available.

The maximum length and versatility of a taxon are classified into three categories (Figure 4), and it is assumed that a taxon can associate with one or more categories with different degrees of membership (0 to 1). A higher membership value means a higher 'probability' that the taxon is associated with that particularly category. The membership values are defined by a pre-specified membership function for each of the length and versatility categories (Figure 4). For example, the Striped bass (*Morone saxatilis*) has a maximum length of 200 cm (TL). Thus, based on the defined membership functions (Figure 4A, left), Striped bass has a large body size with a membership of 1 (membership ranges from 0 to 1). There are maximum length estimates for all of the 1231 exploited taxa in the *Sea Around Us* Project database, obtained from FishBase and other published literature for invertebrates.

In this paper, versatility refers to the taxon's ability to inhabit different habitat types and is defined as the ratio between the number of associated habitats to the total number of defined habitats (Table 1). For instance, based on descriptions in the SPECIES Table of FishBase, Striped bass is associated with estuaries and 'other habitats'. Given that the total number of defined physical habitats is five (coral reef, estuary, seagrass, seamount, other habitats, while excluding shelf/slope/abyssal and inshore/offshore), the versatility of Striped bass is estimated to be 0.4. Based on the defined membership functions (Figure 4B, right), the versatility of Striped bass is classified as low to medium, with a membership of approximately 0.48 and 0.52 respectively.

Determining habitat association

Based on qualitative descriptions from the published sources, databases such as FishBase and/or through personal communications from experts, each taxon's degree of association with different habitats (Table 1) for all exploited taxa in the database was determined. The taxon's degree of association to each habitat is determined from the qualitative descriptions relating to its density or commonness in the particular habitat (Table 2). As noted above, Striped bass prefers estuaries and also occurs in 'other habitats'. Thus, the Striped bass received a score of 0.75 for estuaries and 0.5 for 'other habitats'.

Maximum distance of habitat effect

Maximum distance of habitat effect (maximum effective distance) refers to the maximum distance from the nearest perimeter of the habitat within which the ‘attraction’ effect to their associated taxa exists. This is defined as the maximum effective distance by the maximum length and habitat versatility of the taxa using a heuristic rule matrix (Table 3). For example: IF maximum length is large (1) AND versatility is moderate (0.52), THEN maximum occurrence distance from the associated habitat is high (0.52). Here, the number in parentheses represents the degree of membership to the categories. In this example, the degree of membership is the minimum memberships of the two predicates. When the same conclusion is reached from different rules, the final degree of membership equals the taxon’s average membership value.

Table 2 Common descriptions on taxa’s relative association to habitat and their assigned weighting factor. The weighting factor for ‘other habitats’ is assumed to be 0.1 when no information on habitat association is available.

Description	Weighting factor
Absent/rare	0.00
Occasionally, sometimes	0.25
Often, regularly, seasonally*	0.50
Usually, abundant in, prefer	0.75
Always, mostly, only occurs	1.00

* If a taxon occurs in a habitat, but no description on the strength of the association is found, we assume a default score of 0.5.

Table 3 Heuristic rules that define the maximum effective distance from the associated habitat. The bolded columns and rules represent the predicates (categories of maximum body size and taxon’s versatility), while the italics represent the resulted categories of maximum effective distance.

	Maximum body size		
Versatility	**Small**	**Medium**	**Large**
Low	*Small*	*Small*	*Small*
Moderate	*Moderate*	*Moderate*	*Large*
High	*Moderate*	*High*	*High*

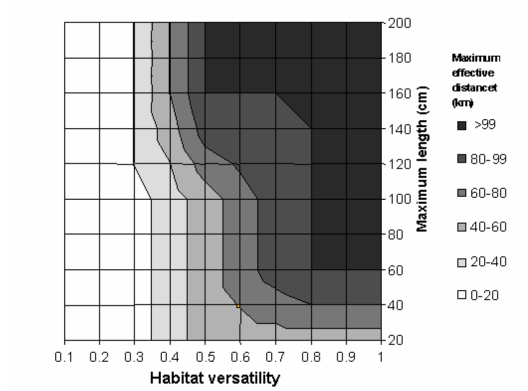


Figure 5 Maximum effective distance for Striped bass (*Morone saxatilis*) estimated from the habitat versatility and maximum length of that species (see text).

The maximum effective distance from the associated habitat can be estimated from the ‘centroid value’ of each conclusion categories, weighted by a taxon’s degree of membership. The centroid values for small, medium and large maximum effective distances were defined as 1 km, 50 km and 100 km, respectively. Thus if, for example, a taxon has membership values of 0.2 and 0.5 to small and medium maximum effective distance, respectively, then the estimated maximum effective distance is: (0.2*1 + 0.5*50 + 0*100)/(0.2 + 0.5 + 0) = 36.1 km (Figure 5). The maximum effective distance is calculated for all exploited taxa in the database.

Estimating relative abundance in a spatial cell

Several assumptions are made to simplify the computations. Firstly, it is assumed that the habitat always occurs in the centre of a cell and is circular in shape. Secondly, the density of a taxon (per unit area) is assumed to be the same across any habitat types. Also, it is assumed that a linear decline in density from the habitat perimeter to the taxon’s maximum effective distance occurs for each taxon. Given these assumptions, the total relative abundance of a taxon in a cell equals the sum of abundance on and around its associated habitat:

$$B'_T = (\alpha_j + \alpha_{j+1} \cdot (1 - \alpha_j)) \cdot (1 - A) \quad \ldots 1)$$

where B'_T is the final abundances, α_j is the density away from the habitat from cell j, and A is the habitat area of the cell. The relative abundance resulting from the different habitat types is the sum of relative abundance, and is weighted by their importance to the taxon.

Although these assumptions on the relationship between maximum length, habitat versatility and maximum distance from the habitat may render predicted distributions at a fine spatial scale uncertain, this routine provides an explicit and consistent way to incorporate habitat considerations into distribution ranges.

Filter 6: Equatorial submergence

The submergence phenomenon was already known to Charles Darwin, who wrote that "we hear from Sir J. Richardson, that Arctic forms of fishes disappear in the seas of Japan & of northern China, are replaced by other assemblages in the warmer latitudes & reappear on the coast of Tasmania, southern New Zealand & the Antarctic islands" (Pauly 2004, p. 198).

Eckman (1967) gives the current definition: "animals which in higher latitudes live in shallow water seek in more southern regions archibenthal or live in shallow water seek in more southern regions archibenthal or purely abyssal waters [...]. This is a very common phenomenon and has been observed by several earlier investigators. We call it submergence after V. Haecker [1906-1908] who, in his studies on pelagic radiolarian, drew attention to it. In most cases, including those which interest us here, submergence increases towards the lower latitudes and therefore may be called equatorial submergence.

Submergence is simply a consequence of the animal's reaction to temperature. Cold-water animals must seek colder, deeper water layers in regions with warm surface water if they are to inhabit such regions at all."

Modifying the distribution ranges to account for equatorial submergence requires accounting for two constraints: (1) data scarcity; and (2) uneven distribution of environmental variables (temperature, light, food, etc.) with depth.

As noted above, there is little information on the depth distribution of most commercial species. As a result, only the following four data points were available for each taxon, namely: the shallow or 'high' end of the depth range (D_{high}), its deep or 'low' end (D_{low}) of the depth range, the poleward limit of the latitudinal range (L_{high}), and its lower latitude limit (L_{low}). These four data points are often available in FishBase for fishes, and can be readily inferred for commercial invertebrates, as noted above. If it is assumed that equatorial submergence is to occur, then it is logical to also assume that D_{high} corresponds to L_{high}, and that D_{low} corresponds to L_{low}.

Data scarcity can be further mitigated by assuming the shape of the function linking latitude and equatorial submergence. In this context, two parabolas are used, one for the upper limits of the depth distribution (P_{high}), and one for the lower limits (P_{low}), with the assumption that both P_{high} and P_{low} are symmetrical about the Equator. In addition, maximum depths are assumed not to change poleward of 60° N and S.

The uneven distribution of the temperature gradient can be mimicked by constraining P_{high} to be less concave than P_{low}. This is achieved by setting D_{gm}, the geometric mean of D_{high} and D_{low}, as the lowest depth that P_{high} can attain. Furthermore, in the case of a distribution spanning both hemispheres, P_{low} will have its lowest point (D_{low}) at the Equator.

Finally, it is assumed that if a computed P_{high} intercepts zero depth at lower latitudes than 60° N and S, then P_{high} is recomputed using the three points D_{oN}=0 at 60° N, D_{oS} at 60° S, and D_{high} and its latitude, which jointly define a parabola.

Figure 6 illustrates three cases of submergence based on different constraints. When this process is applied to a distribution range based on latitudinal range and depth that does not account for submergence, the plots in Figure 7 have the effect of 'shaving off' the shallow end depth values at low latitudes, and similarly, shaving off the deep end depth values at high latitudes. This will have the effect of narrowing the habitat temperature ranges of the corresponding species.

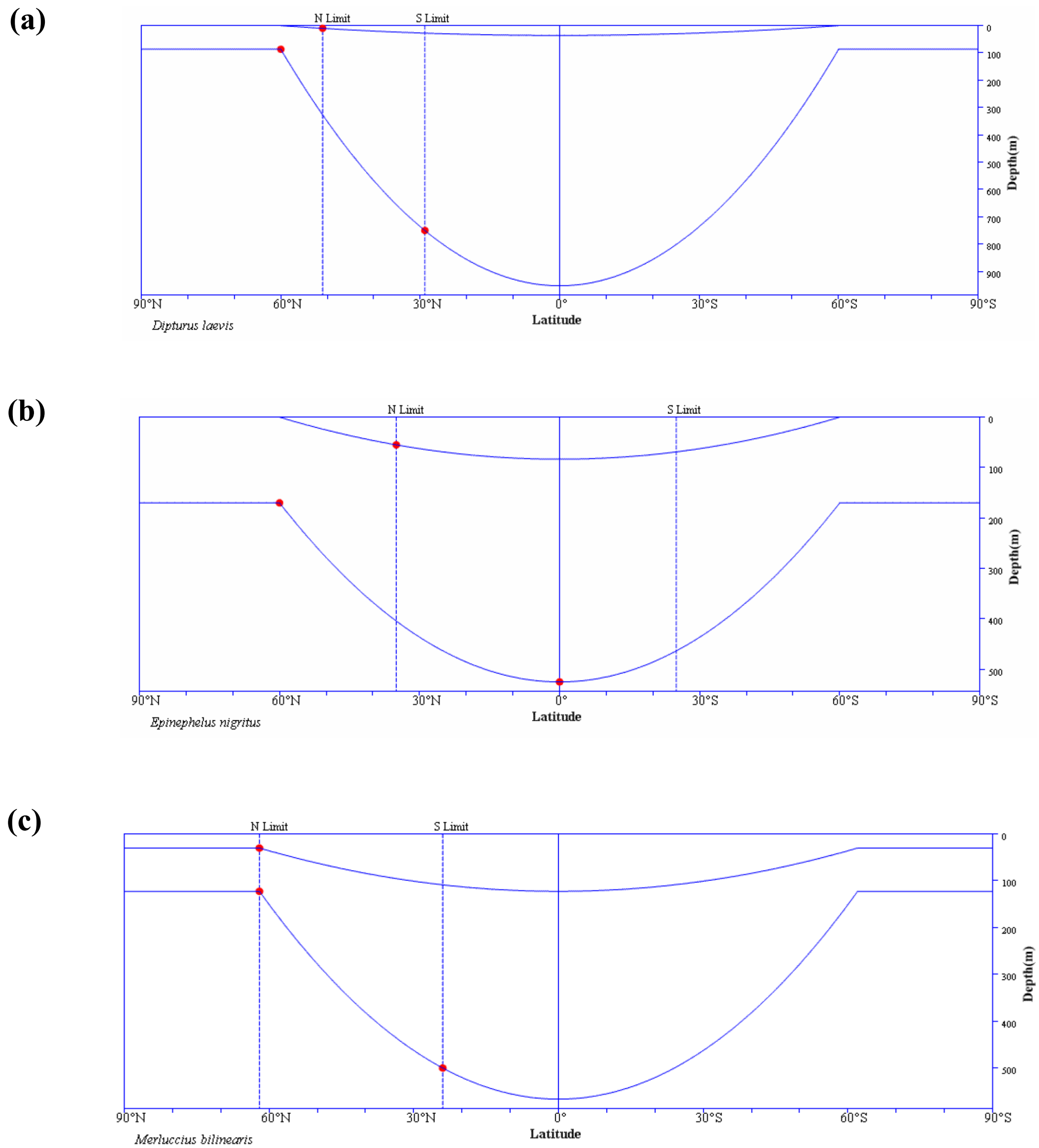


Figure 6 Illustrative representations of 'equatorial submergence', given different depth/latitude data: **(a)** Case 1: Barndoor skate (*Dipturus laevis)* – When the shallow end of the depth range (D_{high}) is at lower latitudes than 60° N and S, the upper limit of the depth distribution (P_{high}) is assumed to intercept zero at 60° N and S; **(b)** Case 2: When distribution range is spanning the North and South hemispheres, as in the case of the Warsaw grouper, *Epinephelus nigritus*, the lowest point of the lower limit (P_{low}) is at the Equator; **(c)** Case 3: Silver hake (*Merluccius bilinearis)*. The poleward limit of the latitudinal range (L_{high}) is at higher latitudes than 60° N and S.

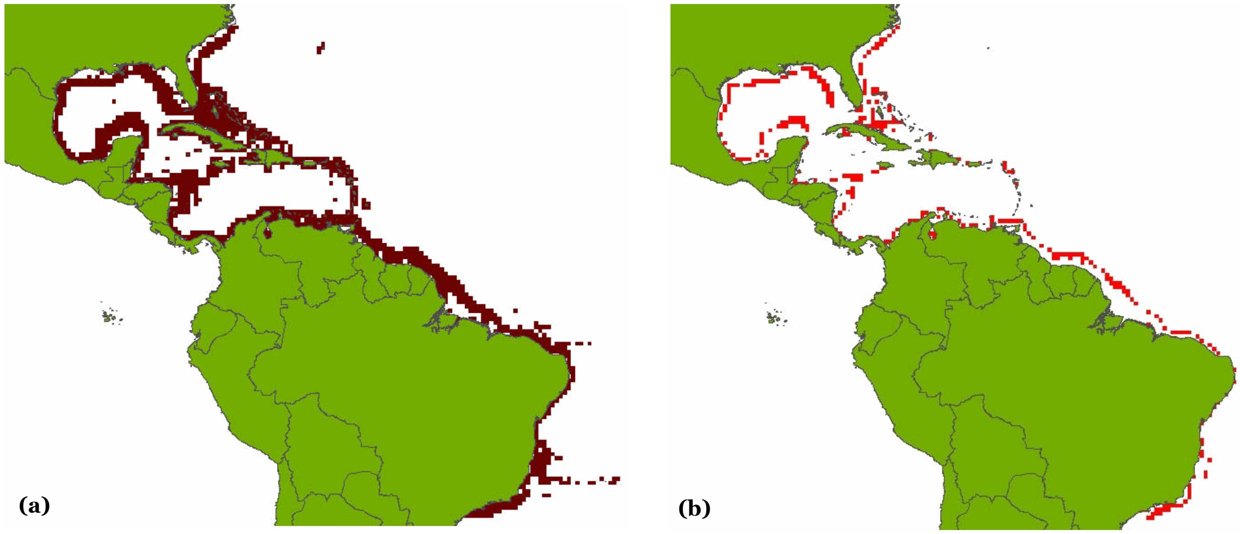


Figure 7 'Equatorial submergence' has the effect of 'shaving off' areas from the distribution range of the Warsaw grouper, *Epinephelus nigritus*: **(a)** Original Distribution; **(b)** Distribution adjusted for 'equatorial submergence'.

Results and Discussion

The results consist of distribution ranges generated through the above methods, incorporated in the *Sea Around Us* database, and available online (see www.seaaroundus.org). They can also be accessed (for fish species) via FishBase (click '*Sea Around Us* distributions' under the 'Internet sources' in the Species Table).

Most importantly, these distribution ranges will serve as basis for all spatial catch allocation done with the *Sea Around Us* Project. Therefore, we would be very thankful for feedback, i.e., suggested comments or corrections, which we will strive to implement as soon as possible.

Acknowledgement

The work documented here is an output of the *Sea Around Us* Project, initiated and funded by the Pew Charitable Trusts, Philadelphia. We thank the Marine Conservation Biology Institute for the support of Sally Hodgson who worked on the distribution ranges of deep sea fish. We thank, finally, Adrian Kitchingman and Ahmed Gelchu for their work on the first generation of *Sea Around Us* distribution ranges.

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