Chapter 4. Distribution of biodiversity in the seas around us, with emphasis on exploited fish and invertebrate species[1]

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Introduction

Ecosystem-based fisheries management (EBFM) must include a sense of place or locale, where fisheries interact with the animals and plants of specific ecosystems. To be useful to researchers attempting to implement EBFM schemes, the *Sea Around Us* presents biodiversity and fisheries data in spatial form onto a grid of about 180,000 half degree latitude and longitude cells which can be regrouped into larger entities, e.g., the Exclusive Economic Zones (EEZs) of Maritime countries (see Chapter 2, and particularly Figure 2.1), or the system of currently 66 Large Marine Ecosystems (LME) initiated by NOAA (Sherman et al. 2007), and now used by practitioners throughout the world.

However, not all the marine biodiversity of the world can be mapped in this manner; thus, while FishBase (www.fishbase.org) includes all marine fishes described so far (more than 15,000 spp.), so little is known about the distribution of the majority of these species that they cannot be mapped. The situation is even worse for marine invertebrates, despite huge efforts (see www.sealifebase.org).

We define as 'commercial' marine fish or invertebrate species that are important enough to be reported in the catch statistics of at least one of the member countries of the Food and Agriculture Organization of the United Nations (FAO). This definition, besides the fact that its application is straightforward, has the advantage that it defines as 'commercial' species that are abundant enough to be targeted by at least one officially monitored fishery. There were about 3,500 such species of fishes in the FAO statistics up to 2012, and for most of them, there was enough data in FishBase for at least tentatively mapping their distribution ranges. Similarly, there were over 800 species of commercial invertebrates, and most had enough information in SeaLifeBase (www.sealifebase.org) for their approximate distribution range to be mapped. (We discuss below the procedure we use for taxa that lacked sufficient data for mapping their distribution, which included few taxa in the FAO statistics, and many from reconstructed catches, including discards).

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In the following, we document how such mapping is done; this contribution builds on Watson et al. 2004) and specifically on Close et al. (2006), of which it is an updated version. Thus, this contribution presents the methods by which all commercial species distribution ranges (totaling over 1100 for the time period 1950-2010) were constructed and/or updated, and consisting of a set of rigorously applied filters that will markedly improve the accuracy of the *Sea Around Us* 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 filtering process, and are referred to in the appropriate section.

Note that the procedures presented here avoid the use of temperature and primary productivity to define or refine distribution ranges for any species, even though these strongly shape the distribution of marine fishes and invertebrates (Ekman 1967; Longhurst and Pauly 1987). This was done in order to allow for subsequent analyses of distribution ranges to be legitimately performed using these variables, i.e., to avoid circularity.

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 species was verified using FishBase (www.fishbase.org) or SeaLifeBase (www.sealifebase.org), two authoritative online encyclopedia covering the fishes of the world, and marine non-fish animals, respectively, and their scientific and English common names corrected if necessary. This information was stored in the *Sea Around Us*' TAXON database.

Filter 1: FAO Areas

The FAO has divided the world's oceans into 18 areas for reporting purposes (**Figure 2.1** in Zeller and Pauly, this volume). Information on the occurrence of commercial species within these areas is available primarily through (a) FAO publications and the FAO website (www.fao.org); and (b) FishBase and SeaLifeBase. **Figures 4.1A** and **4.2A** illustrate the occurrence by FAO area of Florida pompano (*Trachinotus carolinus*) and silver hake (*Merluccius bilinearis*), representing pelagic and demersal species, 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 quote and one 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.*"

The latitudinal range of a species is defined as the space between its northernmost and southernmost latitudes. This range can be found in FishBase for most fishes and in SeaLifeBase for many invertebrates. For fishes and invertebrates for which this information was lacking, latitudes were inferred from the latitudinal range of the EEZs of countries where they are reported to occur as endemic or native species, and/or from occurrence records in the Ocean Biogeographic Information System website (OBIS; www.iobis.org). Note, however, that recent occurrence records (from the 1980s onwards and known range extensions, e.g., of Lessepsian species) were not used to determine 'normal' latitudinal ranges, as they tend to be affected by global warming (Cheung et al. 2013).

A species will not have the same probability of occurrence, or relative abundance throughout its latitudinal range; it can be assumed to be most abundant at the center of its range (McCall, 1990). Defining the center of the latitudinal distribution range is done using the following assumptions:

a) For distributions confined to a hemisphere, a symmetrical triangular probability distribution is applied, which estimates the center of the latitudinal range as the average of the range, i.e., [northernmost + southernmost latitude] / 2;
b) For distributions straddling the equator, the range is 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 abundance is assumed to be the same as in (a). If, however, the equator falls in the middle third of the range, then abundance is assumed to be flat (assigned one value) in the middle third and decreasing to the poles for the remainder of the range.

Figures 4.1B and **4.2B** illustrate the result of the FAO and latitudinal filters combined. Both the Florida pompano and the silver hake follow symmetrical triangular distributions as mentioned in (a) above.

Filter 3: Range limiting polygon
Range limiting polygons help confine species in areas where they are known to occur, while preventing their occurrence in other areas where they could occur (because of environmental conditions), but do not. Distribution polygons for a vast number of species of commercial fish and invertebrates can be found in various publications, notably FAO's (species catalogues, species identification sheets, guides to the commercial species of various countries or regions, and in online resources, some of which were obtained from model predictions, e.g., Aquamaps (Kaschner et al 2007; see also www.aquamaps.org). Such polygons are mostly based on observed species occurrences, which may or may not be representative of the actual distribution range of the species; and working with the assumption that the observer correctly identified the species being reported. These "observational factors" add a level of uncertainty to the validity of distribution polygons. Most often than not, biogeographic experts are needed to manually review and validate a polygon before it is published, e.g., FAO species catalogues. This review process is also important, notably for polygons that are automatically generated via model predictions such as Aquamaps. Note that for commercially important endemic species, this review process can be skipped as the polygon is restricted to the only known habitat and country where such species occurs.

For species without published polygons, range maps were generated using the filter process described here and compared with the native distribution generated in Aquamaps. Differences between these two "model-generated" maps are verified using data from the scientific literature and OBIS/GBIF (i.e., reported occurrences notably by scientific surveys). Note that FAO statistics, where countries reported the species in their catch, were used as occurrence records; except when the species was caught by the country's distant-water fleet, as defined in Zeller and Pauly (this volume). Polygons are drawn based on the verified map (i.e., stripped off of non-referenced occurrences). Additionally, faunistic work covering the high-latitude end of continents and/or semi-enclosed coastal seas with depauperate faunas (e.g., Hudson Bay or the Baltic Sea) were used to avoid, where appropriate, distributions reaching into these extreme habitats. The results of this step, i.e., the information gathered from the verification of occurrences, are also provided to FishBase and SeaLifeBase to fill-up data gaps.

All available polygons, whether available from a publication or newly drawn, were digitized with ESRI's ArcGIS and stored in the *Sea Around Us* TAXON database, along with the latitude ranges derived from them, which were then used for inferences on equatorial submergence (see below). **Figures 4.1C** and **4.2C** 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.

Note that because this mapping process only deals with commercially-caught species, the distribution ranges for higher level taxa (genera, families, etc.) were usually generated using the combination of range polygons from the taxa included in the higher-level taxon. 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 and families 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 than the ones that are never reported in official catch statistics.

Filter 4: Depth range

Similar to the latitudinal range, the 'depth range', i.e., "[the] depth (in m) reported for juveniles and adults (but not larvae) from the most shallow to the deepest [waters]", is available from FishBase for most fish species and SeaLifeBase for many commercial invertebrates, along with their common depth, defined as the "[the] depth range (in m) where juveniles and adults are most often found. This range may be calculated as the depth range within which approximately 95 % of the biomass occurs" (Froese et al. 2000). Given this, and based on Alverson et al. (1964), Pauly and Chua (1988), and Zeller and Pauly (2001), among others, the abundance of a species within the water column is assumed to follow a scalene triangular distribution, where maximum abundance occurs at the top one-third of its depth range.

Filter 5: Habitat preference

Habitat preference is an important factor affecting the distribution of marine species. Thus, the aim of this filter is to enhance the prediction of the probability that a species occurs in an area, based on its association with different habitats. Two assumptions are made here:

- That, other things being equal, the relative abundance of a species in a spatial cell is determined by a fraction derived from the number of habitats that a species associates with in that same cell, and by how far the association effect will extend from that habitat; and
- That the extent of this association is assumed to be a function of a species' maximum size (maximum length) and habitat 'versatility'. Thus, a large species that inhabit a wide range of habitats is more likely to occur far from the habitat(s) with which it is associated, while smaller species will tend to have low habitat versatility (Kramer and Chapman 1999).

The maximum length and versatility of a species are classified into three categories, and it is assumed that a species 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 species 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 4.3**). For example, the striped bass (*Morone saxatilis*) has a maximum length of 200 cm (total length). Based on the pre-defined membership function presented in **Figure 4.3A**, the striped bass has a large body size with a membership of 1. Note that there are maximum length estimates for all of the over 1,100 exploited species in the TAXON database of the *Sea Around Us*, derived from FishBase and SeaLifeBase, and which are displayed on our website along with other information, e.g., affinities to certain habitat types and trophic levels.

The ability of a species to inhabit different habitat types, here referred to as 'versatility', is defined as the ratio between the number of habitats with which a species is associated to the total number of habitats as defined in **Table 4.1**. These habitats are categorized as 'biophysical' (coral reef, estuary, seagrass, seamount, other habitats), 'depth-related' (shelf/slope/abyssal), and 'distance from coast' (inshore/offshore). As species are generally specialized towards 'biophysical' habitats, this filter only takes those five habitats into consideration. Taking our example again, the FishBase species summary page (Biology section) for the striped bass reads "*Inhabit coastal waters and are commonly found in bays but may enter rivers in the spring to spawn*" (Eschmeyer et al. 1983). This associates the striped bass with estuaries (brackishwaters) and 'other habitats' (i.e., when it enters rivers to spawn). Given that the total number of defined biophysical habitats is five, and the striped bass is associated with two of those, then the versatility of striped bass is estimated to be 0.4 (i.e., 2/5). Finally, based on the defined membership functions shown in **Figure 4.3B**, the versatility of striped bass is classified as 'low' to 'moderate', with a membership of approximately 0.4 and 0.6, respectively.

Determining habitat association

Qualitative descriptions relating the commonness of (or the preference of) a species to particular habitats (as defined in **Table 4.1**) are given weighting factors as enumerated in **Table 4.2**. Such descriptions are available from FishBase for most fishes and in SeaLifeBase for most commercially important invertebrates. Going back to our example, we thus know that the striped bass occurs in (and thus prefers) brackishwaters (i.e., estuaries), but enters freshwaters (i.e., 'other habitats') to spawn. Given the weighting system in **Table 4.2**, estuaries is assigned a weight of 0.75 (usually occurs in) and 'other habitats' is given a weight of 0.5 (assuming a seasonal spawning period).

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 which ‘attracts’ a species to a particular habitat. This is defined by the maximum length and habitat versatility of the species using the heuristic rule matrix in **Table 4.3**. Taking our example for the striped bass, with a ‘large’ maximum length (membership=1) and ‘low’ to ‘moderate’ versatility (membership values of 0.4 and 0.6), points to ‘farthest’ maximum effective distance. The degree of membership assigned to maximum effective distance is equal to the minimum membership value of the two predicates[2], in this example, 1 vs. 0.4 = 0.4 and 1 vs. 0.6 = 0.6. When the same conclusion is reached from different rules, the final degree of membership equals the average membership value (in this example, (0.4+0.6)/2=0.50).

The maximum effective distance from the associated habitat can be estimated from the 'centroid value' of each conclusion category[2], weighted by the degree of membership. The centroid values for near, far and farthest maximum effective distances were defined as 1 km, 50 km and 100 km, respectively. In our example, we obtained membership values of 0.4 for near (1 km) and 0.6 for farthest (100 km) maximum effective distance, respectively. This gives an estimate of (0.4*1 + 0*50 + 0.6*100)/(0.4 + 0 + 0.6) = 60.4 km (see **Figure 4.4**). The maximum effective distance is calculated for all exploited species in the TAXON database.

Estimating relative abundance in a spatial cell

Several assumptions are made to simplify the computations. First, it is assumed that the habitat always occurs in the center of a cell and is circular in shape. Second, species density (per unit area) is assumed to be the same across any habitat type; and that density declines linearly from the habitat perimeter to its maximum effective distance. Given these assumptions, the total relative abundance of a species in a cell equals the sum of abundance on and around its associated habitat, expressed as:

$$B'T = (\alpha j + \alpha j{+}1 \cdot (1 - \alpha j)) \cdot (1 - A) \qquad \ldots 4.1)$$

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[2] From predicate logic, a generic term for systems of abstract thought applied in fuzzy logics. In this example, the first order logic predicate is “IF maximum weight is large”, and the second order logic predicate is “AND versatility is moderate”. The resulting function, i.e., the conclusion category based on the predefined rules matrix in **Table 4.3**, is “THEN maximum effective distance is ‘farthest’.

where *B'T* is the final abundance, *αj* 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 species.

Although these assumptions on the relationship between maximum length, habitat versatility and maximum distance from the habitat may render uncertain predicted distributions at a fine spatial scale, 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.*" Equatorial submergence, indeed, is caused by the same physiological constraints which also determine the 'normal' latitudinal range of species, as described above, and its shift due to global warming (Chapter 8), i.e., respiratory constraints fish and aquatic invertebrates experience at temperatures higher than their evolved preferendum (Pauly 1998, 2010).

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. FishBase and SeaLifeBase notwithstanding, there is little information on the depth distribution of most commercial species. However, in most cases, the following four data points are available for each species: 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}). 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}.

Also, we further mitigate data scarcity by assuming the shape of the function linking latitude and equatorial submergence. Here, 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 60^0N and 60^0S. 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 60^0N and 60^0S, then P_{high} is recomputed using the three points $D_{0N}=0$ at 60^0 N, D_{0S} at 60^0 S, and D_{high} and its latitude, which jointly define a parabola.

Figure 4.5 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 did not account for submergence, these have the effect of 'shaving off' parts of the shallow-end of that distribution at low latitudes, and similarly, shaving off part of the deep-end end of the distribution at high latitudes. Also, besides leading to narrower and more realistic distribution ranges, this lead to narrowing the temperature ranges inhabited by the species in question, which is important for the estimation of their temperature preferenda, as used when modelling global warming effects on marine biodiversity and fisheries (Cheung and Pauly, this volume).

The catch reconstruction which form the basis of the Atlas of which this contribution is a chapter generated a large number of 'new commercial taxa', i.e., taxa (mainly species) not included in the catch statistics disseminated by FAO, and for which we did not have the data (or the time) required to produce distributions using the 'filter'procedure outlined here, and to which very small landings (or discarded bycatch) were associated. Pending future dedicated research devoted to providing as soon as possible all taxa with well-founded distribution-related data, and thus, distribution maps, this iteration assigned a number of these 'new commercial taxa' to either the next higher taxa (species to genera, or genera to families, etc), or the distribution of closely related taxa (e.g., species in the same genus with similar or related distribution data).

RESULTS AND DISCUSSION

The key results consist of distribution ranges such as in **Figure 4.6**, generated through the above methods, incorporated in the *Sea Around Us* TAXON database, and available online (see www.seaaroundus.org). They can also be accessed via FishBase or SeaLifeBase (click '*Sea Around Us* distributions' under the 'Internet sources' section of the species summary pages). These distribution ranges serve as basis for all spatial catch allocation done with the *Sea Around Us*, and thus we would be very thankful for feedback, i.e., suggested comments or corrections. The numbers of species used to spatialize fisheries catches in different regions of the globe (as described in Chapter 5) are mapped in **Figure 4.7**; these numbers, pertaining to the mid-2000s, have increased since, given the increasing taxonomic resolution of the catch statistics reported by FAO.

Predictions of distribution from the *Sea Around Us* algorithm are comparable in performance to other species modeling approaches that are commonly used for marine species (Jones et al. 2011). Specifically, AquaMaps (Kaschner et al. 2008), Maxent (Phillips et al. 2006) and the *Sea Around Us* Project algorithm are three approaches that have been applied to predict distributions of marine fishes and invertebrates. Jones et al. (2011) applied these three species distribution modelling methods to commercial fish in the North Sea and North Atlantic using data from FishBase and the Ocean Biogeographic Information System. Comparing test statistics of model predictions with occurrence records suggest that each modelling method produced plausible predictions of range maps for each species. However, the pattern of predicted relative habitat suitability can differ substantially between models (Jones et al. 2013). Incorporation of expert knowledge, as discussed above with reference to Filter 3, generally improves predictions, and therefore was given here particular attention.

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FIGURE & TABLE CAPTIONS

Figure 4.1 Partial results obtained following the application of the filters used for deriving a species distribution range map for the Florida pompano (*Trachinotus carolinus*): (**A**) illustrates the Florida pompano's presence in FAO A reas 21, 31 and 41; (**B**) illustrates the result of overlaying the latitudinal range (43°N to 9°S; see Smith 1997) over the map in A; (**C**) shows the result of overlaying the (expert-reviewed) range-limiting polygon over B; and (**D**) illustrates the relative abundance of the Florida pompano resulting from the application of the depth range, habitat preference and equatorial submergence filters on the map in C.

Figure 4.2 Partial results obtained following the application the filters used for deriving a species distribution range map for 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 (55°N to 24°N; see FAO-FIGIS 2001); **(C)** shows the result of overlaying the (expert-reviewed) range-limiting polygon over B; and (**D**) illustrates the silver hake's relative abundance resulting from the application of the depth range, habitat preference and equatorial submergence filters on the map in C.

Figure 4.3 Fuzzy membership functions for the three categories of (**A**) maximum length and (**B**) versatility of a species. Habitat versatility is defined as the ratio of the number of habitat types with which a species is associated to the total number of defined habitat types in Table 4.1. For example, the striped bass (*Morone saxatilis*) grows to a maximum total length of 200 cm (large body size; degree of membership = 1). It occurs in estuaries and 'other habitats' (2 of 5 defined habitats, i.e., versatility = 0.4, low to moderate; degree of membership = 0.4-0.6).

Figure 4.4 Maximum effective distance for striped bass (*Morone saxatilis*) estimated from the habitat versatility and maximum length of that species (see text).

Figure 4.5 Shapes used to generate 'equatorial submergence', given different depth/latitude data: **(**A**)** Case 1: Barndoor skate (*Dipturus laevis)* – When the shallow end of the depth range (*Dhigh*) is at lower latitudes than 60^0 N and S, the upper limit of the depth distribution (*Phigh*) is assumed to intercept zero at 60^0 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 (*Plow*) is at the Equator; (**C**) Case 3: Silver hake (*Merluccius bilinearis).* The poleward limit of the latitudinal range (*Lhigh*) is at higher latitudes than 60^0 N and S.

Figure 4.6 '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'.

Figure 4.7 Distribution of the richness of 'commercial' species (836 fish and 230 invertebrate spp.) created by the *Sea Around Us* by the mid-2000s for mapping fisheries and studying distribution shifts due to global warming. The number of species available for such map has increased since by about 30 %, as more species are included in FAO FishStat, and thus become 'commercial' (see text).

Table 4.1 Habitat categories used here, and for which global maps are available in the *Sea Around Us*, with some of the terms typically associated with them (in FishBase, SeaLifeBase and other sources).

Table 4.2 Common descriptions of relative abundance of species in habitats where they occur and their assigned weighting factors. The weighting factor for ‘other habitats’ is assumed to be 0.1 when no information further information is available.

Table 4.3 Heuristic rules that define the maximum effective distance from the habitat in which a species occurs. The columns and rules in bold characters represent the predicates (categories of maximum body size and versatility), while those in italics represent the resulting categories of maximum effective distance.

Table 4.1 Habitat categories used here, and for which global maps are available in the Sea Around Us, with some of the terms typically associated with them (in FishBase, SeaLifeBase 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.

Table 4.2 Common descriptions of relative abundance of species in habitats where they occur and their assigned weighting factors. The weighting factor for 'other habitats' is assumed to be 0.1 when no information further information 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 species occurs in a habitat, but no indication of relative abundance is available, a default score of 0.5 is assumed.

Table 3 Heuristic rules that define the maximum effective distance from the habitat in which a species occurs. The columns and rules in bold characters represent the predicates (categories of maximum body size and versatility), while those in italics represent the resulting categories of maximum effective distance.

	Maximum body size		
Versatility	**Small**	**Medium**	**Large**
Low	*Near*	*Near*	*Near*
Moderate	*Far*	*Far*	*Farthest*
High	*Far*	*Farthest*	*Farthest*