

CHAPTER 2

MODELLING SEASONAL DISTRIBUTION OF PELAGIC MARINE FISHES AND SQUIDS²

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ABSTRACT

The distribution of pelagic marine fishes and invertebrates varies seasonally. However, information on the seasonal variation of the distribution of most pelagic marine fishes and invertebrates is scarce. In this paper, seasonal changes in distribution ranges of commercially exploited pelagic fishes and invertebrates are predicted based on the existing *Sea Around Us* Project distribution, a prediction algorithm, the correlation between seasonal changes in north-south boundaries and sea surface temperature. In the northern hemisphere, in summer (July to September), mobile pelagic marine species tend to migrate to the northern part of their distribution range to avoid excessive temperature near the equator, while in winter (January to March), the same species will migrate southward to avoid the low temperature at higher latitudes. The converse applies to the southern hemisphere. The resulting distributions can improve the prediction of temperature preference profile of pelagic species which are important in evaluating the effects of global warming on their distribution ranges. However, this method of predicting summer and winter distributions of pelagic species can only be considered as an approximation as other factors such as food availability, salinity, rainfall and current are not included. On the other hand, such approximation appear reasonable, given the global scope of the application of the predicted seasonal distributions and the large number of evaluated species (> 160).

INTRODUCTION

Temperature is a key factor affecting the physiology (e.g., reproduction, growth) and spatial and temporal distributions of marine fishes and invertebrates. For instance, Pörtner *et al.* (2001) shows that growth rates and fecundity decrease with higher latitude in the case of Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). Thus, marine ectotherms generally inhabit areas where temperature is favorable for their physiological processes. Also, the northern and southern boundaries of a particular species are determined by the water temperatures suitable for survival and reproduction. Such boundaries may fluctuate according to seasonal changes in temperature. Thus, in the northern hemisphere, the northern boundaries may shift southward in winter and northward in summer (Hutchins 1947), and conversely, in the southern hemisphere.

The correlation between distribution ranges and water temperature is a major factor determining the fluctuation in distributions of the highly mobile pelagic fishes and invertebrates. Many pelagic fishes and invertebrates have the ability to migrate over long-distance to find suitable habitats. As sea water temperature fluctuates seasonally and inter-annually, these species migrate to maintain physiologically suitable temperature in their surrounding water. For instance, *Sardinella* and

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other pelagic fishes migrate northward and southward, along the Northwest African coast such that they remain at the same temperature, despite strong seasonal fluctuation (Pauly 1994). Similarly, tuna and billfish migrate according to changes in sea surface temperature (SST) (Buxton & Smale 1989). Higher catch rates of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) were found in regions where SST increased during El Niño and La Niña periods (Lu *et al.* 2001). Specifically, yellowfin tuna displayed movements from tropical to higher latitude when temperatures in the tropical regions were low i.e. during La Niña periods.

Given seasonal sea water temperature data, it is possible to predict intra-annual changes in distribution of marine pelagic fishes and invertebrates. The *Sea Around Us* project predicted annual average distributions of over 1,230 commercial marine fishes and invertebrates, of which over 190 were pelagic species (www.seaaroundus.org). Distributions of the species were predicted based on existing knowledge of species' north-south latitudinal ranges, depth ranges, affinities to habitats, and known distribution boundaries from published literature (Close *et al.* 2006). Assuming that species' north-south latitudinal boundaries are correlated with sea water temperature, their geographic ranges should shift northward and southward as sea water temperature fluctuates seasonally.

Predicting seasonal distributions of pelagic marine fishes and invertebrates allows more accurate modelling of climate change impacts on these species. A dynamic bioclimate envelope model was developed to predict changes in geographic range of marine fishes and invertebrates under climate change scenarios (see Cheung *et al.* this vol.). This model is based largely on species temperature preference, as inferred from predicted species distributions. Assuming that highly mobile pelagic fishes and invertebrates migrate seasonally according to water temperature, ignoring such seasonal migration would over-estimate the temperature limits of the species and, thus under-estimate the impacts of sea water warming. Thus, the temperature preference of a species can be more accurately predicted if seasonal distributions are available. However, since data on seasonal distributions of the majority of marine fishes and invertebrates are lacking, predictions of seasonal distributions have to be based on some simple, but sensible, assumptions that allow application to a wide range of species. This is essentially the objective of this study.

This paper documents an algorithm to predict seasonal changes in distributions of mobile marine fishes and invertebrates. The algorithm based on simple assumptions of correlation between seasonally (summer and winter) changes in species' north-south latitudinal boundaries and fluctuation in sea water temperature. We apply the algorithm to predict distributions of commercially-exploited pelagic fishes and invertebrates. We illustrate the results from the algorithm with examples, and we discuss its *pros* and *cons* and its potential applications.

METHODS

We developed an algorithm that can predict the seasonal distribution of marine pelagic fishes and invertebrates. This algorithm was modified from the species distribution prediction model presented in Close *et al.* (2006). The details of the algorithm, together with its theoretical basis and assumptions, are summarized in the followings:

We assume that the north-south latitudinal limits of species' geographic ranges change according to ocean temperature in different seasons. The monthly average sea surface temperature data from 1956 to 2006 was obtained from Met Office Hadley Centre observation datasets (Rayner *et al.* 2007). The average annual sea surface temperature data within this period were computed. Two seasons were considered: summer and winter. In the northern hemisphere, summer includes July to September and winter includes January to March. On the other hand, Austral summer and winter are January to March and July to September, respectively. Globally, average sea water temperature at each latitudinal zone increases in summer and decreases in winter. As highly mobile fishes and invertebrates generally attempt to occupy regions with their preferred sea water temperature, we assume that their southern range boundaries move northward in summer to avoid the excessive temperatures near the southern boundary. In winter, their northern range boundaries move southward to avoid sea water temperature at the northern boundary being under the species' physiological limits. Also, the contrast between summer and winter temperature increases towards higher latitude (Figure 1). Thus, the extent of seasonal shifting in

north-south range boundaries should be higher in higher latitude as species must migrate further in higher latitude to maintain similar temperature in their surrounding water.

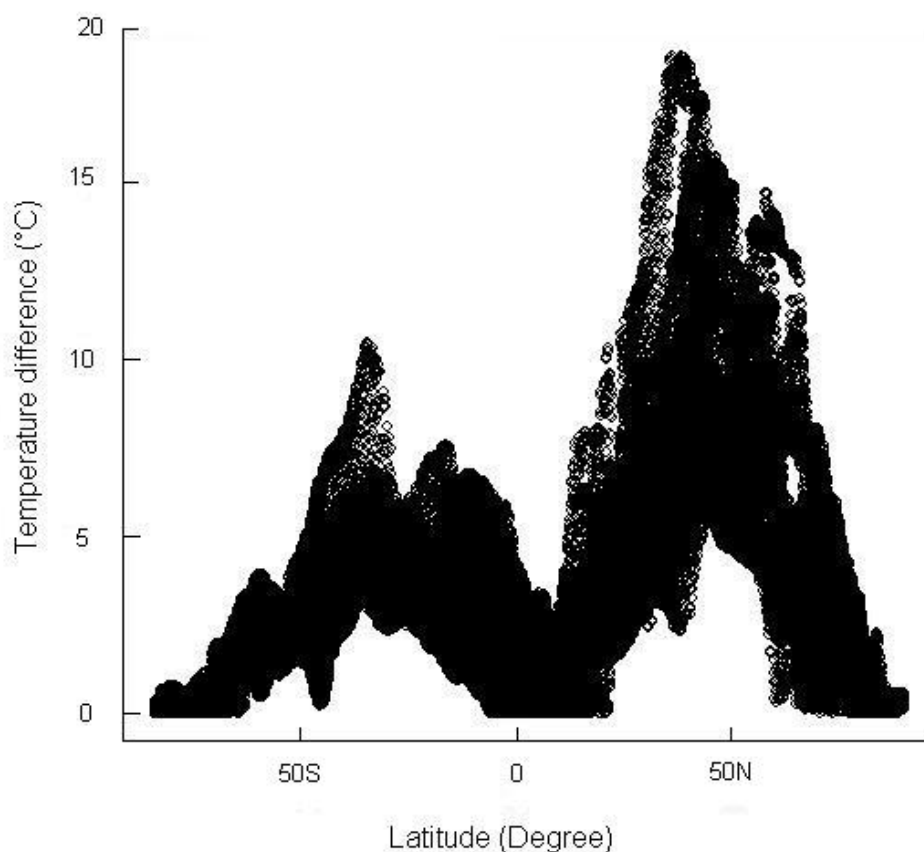


Figure 1. Magnitude of the change in sea surface temperature between summer and winter latitude.

We assume that the centroid of the distribution range also shifts according to temperature. Theoretically, the centroid of a species distribution range generally overlaps with regions where environmental conditions (e.g., sea water temperature) are optimal for the species (MacCall 1990). Thus, we assume that the average temperature at the latitudinal position of the centroid is close to the optimal preferred temperature of the species. We further assume that when latitudinal gradients of sea water temperature shift seasonally, the centroid of the distribution range shifts accordingly. Moreover, the mid-point between the centroid of the distribution range and the north/south range boundary shifts according to temperature. Predicting the seasonal shift in positions of the centroid, range boundaries and the mid-points centroid and range boundaries allow us to calculate seasonal distributions of the species. Longitudinal and vertical movement are not considered here, as these are not generally observed in large-scale seasonal migration patterns of pelagic marine fishes and squids.

We determined the maximum potential shift in centroid and the mid-point based on the annual average distribution of a species, and the annual and seasonal sea surface temperature with such distribution. Firstly, the latitudinal position of the centroid of species' annual average relative distribution, C (*Annual*), was calculated from:

$$C(Annual) = \frac{\sum_{i=1}^n A_i \cdot L_i}{\sum_{i=1}^n A_i} \quad \dots 1)$$

where A_i is the species relative abundance in each spatial cell on the map, L_i is the latitudinal coordinate of the cell, and n is the total number of cells within the species' geographic range. When calculating the latitudinal position of the mid-point, we only include the cells lie within the distribution range between the centroid and northern/southern boundary. The latitudinal position of the mid-point, $MP(Annual)$, was computed from:

$$MP(Annual) = \frac{\sum_{i=1}^m A_i \cdot L_i}{\sum_{i=1}^m A_i} \quad \dots 2)$$

where m is the total number of cells within the distribution range between the centroid and the northern or southern boundary.

Secondly, we calculated the annual average sea surface temperature at $C(Annual)$ and $MP(Annual)$. The temperature at $C(Annual)$ is assumed to be the optimal (preferred) temperature by the species T_a . Moreover, we calculated the average sea surface temperature within the species range by latitudinal bands (every 30') for each season (summer and winter). The latitudinal positions of the centroid in summer and winter, i.e., C_s' and C_w' , respectively, were assumed to be the latitudinal bands with average temperature that was closest to the optimal preferred temperature T_a . Thus, the maximum potential shift in centroid's latitudinal position was calculated from:

$$\begin{aligned} CS_s' &= |C_s' - C(Annual)| \\ CS_w' &= |C_w' - C(Annual)| \end{aligned} \quad \dots 3)$$

where CS_s' and CS_w' are the maximum potential shift in centroid's latitudinal positions in summer and winter, respectively. The latitudinal position of the mid-point in summer and winter i.e., MP_s' and MP_w' , were assumed to be the latitudinal bands with temperature closest to the temperature at $MP(Annual)$. In summer, $MP(Annual)$ was calculated from the latitudinal values of the centroid and the southern bound i.e. MP_s . In winter, $MP(Annual)$ was calculated from the latitudinal values of the centroid and the northern bound i.e. MP_w . The maximum potential shift in the latitudinal position of the mid-point was calculated from:

$$\begin{aligned} MS_s' &= |MP_s' - MP_s| \\ MS_w' &= |MP_w' - MP_w| \end{aligned} \quad \dots 4)$$

where MS_s' and MS_w' are the maximum potential shift in the latitudinal positions of the mid-point in summer and winter, respectively.

The actual shifts in latitudinal positions of the centroid and the mid-point were determined by the motility of the species. Species' motility was represented here by a 'motility index' (MI). This index was calculated by using a fuzzy logic expert system that determines species' motility from species' maximum body length and aspect ratio of caudal fin (i.e., the ratio between the square of the height of fish's caudal fin to the caudal fin area) (Cheung *et al.* this vol.). As aspect ratio is not

available for invertebrates, ordinal levels representing the motility (Sedentary = 1; Low motility = 2; motility = 3; motility = 4) was assigned for each species (see Cheung *et al.* this vol. for details). The calculated motility index scales from 0 to 100. Higher index value indicates higher motility, i.e., higher ability to move, and *vice versa*.

Combining the estimated maximum potential centroid shift and the motility index, we determined the actual seasonal shift in centroid of species distribution range:

$$CS' = CS \cdot \frac{MI}{100} \quad \dots 5)$$

where CS' is the actual shift in centroid of the distribution range (in degree) and MI is the motility index. Similarly, the actual seasonal shift in the mid-point was calculated by:

$$MS' = MS \cdot \frac{MI}{100} \quad \dots 6)$$

where MS' is the actual shift in the latitudinal position of the mid-point (in degree).

Species' latitudinal range limits shifted according to the seasonal shifts in centroid and the mid-point. The latitudinal limits delineated the maximum latitudinal range of the species. Thus, the northern and southern range limits should represent the occurrence limits in summer and winter respectively. We assume that the actual shift in the range boundaries of the species (AS) is the average of the actual shift in the latitudinal positions of the centroid and the mid-point. This value was calculated as:

$$AS = \frac{(CS' + MS')}{2} \quad \dots 7)$$

For species with motility index equal to 100, the northern and southern boundaries of the species will change by the average latitudinal shift of the centroid and the mid-point. In summer, a species moves northward within its total distribution range.

Thus, in the northern hemisphere, the southern range limits would shift northward in summer and the northern range limits would shift southward in winter. The northward shift in southern range limit in summer is calculated from:

$$SL' = SL + AS \quad \dots 8)$$

where SL' is the latitude of the southern bound in summer, SL is the latitude of the original southern bound and AS is the actual shift in distribution range in summer.

Similarly, southward shift in winter in the northern range limit was calculated by:

$$NL' = NL + AS \quad \dots 9)$$

where NL' is the latitude of the northern bound in winter, NL is the latitude of the original northern bound. A schematic diagram of the simulation of range shifting is illustrated in Figure 2.

The calculated seasonal latitudinal boundaries were then used to generate geographic distribution for pelagic fishes and invertebrates using the method documented in Close *et al.* (2006).

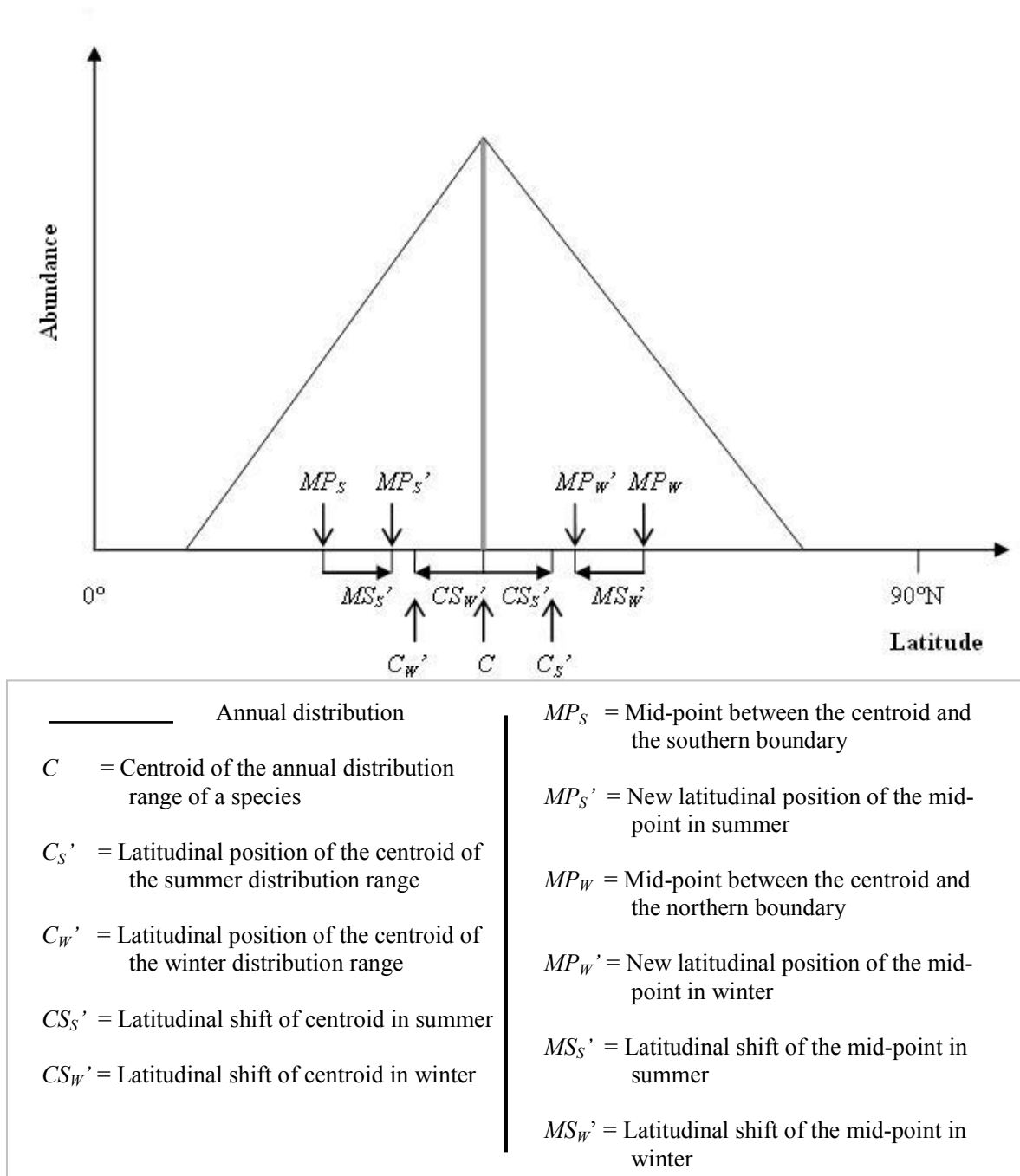


Figure 2a. Schematic diagram showing latitudinal shift in centroid and the mid-point of the distribution range between the centroid and the northern/southern boundary (see text).

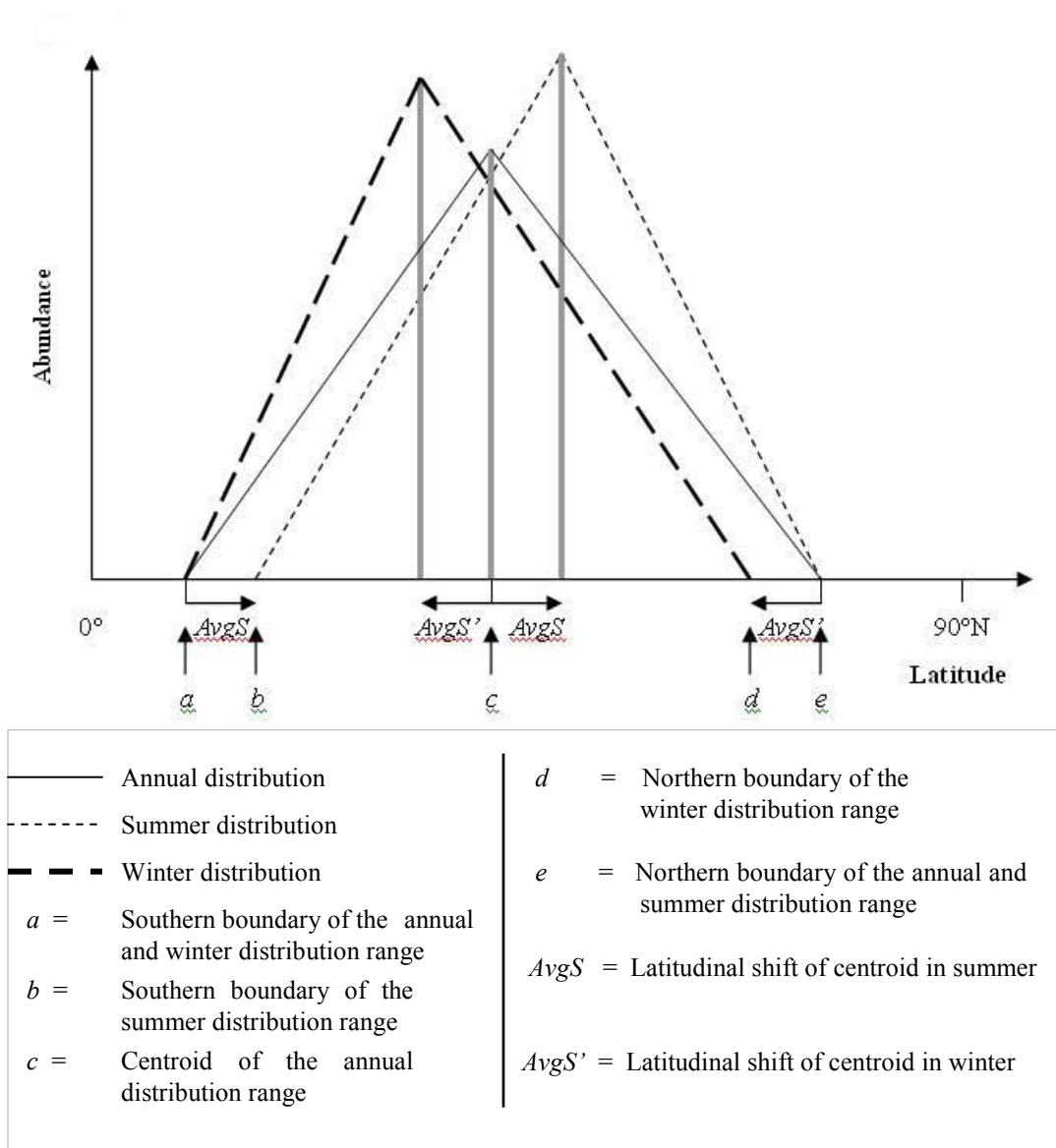


Figure 2b Schematic diagram showing latitudinal shift in the distribution range (see text).

RESULTS

In the Northern hemisphere, the distribution of species shifts to the northern part of their ranges in the summer, whereas the species move to the southern part of their ranges in the winter (and conversely in the Southern hemisphere). The extent of the summer movement may not be necessarily the same as that of the winter movement. Species with longer bodies and higher aspect ratio have a higher capability of shifting to the extreme ends of their ranges with changes in seasonal temperature. Species with smaller bodies and lower aspect ratio of their caudal fin, have a lower motility and their distribution ranges remain more or less the same in summer and winter. We illustrate these general results in the following case studies.

Common dolphinfish (*Coryphaena hippurus*)

The annual distribution range of common dolphinfish extends from 45°N to 38°S. Our model predicted the northward shift of southern boundary of common dolphinfish from 38°S to 30°S in summer and the southward shift of the northern boundary from 45°N to 41°N in winter (Figure 3). In the northern summer, the species migrates largely to the northern hemisphere. On the other hand, the southern boundary extends back into the southern hemisphere in the northern winter while the northern boundary moves slightly southward, e.g. to avoid the cold temperature of the Adriatic Sea in winter.

Common dolphinfish has a high motility index, (= 100), Thus, the shift in boundaries is equal to the entire latitudinal shift of the centroid.

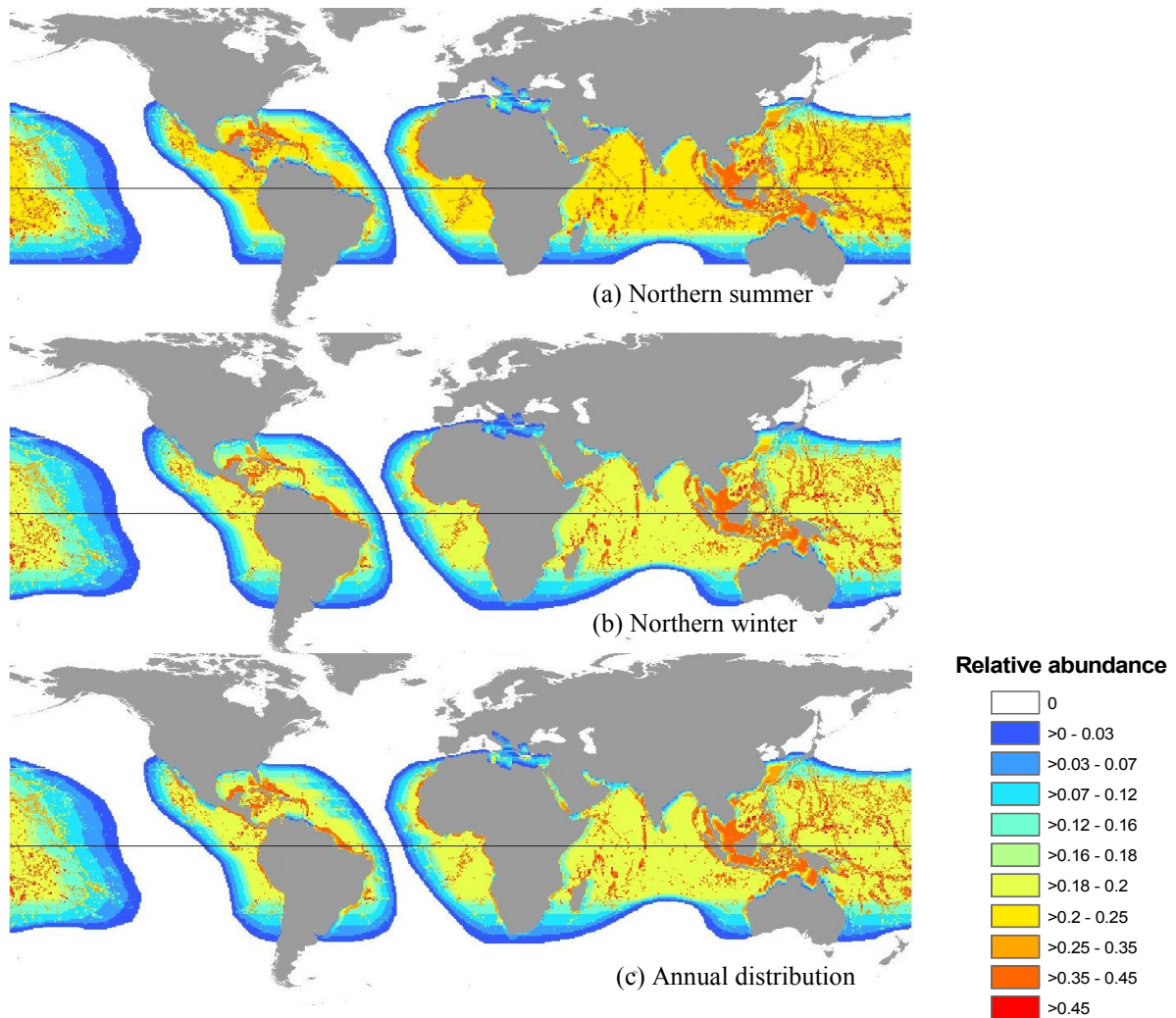


Figure 3. Shift in distribution range of Common dolphinfish in different seasons. (a) Southern boundary shifts northward in summer (b) Northern boundary shifts southward in winter (c) annual distribution range. The straight line on each map marks the equator.

Serra Spanish mackerel (*Scomberomorus brasiliensis*)

This species which has a high motility index (= 77) is distributed along the Caribbean and Atlantic coasts of Central and South America from Belize to Rio Grande do Sul, Brazil. The latitudinal range of its annual distribution extends from 20°N to 35°S. Our model predicts that the southern boundary shifts from Rio Grande do Sul to northern coast of Santa Catarina region, Brazil (28°S) in northern summer (Figure 4). In northern winter, the northern boundary shifts from Belize to Nicaragua (13°N).

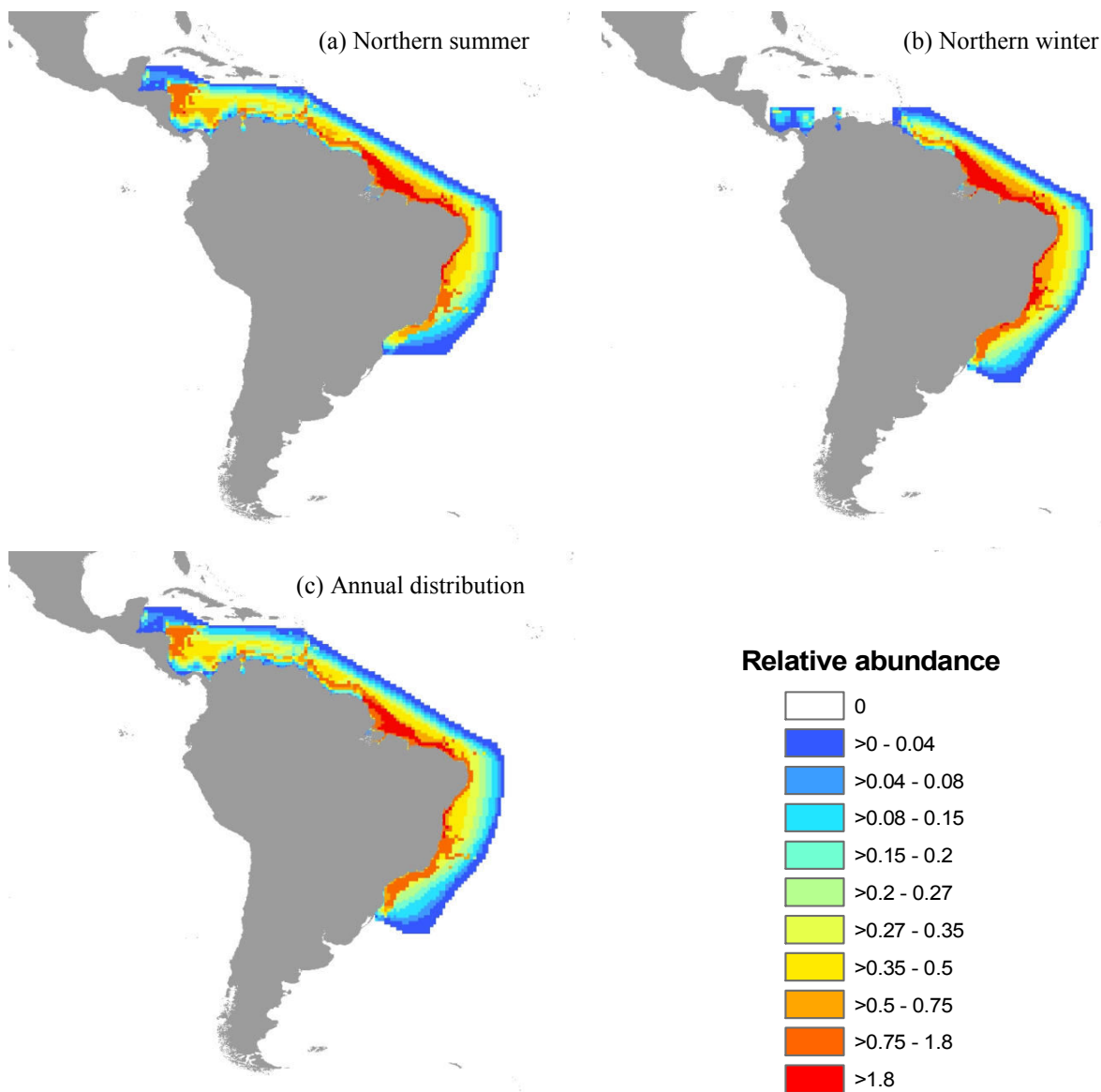


Figure 4. Shift in distribution range of Serra Spanish mackerel in different seasons: (a) southern boundary shifts northward in summer, (b) northern boundary shifts southward in winter, and (c) annual distribution range.

Plain bonito (*Orcynopsis unicolor*)

The plain bonito (motility index = 80) occurs only in the northern hemisphere; its distribution range extends from Bay of Biscay (49°N) to Dakar, Senegal (14°N) (Figure 5). To avoid the excessive summer temperature near the equator in northern summer, the species' southern boundary shifts northward from Dakar (14°N) to the south of Morocco (22°N). In northern winter, the centroid of the distribution shifts southward from south coast of Portugal to the coast of Morocco.

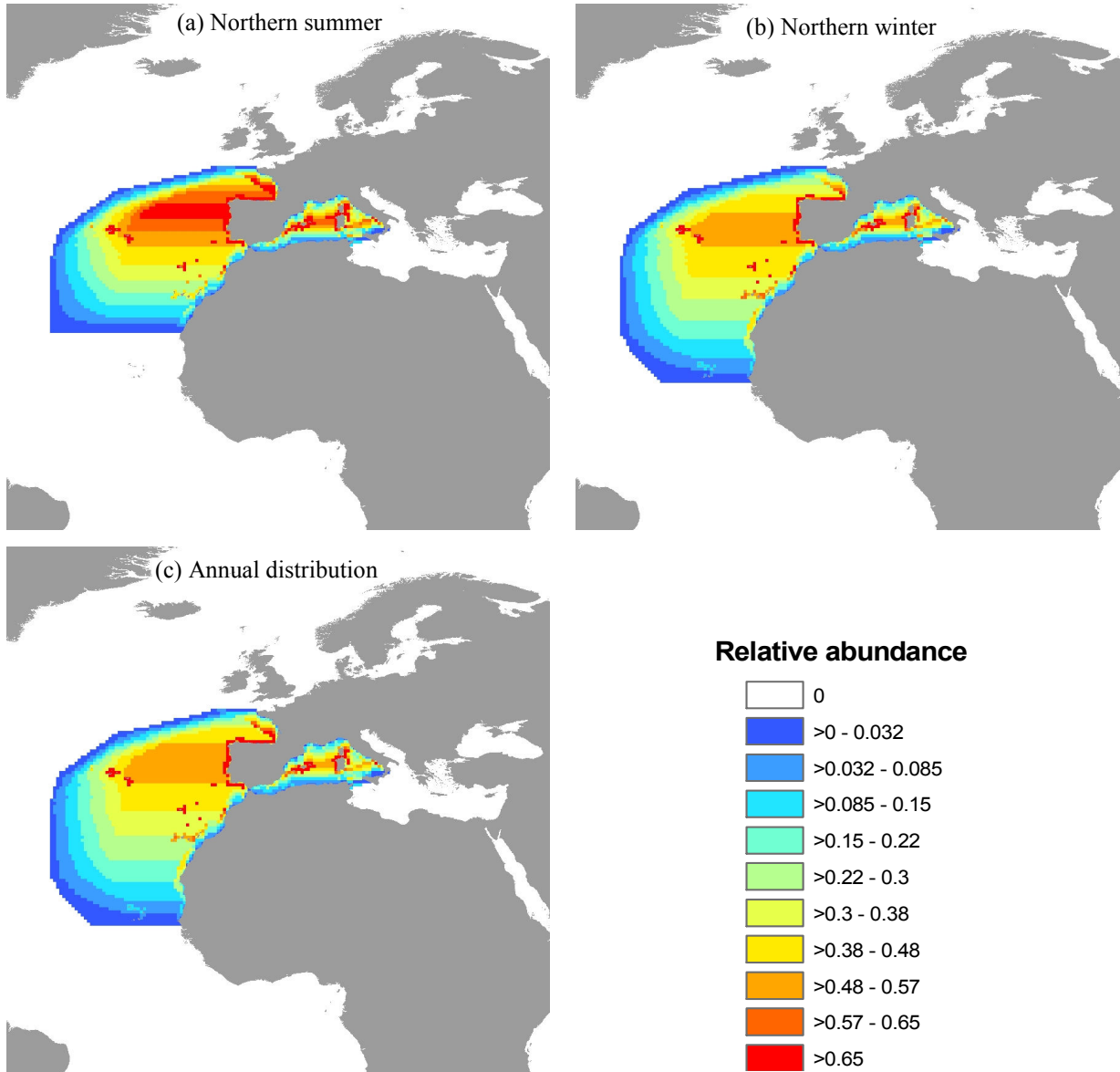


Figure 5. Shift in distribution range of Plain bonito in different seasons: (a) southern boundary shifts northward in summer, (b) northern boundary does not change in winter, and (c) annual distribution range.

DISCUSSION

The distribution ranges of all pelagic fishes and squids are largely dependent on seasonal variations of sea surface temperature (SST). Each species has a specific range of temperature over which the population remains viable. The seasonal migration of these species can be viewed as a strategy to maximize fitness in different seasons (Alerstam *et al.* 2003). Thus, if possible, the species may move to area where water temperature remains within their preferred range. However, long-range migration may not be possible for all species because of limitations in motility. Of the over 1,200 species considered in this study, 116 pelagic species have motility index equal to zero, too low for any seasonal migration to be visible at the scale of this study (i.e., 30' lat. x 30' long.).

The predicted seasonal distributions corroborate with observed seasonal migration patterns of the studied species. Common dolphinfish (*Coryphaena hippurus*) shows seasonal abundance in many tropical and subtropical areas (Massuti & Morales-Nin, 1994, Kraul, 1998). For example, catch records of common dolphinfish show that the adult migrates northward during spring and summer from their wintering grounds in the tropical areas of Atlantic Ocean (Massuti & Morales-Nin, 1994). The species reaches its peak abundance in October in the Mediterranean and decreases again from late November. Many authors suggest that temperature is the controlling factor for the seasonal migration of common dolphinfish and the shift between north and south is correlated with the 23°C isotherm (Kraul, 1998). This 23°C isotherm approaches 36°N in August but goes down to 19°N in February (Kraul, 1998). Some studies also suggest that the peak abundance of Common dolphinfish is found in area with SST of about 25 – 28°C (Massuti & Morales-Nin, 1994). These agree with the temperature preference and migration patterns predicted from our model.

A good match between observed and predicted seasonal migration pattern can also be found in serra (*Scomberomorus brasiliensis*) in northeastern Brazil. The abundance of serra increases along the Brazilian coast in March, but decreases continuously throughout July, August and September (Batista & Fabre, 2001). These observations agree with our model prediction, in which the southern boundary of the distribution range of serra shifts northward in summer. On the other hand, its distribution shifts to the northern part of its range in summer (July to September).

The accuracy of the predicted seasonal distributions of pelagic species can be affected by other factors that can impact on the seasonal migration pattern of the species. A major assumption of our model is the importance of sea water temperature in determining seasonal migration patterns. However, other factors such as food availability, salinity, rainfall and current might also play an important role in the seasonal distribution pattern of species. Williams and Newell (1957) finds that the abundance of Common dolphinfish becomes high when the SST reaches 29°C along with low salinities, while its high abundance may also be due to the seasonal plankton. Moreover, oceanographic condition could affect spawning and migratory patterns of the species (Massuti and Morales-Nin 1995). However, given the global focus of our model, the large number of species from a wide range of groups that the model has to handle, and the limited availability of data for most of these species, the approximations in our model are unavoidable. Furthermore, model predictions appear to agree with the observed patterns of seasonal movement of pelagic species. In addition, the predicted seasonal distributions narrow the Temperature Preference Profiles (TPP) predicted from the maps of distribution range and sea water temperature. These predicted TPP are fundamental to the dynamic bioclimate envelope model developed to study the effects of climate change on distribution ranges of marine fishes and invertebrates (see Cheung *et al.* this vol.).

In conclusion, marine pelagic species and squids shift to the northern or southern parts of their distribution ranges in summer and winter, respectively. These species migrate to areas where SST is optimal (or at least suitable) for their survival and reproduction. Predictions from the model can help us to understand the fluctuation in seasonal catch of marine pelagic species.

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