

CHAPTER 3

ASYMMETRY IN LATITUDINAL, LONGITUDINAL AND BATHYMETRIC DISTRIBUTION OF MARINE FISHES AND INVERTEBRATES³

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ABSTRACT

The distribution ranges of organisms, and marine animals in particular, are a manifestation of their environmental requirements, although they are often modified by the dynamics of prey and predators. Distribution range maps can also be used to infer where an activity occurs which requires the presence of a set of species, e.g., a fishery which targets them.

The distribution of marine fishes and invertebrates serves as the basis for the mapping of fisheries by the *Sea Around Us* Project. Thus, accurate range maps are extremely important, and an earlier contribution by Close *et al.* (2006; FCRR 14(4): 27-37) reviews the step-by-step approach, and the assumptions used to predict the distribution of relative abundance of marine fishes and invertebrates from broad geographical limits, e.g., ocean basins, latitudinal limits, depth limits, etc., to relatively narrow polygons surrounding a number of 1/2 degree lat.-long. cells.

Once established, such distributions, at least those referring to demersal fishes and invertebrates, can be interfaced with a map of sea bottom temperature, and inferred temperature preference profiles (TPP). These can be used, among other things, to verify the distribution ranges as predicted distributions should generate unimodal TPP, with the bulk of the distributions spanning a narrow range of temperature (~10° Celsius).

As a relatively large fraction of the TPP that we obtained at first appeared bimodal, or exhibited a strong kurtosis, the assumption was revisited that the distribution of a species with regard to latitude can be simulated by an equal-sided triangle. It is shown here, for the cod (*Gadus morhua*), and generally for all our over 900 demersal species, that assuming a skewed triangular distribution, whose degree of skew is proportional to the temperature gradient from low to high latitude, generates more realistic distributions when compared to observed species distribution maps, although the narrowing of the uni-modal temperature probability distributions is relatively small. This correction will be implemented in all distribution ranges of demersal fishes and invertebrates in the *Sea Around Us* database, and used for catch allocation, and inferences on climate shifted distributions due to climate change.

³ Cited as: Pauly, D., Cheung, W.W.L., Close, C., Hodgson, S., Lam, V.W.Y. and Watson, R., 2008. Asymmetry in latitudinal, longitudinal and bathymetric distribution of marine fishes and invertebrates, p. 63-72. *In*: Cheung, W.W.L., Lam, V.W.Y., Pauly, D. (eds.) *Modelling Present and Climate-shifted Distribution of Marine Fishes and Invertebrates*. Fisheries Centre Research Report 16(3). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

INTRODUCTION

The distribution range of organisms is, besides their size, the feature that is most informative about their biology. Size largely determines the kind of prey and predators which that organism can have (Pauly & Christensen 2002). The distribution, on the other hand, informs us of the temperature, depth, seasonality, etc., in which they are equipped to live (Helfman *et al.* 1997).

Distribution ranges are also used for practical purposes. In the *Sea Around Us* Project, predicted distribution ranges are used to map fisheries catches (Watson *et al.* 2004). As fisheries maps can be improved by the underlying fish distribution ranges, the *Sea Around Us* Project has worked continuously at improving these ranges, and the last version of the predicted distribution ranges are all available at (www.seaaroundus.org). In Close *et al.* (2006), we reviewed the methods and assumptions used therein, which can be seen as a set of filters:

- 1) FAO area: the fish and invertebrates covered in the *Sea Around Us* database are assigned (or were pre-assigned by FishBase, or FAO) to one or several of the 18 FAO area where they occur;
- 2) Latitudinal range: defined by the northern and southern limits of the distribution, whose relative abundance distribution is assumed to be triangular, with a maximum at the latitude midrange (i.e., symmetry is assumed; see below);
- 3) Range limiting polygon: originating from various sources, and preventing the range from 'spilling over' into water bodies which satisfy (1) and (2), but which are known to have attributes preventing them from being part of the distribution (e.g., low salinities);
- 4) Depth range: defined by shallow and deep limits, with the density of the distribution in between represented by an asymmetrical triangular distribution, with a maximum at 30% of the depth range, thus accounting for larger depth-related changes in shallow than in deep water. Also, we correct for some of 'equatorial submergence' (Ekman 1967) not discussed here, except to mention that this effect is also assumed to be asymmetrical with regard to depth;
- 5) Assignment with regard to habitats (shelves, estuaries, seamounts, etc.). This is not further discussed because this does not concern the point to be made here.

These procedures lead to distribution range maps from which various inferences can be drawn, notably the temperature preference of the fish, since temperature is not used directly in any step in this process. Thus, when distribution ranges are mapped onto a temperature atlas, a temperature preference profile (TPP) can be inferred whose mode should indicate the preferred temperature of the animal in question, while the flanks indicate the normal temperature range of the species (see Figure 1, for an example).

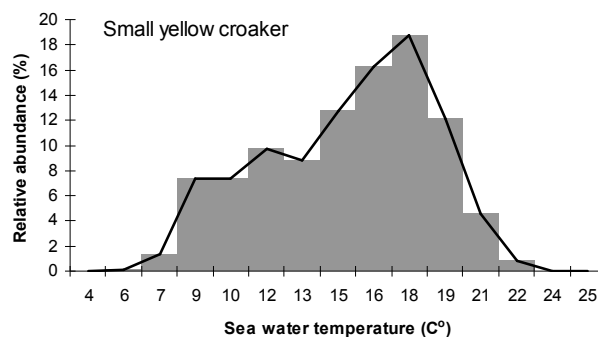


Figure 1. A temperature preference profile (TPP) of the Small yellow croaker (*Larimichthys polyactis*, Sciaenidae) inferred from the predicted species distribution and sea bottom temperature (the latter obtained from Met Office Hadley Centre observations datasets; <http://hadobs.metoffice.com/hadisst/>).

However, a large number of TPP obtained by this method are bi- or multi-modal, while another set of TPP displays extreme kurtosis. Such patterns are not realistic, because marine fish and

invertebrates usually have one temperature optimum, i.e., one mode in a more or less symmetrical, bell-shaped distribution with regard to temperature (Coutant 1987).

We have examined which of the above steps and assumptions of the method of Close *et al.* (2006) could generate these bi- or multi-modal TPP, and identified Step 2 and 3 above, i.e., the assumptions of symmetrical triangular distribution with respect to relative abundance along latitudes, and abruptly-cut range boundary imposed by polygons, respectively, as the likely culprit.

First, the latitudinal distribution of relative abundance should be asymmetrical (step 2). As the underlying environmental variables which affect distribution range are unevenly distributed, uneven gradients of density of animals should be observed (MacCall 1990). For marine ectotherms, temperature is one of the most important parameters affecting their distributions (Coutant 1987; Pörtner 2001). Thus, the assumption of a symmetrical triangular distribution which is probably correct at low latitudes, where the isotherms are widely spaced, would become incorrect at higher latitudes (around 40° N/S), where the isotherms are close to each other (Figure 2).

To represent such asymmetry in latitudinal-temperature gradient, instead of the symmetrical triangular distribution described in Close *et al.* (2006), we should employ asymmetrical triangular distribution, with the degree of skewness being a function of the closeness of the latitudinal isotherms.

Also, range boundaries should not be abruptly cut (Step 3). This problem arises when portions of the potential distribution ranges are excluded by polygons that are constructed from known distribution range of the species. Thus, relative abundance at the edge of the distribution range may become discontinuous in terms of the environmental gradients. However, such abrupt change in abundance at boundary of a range is rarely observed in the sea. This phenomenon is particularly apparent for pelagic species whose predicted distribution ranges are strongly affected by the polygons. Thus, a gradient of relative abundance should be applied to the polygon boundary to make the predicted distribution range more realistic.

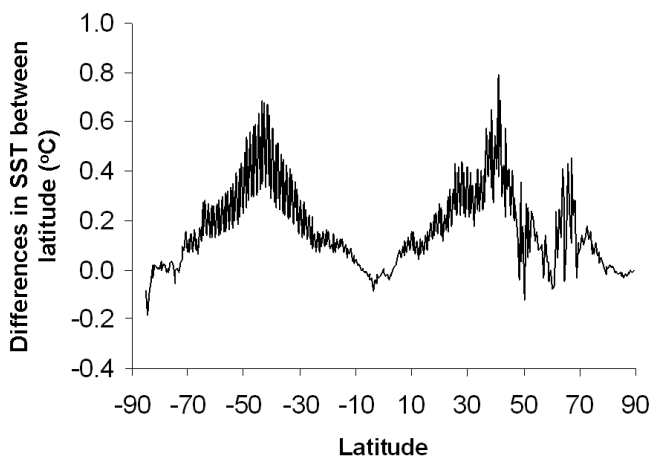


Figure 2. Differences in sea surface temperature between latitudinal zones of the world ocean.

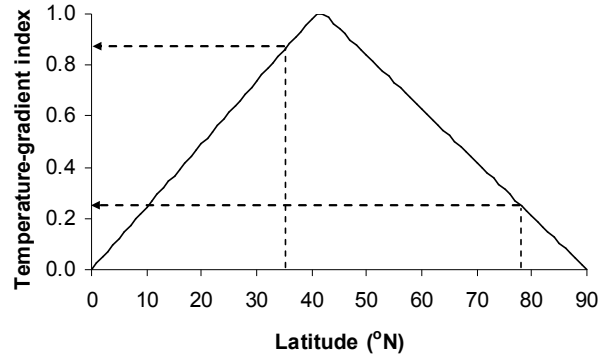
This paper describes the algorithms that improve on the above two assumptions in predicting species distribution range, i.e., latitudinal asymmetry in relative abundance distribution and gradient of relative distribution at range boundaries. We compare the predicted distribution ranges and TPP of selected species to evaluate the effects of implementing the new algorithms.

METHODS

Latitudinal asymmetry

The distribution of relative abundance along latitude was assumed to be triangular-shaped and the mode (peak) of the triangular distribution was assumed to be determined by the steepness of the latitudinal-temperature gradient at range limits. To determine the latitudinal position of the peak, we first constructed a profile of temperature-gradient index (Figure 3a and b for the northern and southern hemispheres, respectively) approximated from the observed sea surface temperature gradients (see Figure 2). The temperature-gradient index represents the marginal changes in temperature by latitude and scales from 0 to 1, with 1 indicating maximum changes in temperature. The profiles are represented by trapezoidal distribution. Latitudinal zones between 40.75° and 42.25° in the northern hemisphere and 42.25° and 43.75° in the southern hemisphere have the maximum temperature-gradient index values of 1, from where the index decreases linearly to the equator and poles (Figure 3). For example, the northern and southern latitudinal limits of Atlantic cod (*Gadus morhua*, Gadidae) are 35° and 78° . Based on the temperature-gradient index profile (Figure 3a), the corresponding temperature-gradient index values are 0.86 and 0.25, respectively.

a)



b)

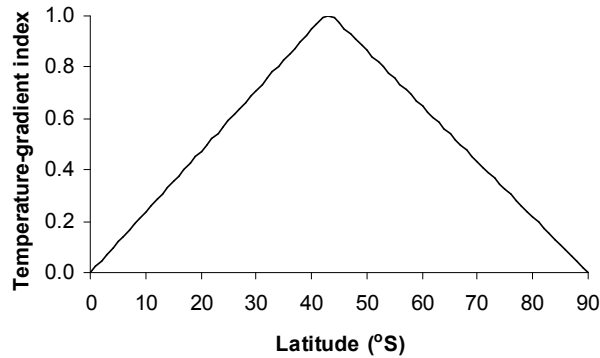


Figure 3. Temperature-gradient index by latitude in (a) northern hemisphere and (b) southern hemisphere. The broken lines on (a) indicate the northern (78°) and southern (35°) latitudinal limits of Atlantic cod.

Secondly, the degree of skewness of the triangular latitudinal-relative abundance distribution is determined by the difference in temperature-gradient index between the north and south latitudinal range margins. We assume that relative abundance declines more rapidly towards the range margin with steeper temperature gradient. The degree of skewness (*Skew*) is calculated from:

$$Skew = a - b \cdot [TG(L^U) - TG(L^L)] \quad \dots 1)$$

and the latitudinal position of the peak of the triangular latitudinal-relative abundance distribution is (L^P):

$$L^P = (L^U - L^L) \cdot (1 - Skew) + L^L \quad \dots 2)$$

where a and b are constants that determine the maximum and minimum degree of skewness; TG is a function to calculate the temperature-gradient index at the upper and lower latitudinal limits (L^U and L^L , respectively). The default values of a and b are 0.5 and 0.3, respectively. Since temperature-gradient tends to be steeper at mid-latitude (around 40° N/S), the calculated latitude-relative abundance distributions will also be skewed towards the mid-latitudinal zone (Figure 4). For example, given the L^U and L^L of Atlantic cod (78° and 35° N), the calculated S is 0.68 and the peak of the triangular distribution is at 48.7° N (see distribution c in Figure 4).

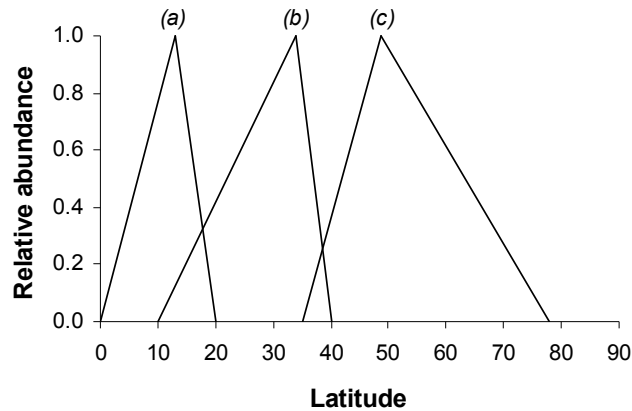


Figure 4. Asymmetric triangular relative abundance – latitudinal distributions generated from three sets of latitudinal range limits: (a) 0° – 20° N, (b) 0° – 40° N, and (c) 35° – 78° N.

This algorithm applies to distribution ranges that cover either the northern or southern hemisphere only, or across the equator with a bimodal latitudinal distribution. The latter is represented by two triangular distributions in each hemisphere which extend from the equator to its northern and southern latitudinal limits. Equatorial species with ranges covering across the equator are assumed to have a symmetrical triangular latitudinal-relative abundance distribution (Close *et al.* 2006).

Abundance gradient at polygon boundaries

We apply a gradient of abundance for distribution range boundaries of a species, as delineated by pre-specified polygons. We assume a trapezoid distribution to each segment of spatial grid within a polygon along the same latitude and longitude (Figure 5). Along a seaward polygon boundary, we assume that relative abundance declines linearly from a maximum at 1/5 of the segment length away from the boundary to zero at the boundary edge. If the polygon boundary is land-bounded, we assume a steeper relative abundance gradient that declines from 1/20 of the segment length away from the boundary edge with relative abundance being half of maximum at the boundary (see Figure 5). In addition, the minimum lengths of the gradient at seaward and landward boundaries are 10 and 5 spatial cells, respectively.

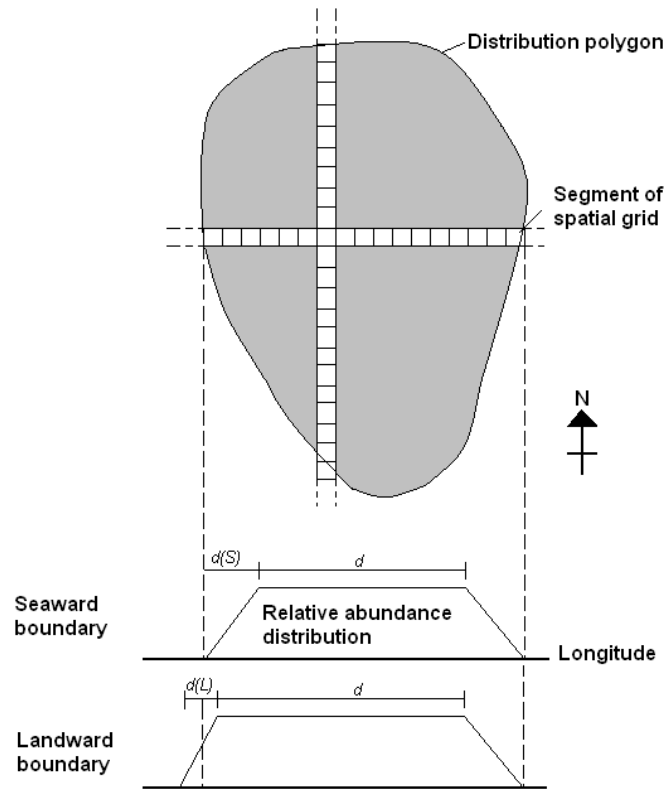


Figure 5. Schematic diagram showing the distribution of relative abundance along the same latitude with a specified polygon. The gradient of relative abundance at the boundary edge is dependent on (1) whether the edge is sea- or land- bounded, and the length of the segment (d). The distances $d(S)$ and $d(L)$ are set as $1/5$ and $1/20$ of d . Also, at the seaward boundary, the relative abundance at the edge is zero while, at the landward boundary, the relative abundance at the edge is half of the maximum relative abundance.

Application examples

To test the effects of these new assumptions, we applied the algorithms on latitudinal asymmetry and abundance gradient at polygon boundary to two species: Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*). We generated predicted distribution maps of the two species with the original routine documented in Close *et al.* (2006) and the routine with the modified assumptions and algorithms as described above. We superimposed the distributions of Atlantic cod and Atlantic herring on maps of sea bottom and sea surface temperature, respectively (Met Office Hadley Centre observations datasets, <http://hadobs.metoffice.com/hadisst/>). We also constructed TPP from the two sets of maps and compared their validity based on uni-modality and variance of the TPP.

RESULTS

Based on visual inspection, the new algorithms provided a predicted distribution of Atlantic cod that appears to be a closer match to reality (Figure 6). Distribution range of cod predicted from the original Close *et al.* (2006) algorithm centers at higher latitude (Figure 6a and c). The new distribution for cod, predicted from a latitude-abundance distribution that is skewed towards lower latitude (Figure 6b and d), has centers of abundance at the Grand Bank, Newfoundland coast, southern parts of Greenland, Iceland, and around Faroe Island.

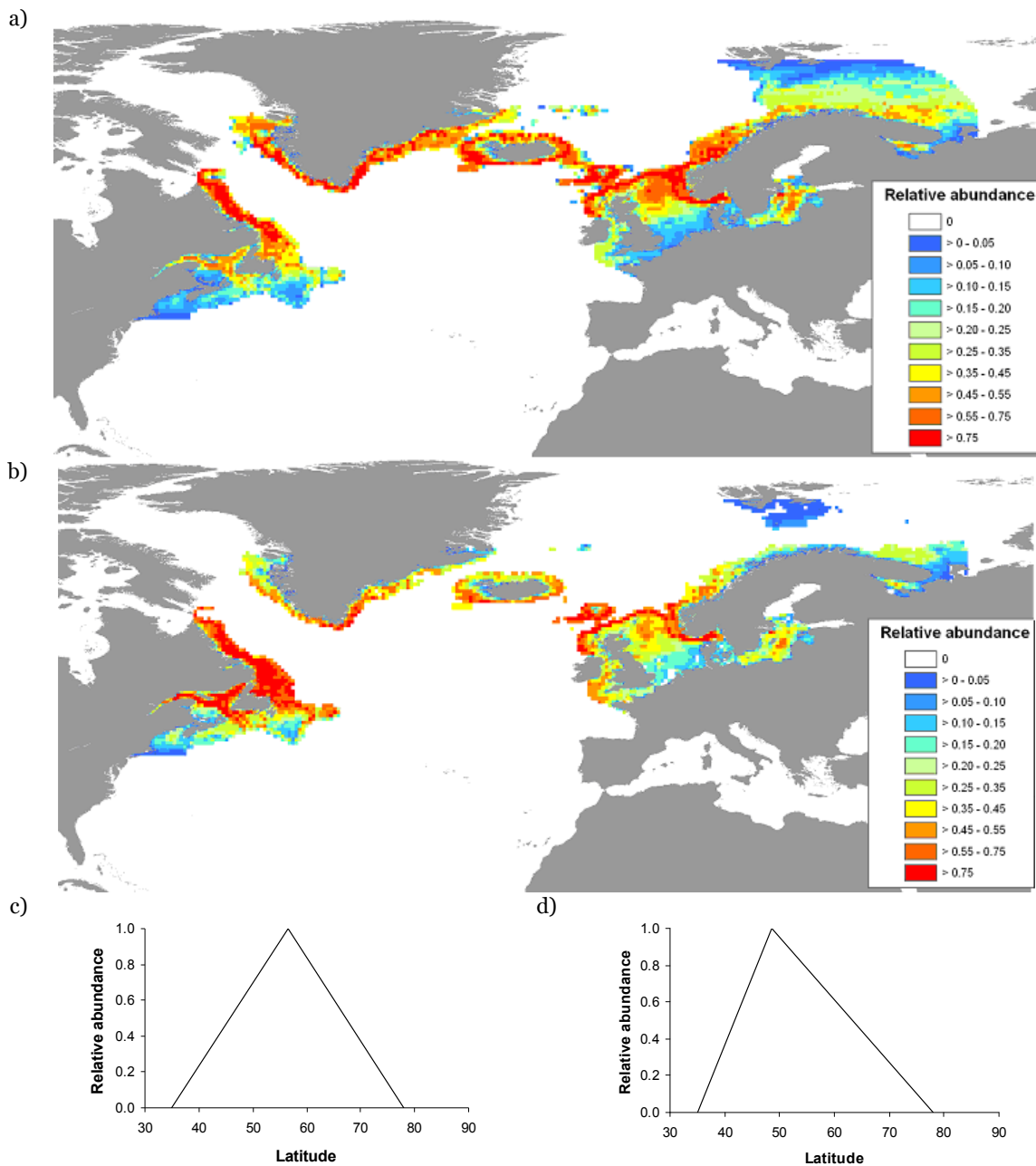


Figure 6. Predicted distribution ranges and the underlying assumptions on the latitudinal gradient of relative abundance of Atlantic cod with (a, c) symmetric triangular distribution and (b, d) asymmetric triangular distribution of relative abundance.

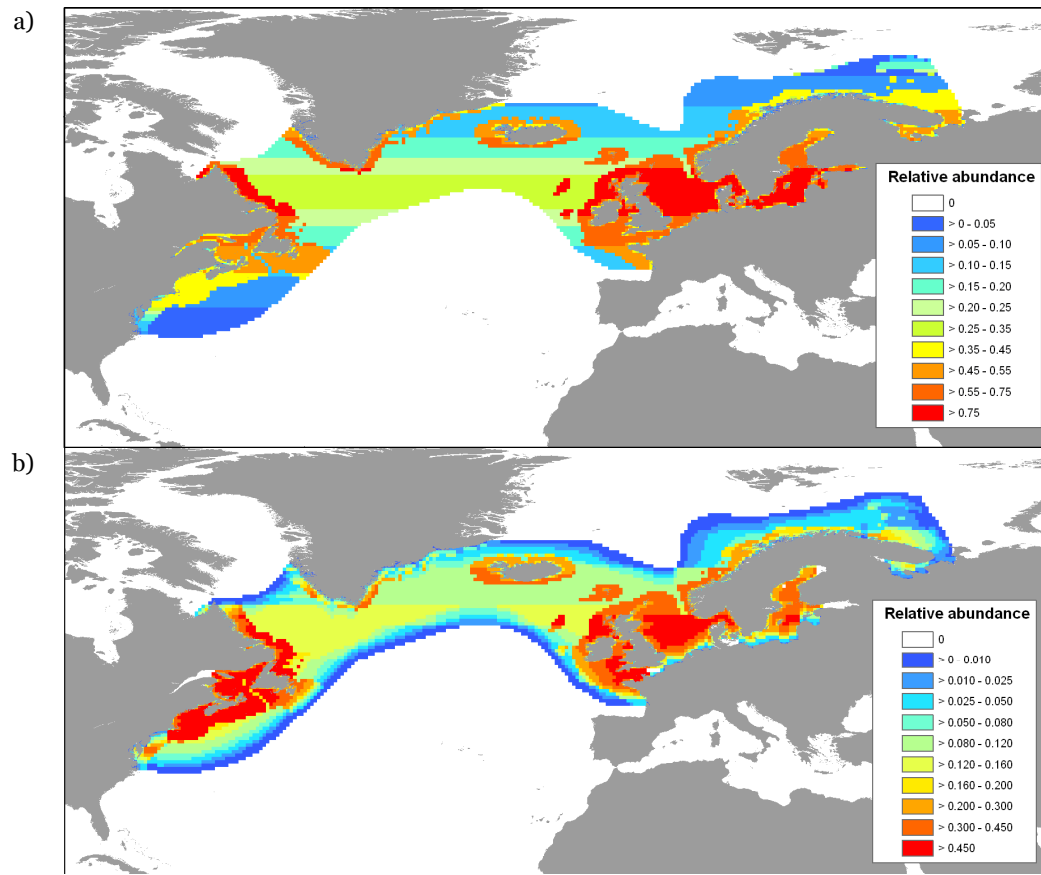


Figure 7. Predicted distribution ranges of Atlantic herring predicted with (a) the original Close *et al.* (2006) algorithm and (b) with additional assumption on abundance gradient at the edge of specified polygons.

Application of the abundance gradient at the edge of polygons eliminated the unrealistic boundary with abrupt drop in relative abundance of Atlantic herring (Figure 7). For example, adjacent to the southern coast of Iceland, the distribution range predicted from the original Close *et al.* (2006) algorithm results in an abrupt drop in relative abundance from medium level to zero at the range boundary (Figure 7a). In the case of the revised algorithm, the predicted distribution shows gradual decline in relative abundance towards the boundary edge (Figure 7b).

Temperature profiles, or TPP, obtained from the revised algorithms appear slightly more unimodal than TPP obtained from the original Close *et al.* (2006) algorithm (Figure 8). With the revised algorithm, the relative abundance of Atlantic cod is more concentrated near sea bottom temperature of around 2 °C (Figure 8a), while the abundance of Atlantic herring is more concentrated at sea surface temperature of around 9 °C (Figure 8b).

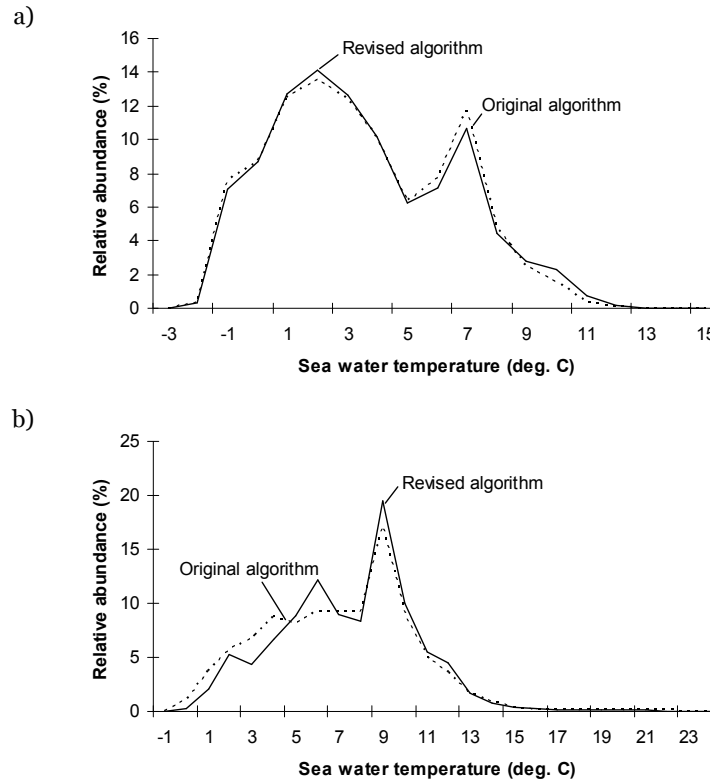


Figure 8. Temperature Preference Profile (TPP) of Atlantic cod calculated based on the distribution ranges that are predicted from the revised algorithm (solid line) and the original algorithm described in Close *et al.* (2006).

DISCUSSION

While the procedure proposed here may seem *ad hoc*, it actually corrects for an inconsistency in our treatment of distribution range maps which we had overlooked earlier. With regard to depth, we had taken asymmetry into account, i.e., we had considered that, e.g., a 10 m depth change has a much stronger effect at shallow than at great depth. The correction suggested here does the same with latitude, as a 1° change of latitude in temperate areas implies a greater change of environmental parameters (especially temperature) than in tropical areas. This correction to our distribution ranges will be fully implemented in our next catch allocation (i.e., the update from time series that end in 2004 to series ending in 2005).

Although the improvement in the predicted TPP in terms of uni-modality and variance of the distribution from considering distributional asymmetry is relatively small, the predicted distributions appear more realistic when compared to observed species distribution maps. Realistic distribution maps are pre-requisites of simulating changes in distribution range under global climate change scenarios (see Cheung *et al.* this vol. for details).

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