Collect. Vol. Sci. Pap. ICCAT, 74(3): 1235-1250 (2017)

CREATING A SPECIES DISTRIBUTION MODEL FOR SWORDFISH: EVALUATIONS OF INITIAL HABITAT VARIABLES

C. Phillip Goodyear[1] Michael Schirripa[2] and Francesca Forrestal[3]

SUMMARY

This study develops a species distribution model (SDM) for swordfish using a habitat suitability framework. When suitably parameterized, the model is intended to estimate the time-varying, three dimensional (3D) distribution of swordfish habitat that would be useful for many aspects of stock assessment, including visualizing stock boundaries and estimating abundance from catch per unit effort (CPUE) data. Currently, the model integrates ocean depth, annual average estimated total chlorophyll by latitude and longitude, and temperature and oxygen by latitude, longitude, depth, month and year. Model predictions and general distributions of North Atlantic swordfish catches are used as criteria for the inclusion and treatment of variables. Initial trials demonstrated that the habitat cannot be predicted using temperature and oxygen alone. The inclusion of the spatial annual average productivity via chlorophyll markedly improved distribution predictions. The current formulation predicts the north-south seasonal migration in the North Atlantic but also predicts high abundance in areas of low swordfish catch. Better, time-varying data for ecosystem productivity relevant to swordfish might resolve this problem, but important habitat features may also be missing.

RÉSUMÉ

Dans le cadre de la présente étude, un modèle de distribution des espèces (SDM) pour l'espadon a été mis au point à l'aide d'un cadre d'adéquation de l'habitat. Lorsqu'il est correctement paramétrisé, le modèle vise à estimer la distribution tridimensionnelle (3D) variant dans le temps de l'habitat de l'espadon qui pourrait être utile pour de nombreux aspects de l'évaluation des stocks, y compris la visualisation des limites des stocks et l'estimation de l'abondance à partir des données de capture par unité d'effort (CPUE). Actuellement, le modèle intègre la profondeur de l'océan, la chlorophylle totale annuelle estimée moyenne par latitude et longitude, et la température et l'oxygène par latitude, longitude, profondeur, mois et année. Les prédictions du modèle et les distributions générales des prises d'espadon de l'Atlantique Nord sont utilisées comme critères pour l'inclusion et le traitement des variables. Des premiers essais ont démontré que l'habitat ne peut pas être prédit uniquement au moyen des données relatives à la température et l'oxygène. L'inclusion de la productivité moyenne annuelle spatiale par l'intermédiaire de la chlorophylle a considérablement amélioré les prévisions de distribution. La formulation actuelle prévoit la migration saisonnière Nord-Sud dans l'Atlantique Nord, mais prévoit également une abondance élevée dans les zones de faibles captures d'espadon. De meilleures données variant dans le temps concernant la productivité de l'écosystème pertinente pour l'espadon pourraient résoudre ce problème, mais d'importantes caractéristiques de l'habitat pourraient également encore faire défaut.

RESUMEN

Este estudio desarrolla un modelo de distribución de especies (SDM) para el pez espada con un marco de idoneidad de hábitat. Cuando se incluyen los parámetros adecuados, el modelo está concebido para estimar la distribución tridimensional (3D) variable en el tiempo del hábitat de pez espada que sería útil para muchos aspectos de la evaluación de stock, lo que incluye visualizar los límites del stock y estimar la abundancia a partir de los datos de la captura por unidad de esfuerzo (CPUE). Actualmente, el modelo integra la profundidad del océano, la media anual de la clorofila total estimada por latitud y longitud y la temperatura y el oxígeno por latitud, longitud, profundidad, mes y año. Se usan las predicciones del modelo y las

[1] 1214 North Lakeshore Drive, Niceville, Florida 32578, USA. phil_goodyear@msn.com

[2] NOAA Fisheries, Southeast Fisheries Center, Sustainable Fisheries Division, 75 Virginia Beach Drive, Miami, FL, 33149-1099, USA. Michael.Schirripa@noaa.gov

[3] CIMAS/RSMAS University of Miami, 4600 Rickenbacker Cwy. Miami, FL 33149. fforrestal@rsmas.miami.edu

distribuciones generales de las capturas de pez espada del Atlántico norte como criterios para la inclusión y tratamiento de las variables. Las pruebas iniciales demostraron que el hábitat no se puede predecir usando únicamente datos de temperatura y oxígeno. La inclusión de la productividad media anual espacial a través de la clorofila mejoró notablemente las predicciones de distribución. La formulación actual predice la migración estacional de norte a sur en el Atlántico norte, pero también predice alta abundancia en zonas con bajas capturas de pez espada. Unos datos mejorados que varíen en el tiempo para la productividad del ecosistema relevante para el pez espada podrían resolver este problema, pero podrían seguir faltando características importantes del hábitat.

KEYWORDS

Swordfish, Habitat, Stock assessment, Statistics, Species Distribution, Data simulation, Population modeling

1. Introduction

Knowledge of the physical distribution of the utilized habitat of "highly migratory" pelagic fishes is key to understanding the species as a resource. The term migration brings to mind directed seasonal movements, often over large distances. Some or all of this behavior can simply be the result of the movement of acceptable physical habitat caused by seasonal or longer term shifts in acceptable thermal regimens or other habitat features. The habitat itself is migrating, independent of fish behavior. These are first order effects that constrain all of the remaining population processes, including population dynamics and seasonal distributions of the fisheries. Quantitative models of this habitat space are important for most aspects of management and related research, but are not generally available. One such use is in the simulation of longline catch data for studying methods for standardizing CPUE data. Goodyear (2016) described a relatively simple, generic approach for modeling the distribution of a species-specific pelagic habitat using Atlantic blue marlin as an example. The approach relies heavily on the availability of oceanographic data in time and space and behavioral information derived from satellite tags. The current work begins an implementation of that approach for swordfish in the Atlantic using temperature and depth utilization patterns recorded with 15 PSAT tags. These data were coupled with time-varying oceanography to explore the potential value of several important habitat variables.

2. The species distribution model

Swordfish habitat distribution is predicted using a mix of standard habitat suitability index (HSI) models to compute weighted habitat volume (*H*) following the methods described in Goodyear (2016). With appropriate inputs, the approach can be used to quantify the amount and distribution of usable habitat at any point in time. The value of the weighted habitat volume H_{ijk}, for a segment of the water column at latitude i, longitude j, and depth layer k at time is given by:

$$H_{ijk} = X_{ijk} V_{ijk}$$

were X_{ijk} is the cumulative HSI weighting based on the values of the environmental variables existing at *ijk* at that point of time, and V_{ijk} is the volume of the corresponding segment of the water column. The cumulative weighted habitat volume is simply the sum of the H_{ijk} over the whole of the modeled region, ideally a single stock isolated by a boundary of unsuitable habitat. The X_{ijk} can consist of both additive and multiplicative factors such that cumulative HSI weighting is given by:

$$X_{ijk} = \left(\frac{\sum_{l=1}^{L} A_{ijkl}}{L} \right) \left(\prod_{n=1}^{N} G_{ijkn} \right)^{1/N}$$

where A_{ijkl} and G_{ijkn} are the values of additive factors (l) and multiplicative factors (n), at location ijk, and L and N are the number of additive and multiplicative factors, respectively. The numerical values of the A and G are the habitat suitability values at the magnitudes of the associated environmental variables (i.e., temperature and DO, respectively) at location ijk. The magnitude of the habitat suitability values range from 0.0 to 1.0 and are often drawn from histogram representations of their respective distributions. The density distribution in the volume occupied by the species is proportional to the X_{ijk} such that the relative density R_{ijk} is given by:

$$R_{ijk} = H_{ijk}V_{ijk} \Big/ \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{k=1}^{K} H_{ijk}V_{ijk}$$

The product of R_{ijk} and population abundance can be used to calculate the absolute average density in time and space for any total number of fish in the population. The sum of products of layer densities and volumes for a latitude-longitude grid provides an estimate of the average relative abundance at that location, i.e.,

$$N_{ij} = \sum_{k=1}^{K} R_{ijk}V_{ijk}$$

Swordfish exhibit diurnal cycles in vertical distribution, spending more time near the surface at night and are deeper in the water column during daylight hours (e.g., Abascal et al., 2010; Dewar et al., 2011;.Abecassis et al., 2012; Chang et al. 2013, Lerener et al. 2013 Braun et al., 2015) It is important to capture this effect for applications such as the simulation of longline catches because of the variability of fishing depths by different gears. This pattern is probably a local accommodation to factors ultimately related to the diel cycle in ambient light intensity, but the cyclic variation causes the fish to spend different amounts of time at different temperatures because of the thermal stratification of the ocean. This phenomenon makes it possible to predict depths from temperature using data describing thermal stratification in a location as was done for blue marlin (Goodyear 2016). That approach could be extended to swordfish, but accuracy and precision would be seriously degraded because swordfish spend large parts of their daytime much deeper in the water column where temperature changes very slowly with depth (Boyer and Mishonov 2013; Chang et al. 2013, Lerener et al. 2013 Braun et al., 2015). Here we employ the day-night cumulative depth distributions estimated directly from satellite tags P_{kt}, to repartition the N_{ij} into the depth strata. But since this process may assign part of the local population to depth layers with unsuitable habitat (e.g., rock, toxic DO, etc.) the weightings (D) at each depth are corrected for critical HSI factors as:

$$D_{ijkt} = (P_{kt})\left(\prod_{n=1}^{N} G_{ijkn}\right)^{1/N}$$

The local vertical density fractions can then converted back to population relative density, Y_{ijkt}, for the location, depth and time of day after normalizing the D_{ijkt} to account for the effects of critical habitat weightings:

$$Y_{ijkt} = N_{ij}D_{ijkt}V_{ijk} \Big/ \sum_{k=1}^{K} D_{ijkt}V_{ijk}$$

The Y_{ijkt} are now estimates of the weighted proportions of the habitat available at the latitude, longitude, depth, and time of day given the distribution of oceanographic features existing at the time evaluated. This reaggregation does not modify the areal distribution of the population within each latitude-longitude stratum. It moves the local population densities vertically among depths in response to their day-night movements. When populated with oceanographic data and appropriate habitat suitability functions, the model can be used to predict 2- and 3-D distributions of the species by month and year. These predictions are a guide to understanding the species population as an entity, and a quantitative framework for testing what and how environmental variables shape swordfish distributions.

3. Implementation

The model is at a formulative stage of development. Temperature and dissolved oxygen are features known to profoundly affect species distributions and so are included. The depth layering is designed to accommodate the spatial structure of environmental data of the Community Earth System Model (CESM1), which is a global ocean-sea-ice coupled model coupled to a biogeochemistry model as known BEC (Biogeochemical Elemental Cycle). It provides data monthly from the late 1940's to the near present and is intended to be the primary source of environmental data. The current model is partitioned into cells of 1º latitude and longitude and 46 depth layers from the surface to just shy of 2 km (**Table 1**, **Figure 1**). In addition, the spatial distribution of chlorophyll is included as a variable to examine how productivity patterns might influence swordfish dynamics (data from the World Ocean Atlas 2001 https://www.nodc.noaa.gov/OC5/WOA01/1d_woa01.html).

3.1 Habitat suitability

The aggregate of the selectivity functions and habitat values that will describe the distribution of swordfish habitat is a complex research agenda. The estimation of the spatial distribution of the X_{ijk} requires estimation of the A_{ijk} and G_{ijk} from habitat suitability values and the values of the corresponding environmental variables. The initial design here applied some patterns derived from tagging data or functions designed to test if variables, such as chlorophyll are potentially explanatory.

3.1.1. Oxygen

Although brief excursions into hypoxic conditions are possible or even routine, at some level the concentration of oxygen must be a limiting factor. A precise model of oxygen suitability is not available for swordfish, but observations from several studies indicate swordfish are more tolerant of low DO than many other pelagic species (Abascal *et al*., 2010; Abecassis *et al*., 2012 Braun *et al*., 2015; Dewar et al., 2011). Pending a more accurate analysis, the oxygen selectivity curve used for the blue marlin SDM in Goodyear (2016) was modified for swordfish by adjusting the transition downward by 1 ml/l so that the median corresponds to 2.5 ml/l (**Figure 2**.).

3.1.2. Temperature

Swordfish exhibit a wide thermal plasticity in occupied habitat. They also show a well documented propensity for spending daytime hours deeper in the water column (Abascal *et al*., 2010; Abecassis *et al*., 2012 Braun *et al*., 2015; Dewar *et al*., 2011; Neilson *et al*., 2009; Neilson *et al.*, 2014). This trend was also clearly evident in the tag data available for this study and results in a strong diel cycle in the temperatures of the habitat utilized (**Figure 3**).The large amount of time spent in cooler environments during the daytime subverts using the temperature utilization pattern to map the spatial extent of suitable habitat from temperature as was done for blue marlin. This is partly because the lower daytime mode of temperature occurs at temperatures present in nearly every latitude-longitude ocean grid, and partly because like temperatures extend beyond the modeled region. Nonetheless, temperature is an important determinant of suitable habitat.

It is reasonably clear that the temperatures at which swordfish spend daytime hours in **Figure 3** are not limiting areal distributions because such temperatures are nearly everywhere present in the water column. In contrast, the nighttime temperature utilization pattern may have predictive value, and we apply the relative proportions at temperatures from 15º C and above as weightings for the temperature selectivity curve for use in the SDM to obtain the 2-D spatial distribution pattern. The method used here to predict the day/night distribution from the global observed depth distributions pattern can predict swordfish to be in depths that are either too warm or cold based on the local oceanographic conditions at time and place. The current model avoids that possibility with a second HSI model of temperature tolerances imposed on the vertical predictions to limit the values to the range of observed values (**Figure 4**).

3.1.3. Chlorophyll

The potential importance of primary productivity as a predictor of swordfish spatial distribution is being evaluated with an arbitrary selectivity curve. The intent is to examine the impact of alternative assumptions about the importance of productivity on the ocean-wide relative habitat value. Alternative weightings (W) have used the expression: $W = (1 - e^{-r*c})^2$; where c is the chlorophyll concentration at the surface and r is an arbitrary constant. The analyses presented here use a value of r=10.0 (**Figure 5**). The WOA data used were available only as a mean of annual conditions by 1º latitude and longitude, surface only, so there were no seasonal or depth effects from this feature.

3.1.4 Ocean depth

The depth of the ocean is considered a habitat variable. Presently only latitude-longitude cells that average 200 m or greater are included and no additional weighting for ocean depth is considered in determining the areal distribution. However, the vertical distribution of swordfish within the volume of water at a location is partitioned day and night by the observed proportions from swordfish monitored with satellite tags (**Figure 6**).

4. Model predictions

The SDM needs to first capture the main features that affect species distributions to provide a framework within which other features of the habitat can be expressed. The modeling approach and selection of variables progresses from postulation to acceptance based on qualitative and quantitative examinations of SDM predictions. Many possible combinations of conditions can be excluded, thus providing useful directions for continued research. The approach here begins with the evaluation of abiotic features (oxygen and temperature) and is extended to investigate if an index of productivity improves model predictions. The criteria for judging model performance at the current stage of development is the simple qualitative inspection of the distribution of predicted population abundance and the distribution of longline catch in the ICCAT Catdist data file (downloaded from http://www.iccat.int/en/accesingdb.htm). For reasons arbitrary to the results presented here, all SDM predictions use the CESM estimates of temperature and oxygen by month and 1º latitude-longitude cell for the years 1976 and 2010 respectively.

4.1 Oxygen

The effect of oxygen concentrations and the oxygen tolerance assumption (**Figure 2**) on the predicted swordfish distribution was not evaluated separately from other variables. In the Atlantic, oxygen is only potentially important as a variable limiting swordfish where it often diminishes below the thermocline in tropical regions. Its effects would be confounded with those of temperature and error in the accuracy of the selectivity curve would only marginally change the depth of the acceptable habitat. Further, oxygen also does not exhibit the large scale seasonal fluctuations seen with temperature. Consequently, the influence of the oxygen selectivity function on spatiotemporal variability in swordfish habitat is of secondary importance. It is maintained constant in all analyses and was not specifically investigated here.

4.2 Temperature and oxygen only

Application of the nighttime temperature utilization pattern of **Figure 3** with the oxygen selectivity curve produced a monthly average predicted distribution shown in **Figure 7**. The seasonal, 3-D distributions of temperature and oxygen are too complex to condense meaningfully into a graphic for comparison, but the SDM predictions with these data alone show significant departure from patterns in average swordfish catch. A primary example of the discrepancy is the area of the Sargasso Sea and southeastward at about 20º-25º N in the central Atlantic where average predicted abundance is high but in an area where the catch is low.

4.3 Chlorophyll and oxygen only

Chlorophyll was explored to examine the potential of productivity in the context of the SDM. The WOA 2001 annual average distribution used for input is presented in **Figure 8**. The distribution of monthly average predicted values using the selectivity function of **Figure 7** in concert with oxygen data are presented in **Figure 9**. Note that the chlorophyll selectivity was arbitrary and derived by trial and error to get reasonable spatial contrast in the predictions. The resulting pattern of predicted values is exaggerated to the north compared to landings, but the mid-Atlantic area of predicted high abundance by the temperature-oxygen model is diminished in the chlorophyll-oxygen model.

4.4 All variables combined

The month by month SDM predictions averaged for the years 1974 and 2010 from model that combines the effects of temperature, chlorophyll and oxygen are in **Figure 10.** The results seem more reasonable than either of the analyses that omitted a variable, but no quantitative assessment of accuracy has been attempted. The month by month averages of the 1974 and 2010 predictions are given in **Figure 11**. Inspection of these plots reveals the expected north-south movement of the distribution in the northern hemisphere. The magnitude of the seasonal variability caused by temperature is suppressed by the constant annual chlorophyll data used in the analysis. This weakness would presumably be eliminated by monthly chlorophyll data that was not available at the time of the analysis. There is a persistent area of high estimated abundance in the north at about 40W and 20N that is not apparent in the catch. Also, the predicted abundance in region to the west of Portugal seems to be insufficient to support the catch in the area. A more thorough analysis that accounts for the amount of effort will be required to clarify the extent of disagreement.

5. Discussion

Regions of low oxygen were of limited interest at this stage of model development. Based on catch and other observations, swordfish habitat in the Atlantic extends well away from the tropics where low oxygen zones are present. Swordfish are relatively tolerant of low oxygen. The effects of oxygen depletion in these areas may be important; but the major effects would be spatially confined to these tropical regions. Seasonal cycles in oxygen are also minor when compared with temperature, and so would not be expected to be evident in seasonal variations of either catches or the SDM predictions. This topic may become more important as the study progresses, particularly if an application of the SDM might be focused on areas or times where a gradient in DO is an important consideration.

The temperature utilization patterns seen in the tag data used here and elsewhere in the Literature show swordfish have a remarkable plasticity in their use of available habitat (Braun et al., 2015). The results of the SDM predictions with just oxygen and temperature appeared to depart substantially from what would be expected given the distribution of catch. This result could be the consequence of an inappropriate selectivity curve, a strong influence of other factors on habitat quality, or likely both. Among many other possibilities, the individual swordfish used to derive the selectivity curve are unlikely to be a representative sample of the population because of biases in the sample selection, including sizes, sexes and geographic region. Fish are known to accommodate to prevailing ambient temperatures and so estimation of temperature preference/utilization norms would be expected to benefit from random sampling of the spatiotemporal habitat.

The estimation of the selection curve for temperature is an important problem. In blue marlin, the selection curve used PSAT tag data to essentially map habitat space using temperature data. The method exploited the fact that, within the modeled region, marlin spent more than 90% of their time in less than 2% of the ocean. In contrast, swordfish monitored in this study spent significant amounts of time at temperatures as low as 6ºC so that the volume of the commonly utilized temperatures constitutes about 60% of the volume of the ocean (volumes for both species from WOA 2013 monthly means). This makes it impossible to meaningfully predict location from the overall temperature utilization pattern recorded by the tags. The situation id improved somewhat by assuming only the nighttime temperature patterns are relevant to defining the limits of suitable areal habitat as was done here, but the volume improves to only 17.8%, so the pattern is still not well defined by the data. The accumulation of more temperature utilization data from tagging or other means would help to define the relationship, particularly where temperature becomes a principal determining factor at the extremes of the range. This region would be where the volume of acceptable ranges in water temperature might become limiting. Extraction of an informative selectivity curve from this information would likely involve detailed analysis of the change in time at temperature and depth in areas of diminishing volumes of acceptable temperatures.

The addition of chlorophyll improved the SDM predictions but the data used are incompatible with any application requiring time-varying predictions. More important, the model is clearly insufficient when viewed against the background of the catch. However, the improvement implies that environmental variables related to productivity will likely prove valuable features to include in a final SDM. For instance, Change et al. (2013) found mixed layer depth as well as sea surface height anomalies partially explained suitable habitat in the equatorial Atlantic Ocean. The CESM model provides several such variables that yet to be explored. The inclusion of one or more of these variables has the possibility of improving the overall SDM considerably, and a practical working SDM may emerge. Additionally, the HSI structure of the basic model permits inclusion of additional important features that may be identified by research into swordfish ecology. This flexibility fosters refinements that should lead to one or more swordfish SDM tools for different life stages or sexes that will be useful across different levels of spatiotemporal resolutions.

The cpue standardizations routinely employed in stock assessments amply document the fact that swordfish distributions vary by season and location (Anon 2014). The ariel distribution varies not only seasonally, but annually as well. Schirripa et al. (2017) provided evidence that the distribution of suitable swordfish habitat in the north Atlantic can change in relation to decades scale cycles of temperature based on such indicators as the Atlantic Multidecadal Oscillation (a broad scale index of sea surface temperature in the North Atlantic) and the size of the Atlantic Warm Pool (waters with temperatures greater than 28.5 degrees C). Fishery dependent indices of abundance indicated that swordfish may have sought to avoid the higher temperatures of both the decadal cycle of the AMO as well as the seasonal, but variable, cycle of the AWP by redistributing to more northern latitudes in years of positive phases of the AMOs or years of particularly large AWPs. The SDM predictions can be easily tested against these longer term trends by performing the same analysis with the predictions that produced the test results with the observed data. However, an additional step of using the SDM in a simulation of longline catches may be required to make the data compatible for the test. Mejuto et al. (2014) concluded that indices of abundance from fisheries dependent data was correlated not only with the North Atlantic Oscillation (also an indicator of sea surface temperature) but was age dependent as well. Based on ages inferred from swordfish lengths, these authors found that indices of abundance of fish ages 1 to 2 showed a positive relation to cycles of the NAO, while those of ages 4 and 5 showed a negative relation. Modeling age or size-specific habitat preferences with the SDM platform would require separate models for each category into which the species is partitioned. Partitioning would decrease the sample sizes available from the pool of tagged fish in order to estimate selectivities for each. Further, if habitat is age or sex is specific, the partitions would require problematic assignment of tagged animals. Consequently, the number of tags necessary to extract data needed to define selection curves might become problematical as treatments becomes more detailed. It is important therefore to maximize the number of datasets from PSAT and possibly other study sources to identify and quantify participating factors.

Acknowledgements

CPG's contribution to this study was supported by The Billfish Foundation. FCF's contribution was supported by the NOAA Southeast Fisheries Science Center via the University of Miami Cooperative Institute of Marine Science. The authors wish to thank Sang-ki Lee and Yanyun Liu of NOAA Atlantic Oceanographic and Meteorological Laboratory for gathering and compiling oceanographic data.

References

Abascal, FJ, Mejuto J, Quintans M, Garcia-Cortes,B. and Ramos-Cartelle, A. 2010. Horizontal and vertical movements of swordfish in the southeast Pacific. ICES J Mar Sci 67, 466−474

Abascal, FJ, Mejuto J, Quintans M, and Ramos-Cartelle, A. 2015. Tracking of the broadbill swordfish, Xiphias gladius, in the central andeastern North Atlantic. Fisheries Research, 162, 20-28.

Abecassis, M., Dewar, H., Hawn, D., amd Polovina, J. 2012. Modeling swordfish daytimevertical habitat in the North Pacific Ocean from pop-up archival tags. Mar. Ecol.Prog. Ser., 452, 219–236.

Anon. 2014. Report of the 2013 Atlantic Swordfish Stock Assessment Session. Collect. Vol. Sci. Pap. ICCAT, 70(4): 1484-1678.

Anon. 2016. Report of the 2015 meeting of the ICCAT Working Group on Assessment Methods. Collective Volume Scientific Papers, ICCAT, 78(8), 2249-2303.

Bigelow, K.A., and. Maunder, M.N. 2007. Does habitat or depth influence catch rates of pelagic species? Can. J. Fish. Aquat. Sci., 64, 1581–1594.

Boyer, T., Mishonov, A. 2013. World Ocean Atlas 2013 Product Documentation. T. Boyer, Ed.; A. Mishonov, Technical Ed. 1-14. http://www.nodc.noaa.gov/OC5/indprod.html

Braun, C. D., Kaplan, M. B., Horodysky, A. Z., Llopiz, J. K. 2015. Satellite telemetry reveals physical processes driving billfish behavior. Anim. Biotelemetry 3:2 DOI 10.1186/s40317-014-0020-9

Campbell, R.A. 2015. Constructing stock abundance indices from catch and effort data: some nuts and bolts. Fisheries Research 161:109-130.

Chang, Y.-J., Sun, C.-L., Chen, Y., Yeh, S.-Z., DiNardo, G., and Su, N.-J. 2013. Modelling the impacts of environmental variation on the habitat suitability of swordfish, Xiphias gladius, in the equatorial Atlantic Ocean. – ICES Journal of Marine Science, doi:10.1093/icesjms/fss190.

Dewar H, Prince E, Musyl R.M.K, Brill R.W, and others. 2011.Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. Fish Oceanogr 20, 219−241

Forestall, F.C., Goodyear, C.P., Schirripa, M., Babcock, E., Lauretta, M., and Sharma, R. 2017. Testing robustness of CPUE standardization using simulated data: findings of initial blind trials. ICCAT SCRS/2017-??.

Goodyear, C.P. 2017. Simulating longline catch with LLSIM: a user's guide (version 2). pp 1-23.

Goodyear, C.P. 2016. Modeling the time-varying density distribution of highly migratory species: Atlantic blue marlin as an example. Fisheries Research, 183: 469-481.

Lerner JD, Kerstetter DW, Prince ED, Talaue-McManus L, Orbesen ES, Mariano A, Snodgrass D, Thomas GL. 2013. Swordfish vertical distribution and habitat use in relation to diel and lunar cycles in the western North Atlantic. Trans Am Fish Soc. 142(1):95–104. http://dx.doi.org/10.1080/00028487.2012.720629

Maunder, M.N., Hinton, M.G., Bigelow, K.A., and Langley, A.D. 2006. Developing indices of abundance using habitat data in a statistical framework. Bulletin Of Marine Science, 79(3): 545-559.

Maunder, M.N. and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research, 70:141-159.

Mejuto, J., García-Cortés, B. and Ramos-Cartelle, A., 2014. Standardized catch rates in number of fish by age for the North Atlantic swordfish (Xiphias gladius) of the Spanish longline fleet, for the period 1983-2011. *Collect. Vol. Sci. Pap. ICCAT, 70*(4), pp.1812-1825.

Muhling, B.A., Brill , R., Lamkin, J.T., Roffer, M.A., Lee, S.-K., Liu, Y., and Muller-Karger, F. 2016. Projections of future habitat use by Atlantic bluefin tuna: mechanistic vs. correlative distribution models. ICES Journal of Marine Science 74: 698-716.

Neilson, J.D., Smith, S., Royer, F., Paul, S.D., Porter, J.M., Lutcavage, M., 2009. Investigations of horizontal movements of Atlantic swordfish using pop-up satellitearchival tags. In: Nielsen, J.L., Arrizabalaga, H., Fragoso, N., Hobday, A., Lutcavage, M., Sibert, J. (Eds.), Tagging and Tracking of Marine Animals with Electronic Devices, Reviews: Methods and Technologies in Fish Biology and Fisheries, 9.Springer, New York, pp. 145–159 (452 pp).

Neilson, J.D., Loefer, J., Prince, E.D., Royer, F, Calmettes B, Gaspar, P., Lopez, R., and Andrushchenko, I. 2014. Seasonal Distributions and Migrations of Northwest Atlantic Swordfish: Inferences from Integration of Pop-Up Satellite Archival Tagging Studies. PLoS ONE 9(11), 1-10. e112736. doi:10.1371/journal.pone.0112736

Schirripa, M.J., Abascal, F., Andrushchenko, I., Diaz, G., Mejuto, J., Ortiz, M., Santos, M.N. and Walter, J., 2016. A hypothesis of a redistribution of North Atlantic swordfish based on changing ocean conditions. *Deep Sea Research Part II: Topical Studies in Oceanography*.

Table 1. Depth range and layer volumes (km^3) for the 46 depth layers used in the SDM at select latitudes.

	Latitude of midpoint of 1° cell										
	0.5	5.5	10.5	15.5	20.5	25.5	30.5	35.5	40.5	45.5	50.5
Area (km^2)	12371	12314	12164	11921	11588	11166	10659	10072	9407	8671	7869
Depth range (m)											
0-5	62	62	61	60	58	56	53	50	47	43	39
5-15	124	123	122	119	116	112	107	101	94	87	79
15-25	124	123	122	119	116	112	107	101	94	87	79
25-35	124	123	122	119	116	112	107	101	94	87	79
35-45	124	123	122	119	116	112	107	101	94	87	79
45-55	124	123	122	119	116	112	107	101	94	87	79
55-65	124	123	122	119	116	112	107	101	94	87	79
65-75	124	123	122	119	116	112	107	101	94	87	79
75-85	124	123	122	119	116	112	107	101	94	87	79
85-95	124	123	122	119	116	112	107	101	94	87	79
95-105	124	123	122	119	116	112	107	101	94	87	79
105-115	124	123	122	119	116	112	107	101	94	87	79
115-125	124	123	122	119	116	112	107	101	94	87	79
125-135	124	123	122	119	116	112	107	101	94	87	79
135-145	124	123	122	119	116	112	107	101	94	87	79
145-155	124	123	122	119	116	112	107	101	94	87	79
155-165	125	124	123	120	117	113	108	102	95	88	79
165-175	128	128	126	124	120	116	111	105	98	90	82
175-186	134	133	132	129	125	121	115	109	102	94	85
186-197	141	140	138	136	132	127	121	115	107	99	89
197-209	149	148	147	144	140	135	128	121	113	105	95
209-222	159	159	157	153	149	144	137	130	121	112	101
222-236	171	170	168	165	160	154	147	139	130	120	109
236-251	185	184	182	178	173	167	160	151	141	130	118
251-267	201	201	198	194	189	182	174	164	153	141	128
267-285	221	220	217	213	207	199	190	180	168	155	140
285-305	243	242	239	234	228	219	209	198	185	170	155
305-326	269	268	265	259	252	243	232	219	205	189	171
326-351	300	298	295	289	281	270	258	244	228	210	191
351-378	336	334	330	324	315	303	289	273	255	235	214
378-408	378	376	372	364	354	341	326	308	287	265	240
408-443	428	426	421	413	401	386	369	349	326	300	272
443-482	487	485	479	469	456	440	420	396	370	341	310
482-527	557	554	547	536	521	502	480	453	423	390	354
527-579	639	636	628	616	598	577	550	520	486	448	406
579-638	736	733	724	709	689	664	634	599	560	516	468
638-707	850	846	836	819	796	767	732	692	646	596	541
707-787	983	978	966	947	921	887	847	800	747	689	625
787-878	1136	1131	1117	1095	1064	1025	979	925	864	796	723
878-984	1310	1304	1288	1262	1227	1182	1129	1066	996	918	833
984-1106	1503	1496	1478	1448	1408	1357	1295	1224	1143	1053	956
1106-1244	1712	1704	1683	1650	1603	1545	1475	1394	1302	1200	1089
1244-1400	1929	1920	1897	1859	1807	1741	1662	1570	1467	1352	1227
1400-1573	2146	2136	2110	2068	2010	1937	1849	1747	1632	1504	1365
1573-1764	2351	2340	2312	2266	2202	2122	2026	1914	1788	1648	1496
1764-1968	2535	2524	2493	2443	2375	2288	2185	2064	1928	1777	1613

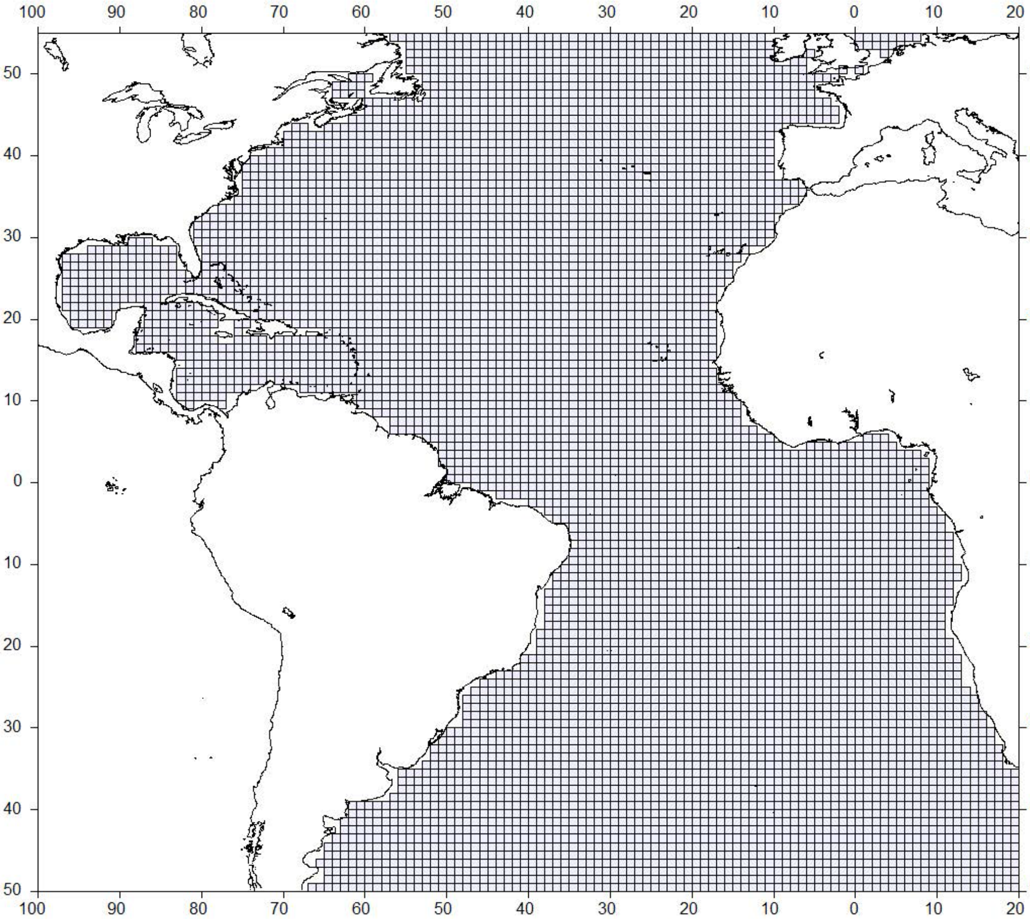

Figure 1. Spatial grid of the model being used to quantify the swordfish habitat distribution. Each 1º cell of latitude and longitude is additionally partitioned into 46 depth layers from the surface to 1968 m.

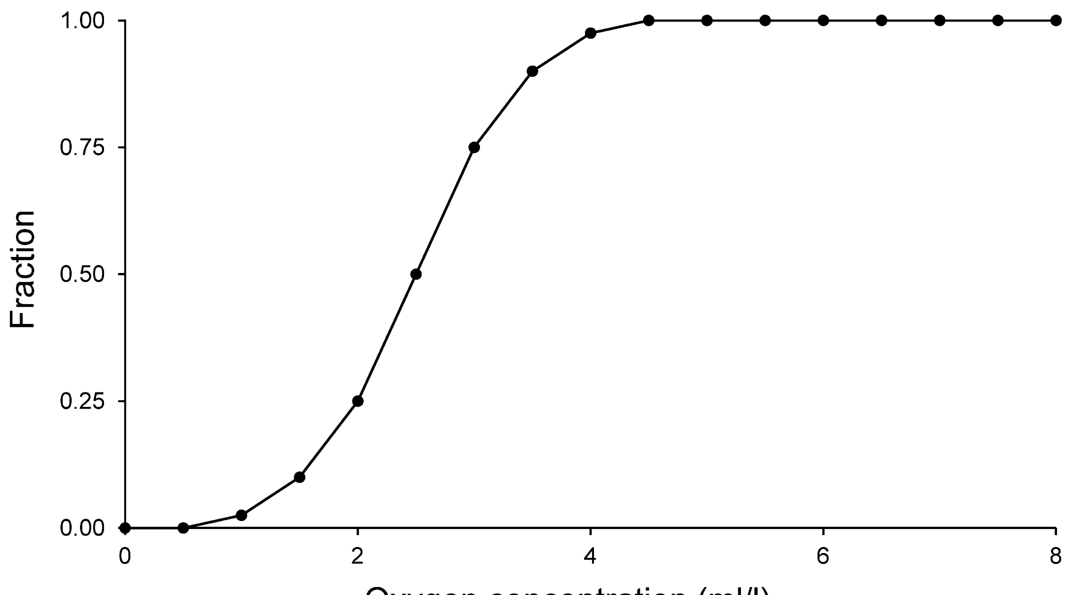

Figure 2. HSI selectivity curve for oxygen used in this study.

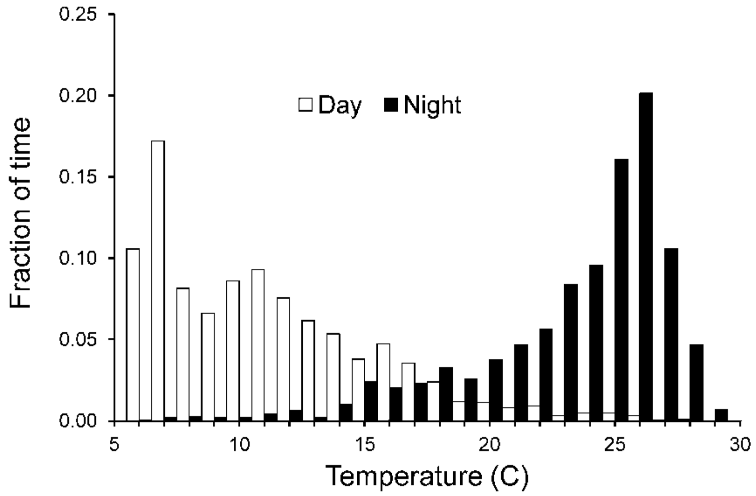

Figure 3. Proportions of time spent at temperature during hours of daylight and darkness from the swordfish tagged in this study.

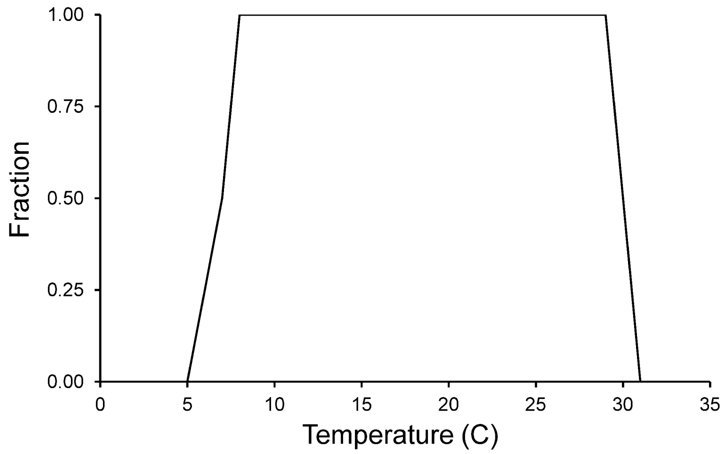

Figure 4. Temperature tolerances applied to depth-distribution predictions.

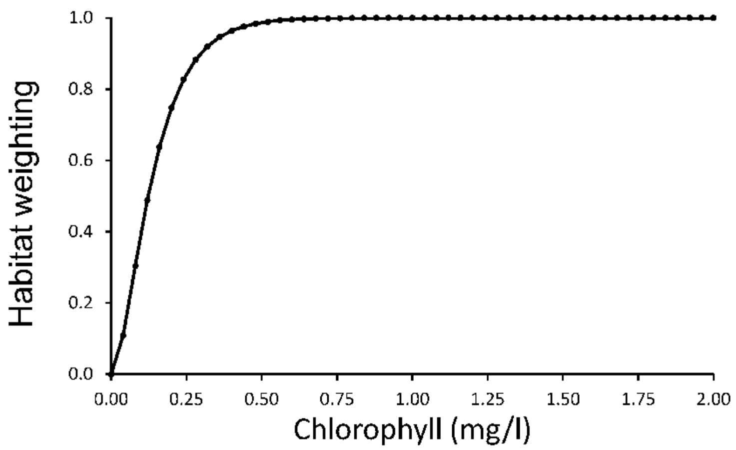

Figure 5. Chlorophyll suitability curve used in the swordfish trial SDM predictions presented herein.

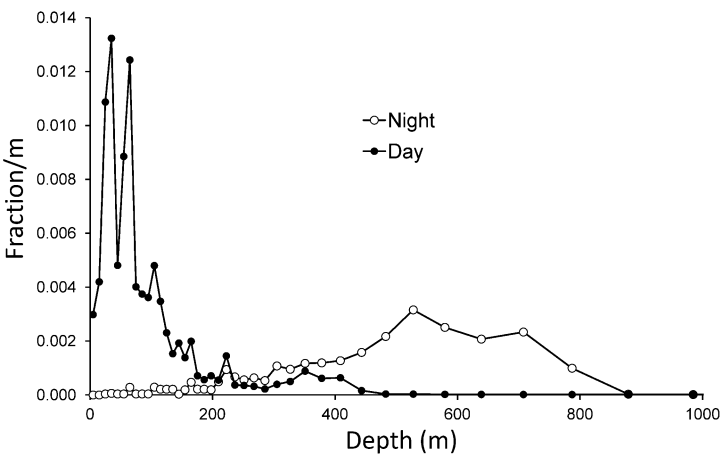

Figure 6. Day and nighttime depth distributions observed for swordfish monitored with satellite tags and used here to quantify that behavior in the SDM.

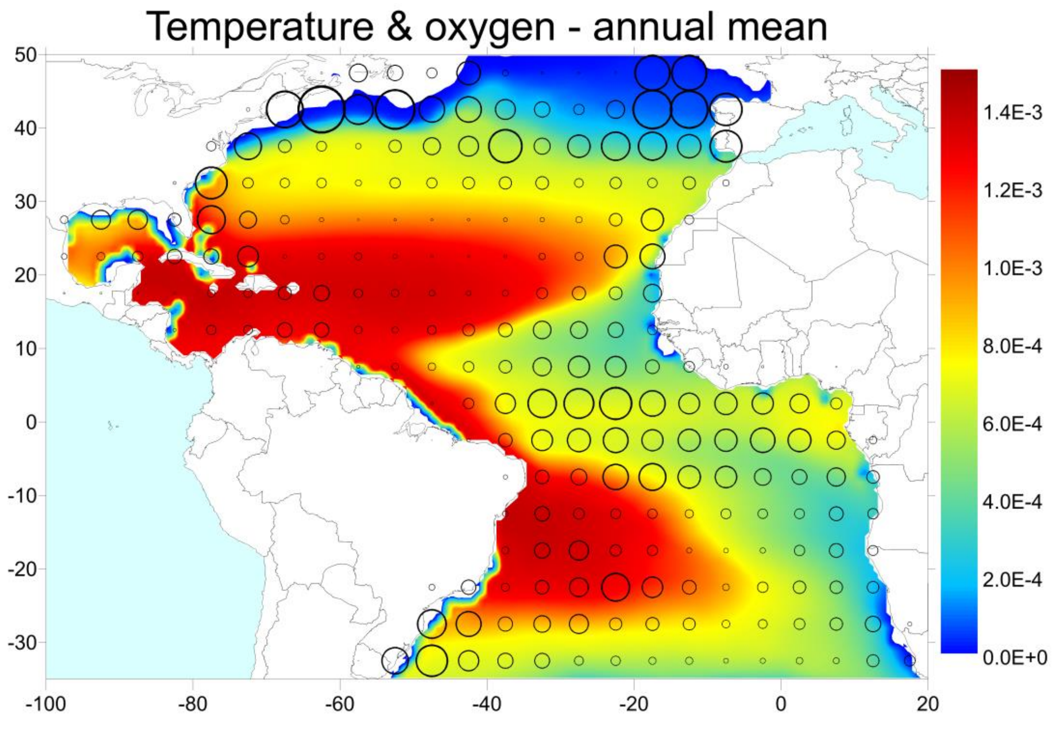

Figure 7. Distribution of average SDM predictions using only temperature and oxygen data, and the 1950-2014 total longline swordfish catch from the ICCAT catdist data file (circles, area is proportional to the magnitude of catch).

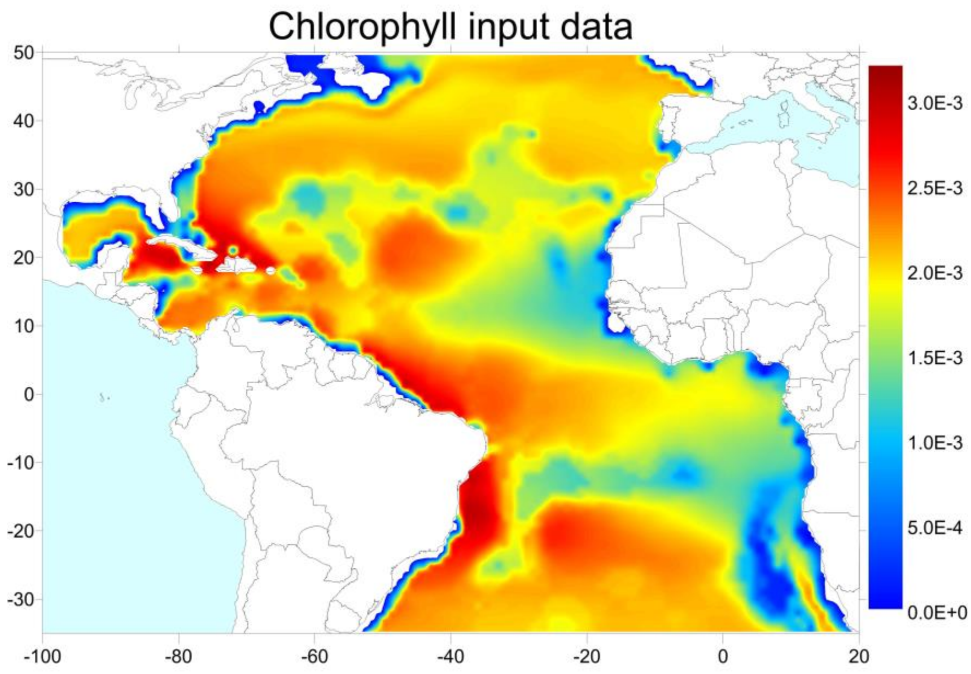

Figure 8. Distribution of WOA 2001 annual average chlorophyll concentration.

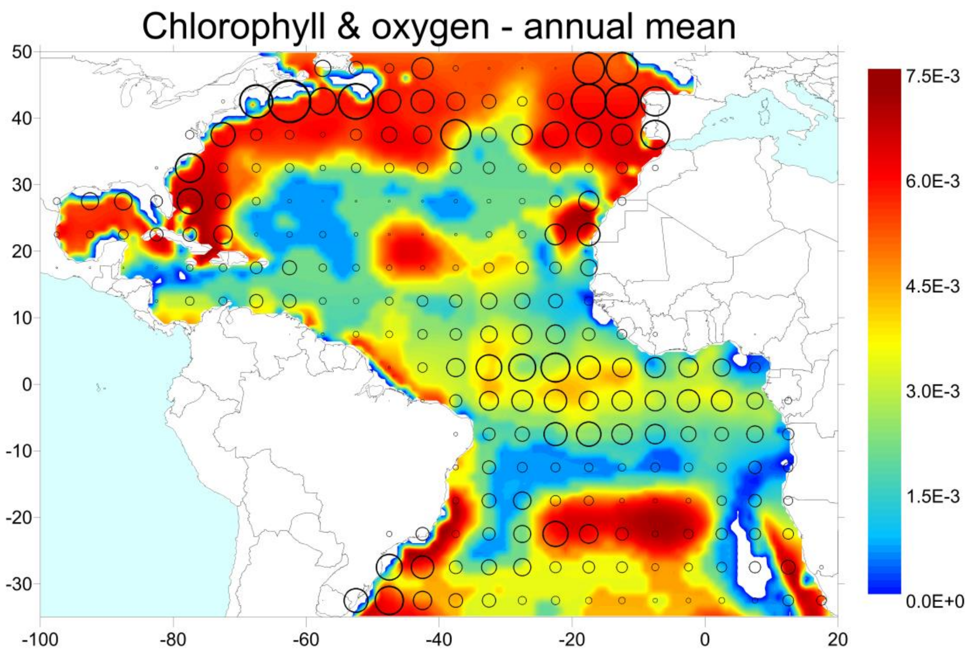

Figure 9. Distribution of annual average SDM predictions based on oxygen and chlorophyll only, and the 1950-2014 total longline swordfish catch from the ICCAT catdist data file (circles, area is proportional to the magnitude of catch).

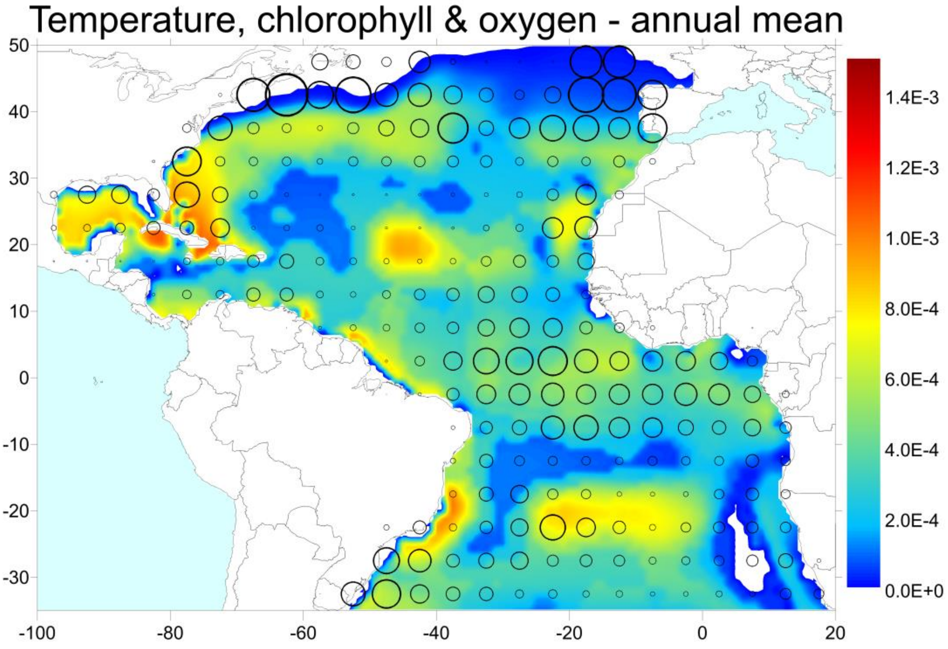

Figure 10. Distribution of annual average SDM predictions based on the combination of oxygen, temperature, and chlorophyll, and the 1950-2014 total longline swordfish catch from the ICCAT catdist data file (circles, area is proportional to the magnitude of catch).

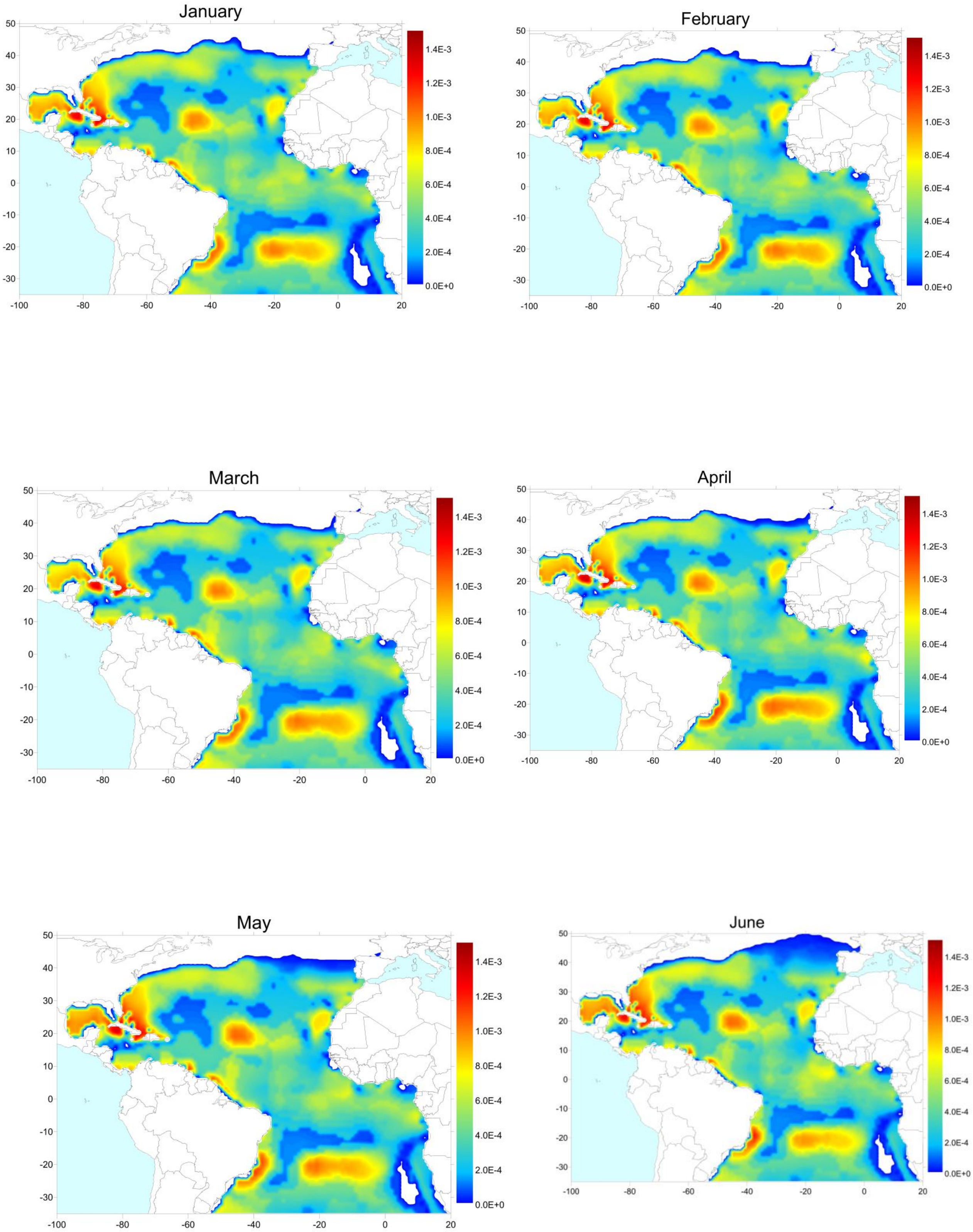

Figure 11. Distribution of average of 1974 and 2010 SDM predictions by month based on the combination of oxygen, temperature, and chlorophyll.

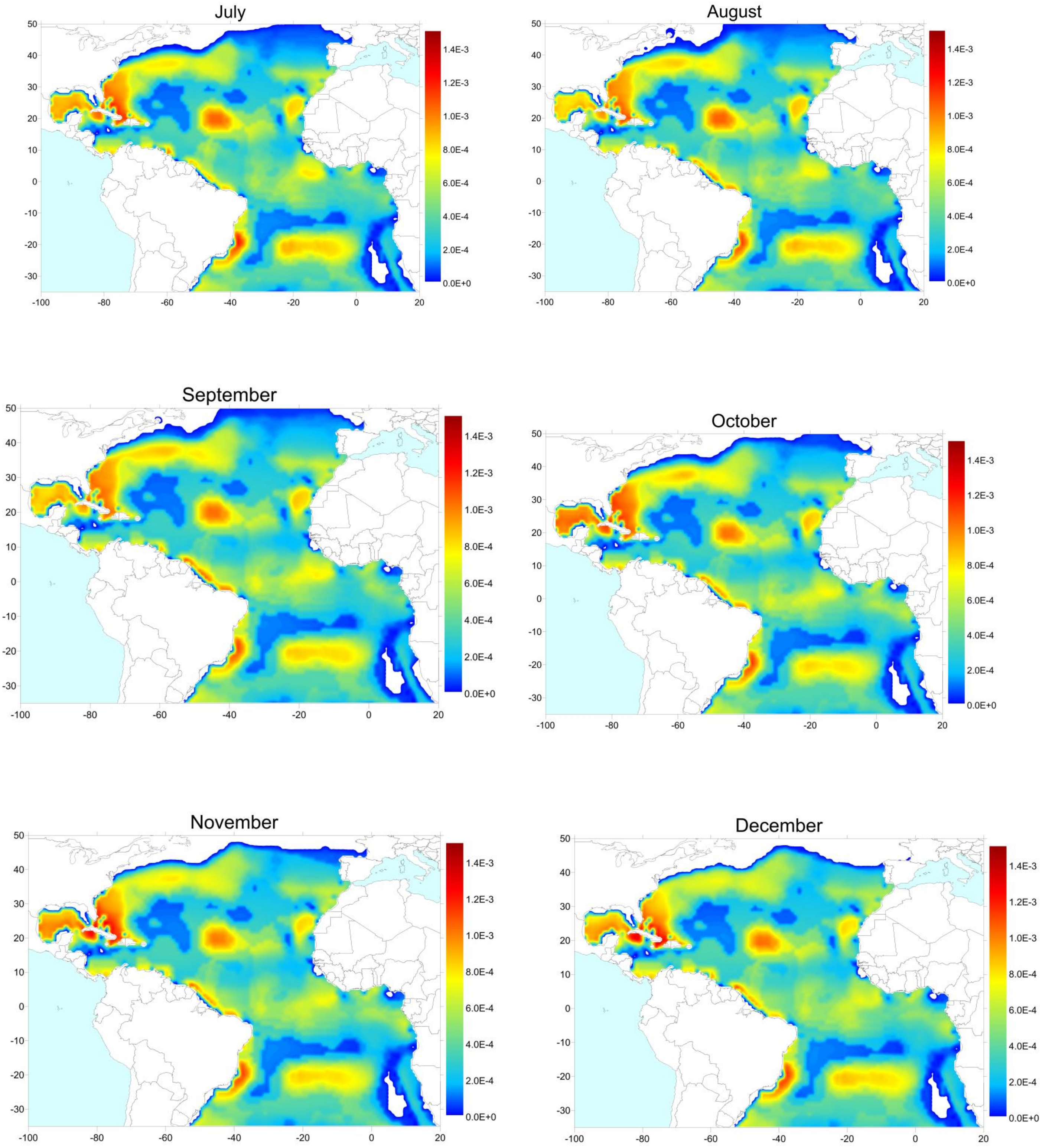

Figure 11. Distribution of average of 1974 and 2010 SDM predictions by month based on the combination of oxygen, temperature, and chlorophyll (continued).