



Modeling the time-varying density distribution of highly migratory species: Atlantic blue marlin as an example



C. Phillip Goodyear

1214 North Lakeshore Drive, Niceville, FL 32578, USA

ARTICLE INFO

Article history:

Received 1 May 2016

Received in revised form 12 July 2016

Accepted 13 July 2016

Handled by: A.E. Punt

Available online 21 July 2016

Keywords:

Habitat

Fishery management

Spatial distribution

Blue marlin

Climate

ABSTRACT

Blue marlin (*Makaira nigricans*) are among many species of tunas and billfishes that require pelagic longline catch-effort statistics for stock assessments. Major controversies about stock status have arisen because of issues concerning habitat influences on catch rates, but models to describe how the species is distributed throughout its entire habitat are lacking. A habitat suitability model (HSM) of the size and spatial distribution of blue marlin habitat by month using habitat weighted-volume (H) is presented. It is estimated from oceanographic data partitioned by 1° of latitude and 1° of longitude in 50 layers from the surface to a depth of 1200 m using dissolved oxygen tolerances and temperature preferences compiled from electronic tagging. The physical habitat is an amorphous 3-dimensional space whose boundaries are constantly changing with seasonal and longer-term variations in climate. Fluctuations in habitat volume likely contribute to fluctuations in CPUE that are independent of population abundance and add unrecognized uncertainty to abundance indices used to estimate population benchmarks. The results highlight the need to expand stock assessments to include seasonal and annual climatology. The HSM-based habitat weighted volume model offers a way to validate analytical methods for using longline CPUE to monitor population health.

© 2016 The Author. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Highly migratory pelagic marine species, such as Atlantic Blue Marlin (*Makaira nigricans*) move extensively about the oceans but are still confined by physical and biological processes to a discrete spatial subset of that environment (Prince et al., 2010; Braun et al., 2015). This envelope of compatible factors that constitutes acceptable habitat is constantly changing in response to annual and long-term trends and cycles in climatology (Robinson et al., 2015). The narratives of assessment documents usually include sections of text devoted to descriptions of these and other environmental aspects of the habitat and behaviors of the species (e.g., Anon., 2011, 2012). However, the stock assessments usually limit consideration of the physical aspects of habitat to the identification of the geographical scope of the unit stock for the assessment. The exception to this generality is that considerable effort is often devoted to explicitly account for habitat effects on longline catch rates (CPUE) while aggregating the data over time, space, and gear configurations to estimate trends in population abundance (Maunder and Punt, 2004; Maunder et al., 2006). The goal of such

efforts is to remove bias in catch-rate estimates of population abundance trends used to fit stock assessment models (Hinton and Nakano, 1996; Hinton and Maunder, 2004; Maunder et al., 2006). The accuracy of the aggregated “habitat-standardized” time series is essential for the models used to estimate the population benchmarks and which are relied upon for the scientifically-based catch limit recommendations for the fisheries (Punt et al., 2015). Ignoring these issues has a history of sparking major controversy (e.g., see Myers and Worm, 2003; Polacheck 2006). The need to remove confounding effects of environment-related differences in catch rates is clear, but the best method is not. Efforts to accomplish this task usually dominate the workload at stock assessment workshops. The main statistical tools involve use of statistical models such as the GLM to remove effects of factors that are correlates of environmental variation (e.g., month, spatial grid, hooks between floats, etc.), but environmental variables are often also explicitly included (Maunder and Punt 2004; Bigelow and Maunder, 2007).

Research on the topic of “habitat standardization” has been framed by the paradigm that longline catch is influenced primarily by the relationship between the distributions of the hooks and the species vulnerability with vulnerabilities a function of either depth or some suite of environmental variables (e.g., Hinton and Nakano, 1996; Bigelow and Maunder, 2007). The habitat standardizations do not model the entire habitat of the species, but

E-mail address: phil.goodyear@msn.com

apply distribution pattern assumptions to account for variation in the overlap of the species and longline hook depths. Broader issues that might arise from large-scale trends in acceptable habitat are not considered in the process. Such trends are the inevitable outcome of the warming global climate (Saba et al., 2015). They will impart important sources of annual variability that cannot be accommodated by habitat standardizations typically used to process the CPUE data in advance of model fitting exercises that are the core of most stock assessments. The explicit consideration of the entire population in three-dimensional (3-D) space is important because climate-induced density changes in one area can be offset elsewhere without concomitant changes in overall population abundances. Data simulations have been used to evaluate assessment model performance for Atlantic blue marlin (Goodyear, 2003b; Lynch et al., 2012) and can be extended to evaluate alternative assessment methodologies that incorporate climate effects. However this approach requires a way to predict marlin distributions for changing climatology. Here, a model is developed to describe the 3-D density distribution of Atlantic blue marlin based on physical oceanography, species temperature preferences and tolerances for dissolved oxygen (DO) to predict the effects of changing climatology on the distribution of the entire population. The method is used to explore the month-to-month variability in average blue marlin abundance and density in 3-D space.

2. Methods

2.1. Model

Blue marlin is a tropical pelagic species seldom encountered where surface water temperatures dip below 15 °C (e.g., Goodyear, 2003a; Su et al., 2008). It is managed as a single population in the Atlantic (Anon., 2012); consequently, the areal extent of the modeled population includes the entire Atlantic from 60° S to 60° N latitude exclusive of major land masses. Data describing the physical environment within this region were used to predict blue marlin abundances using a habitat suitability model (HSM). This approach is in common use for predicting habitat quality from habitat suitability indices (HSI) based on ecological niche theory (Hirzel and Lay, 2008). Applications to billfish species include the identification of potential new fishing grounds (Chang et al., 2012, 2013a), and forecasts of the effects of climate change (Robinson et al., 2015). Habitat models have also proved useful for predicting species concentrations for near real-time effort control in the context of quota management (Hobday and Hartman, 2006; Hobday et al., 2010). I extend the HSM approach to predict the relative concentration of blue marlin by latitude, longitude, depth and month that can be expanded to absolute densities in the same parameter space for known or hypothetical total populations. The approach estimates habitat weighted volume (H) to quantify the amount and distribution of usable habitat for the oceanographic features at a point in time. The value of the habitat weighted volume H_{ijk} , for a segment of the water column at latitude i , longitude j , and depth layer k at any point of time is given by:

$$H_{ijk} = X_{ijk} V_{ijk} \quad (1)$$

where X_{ijk} is the cumulative HSM weighting based on the values of the environmental variables existing at ijk , and V_{ijk} is the volume of the corresponding segment of the water column. The cumulative habitat weighted volume is simply the sum of the H_{ijk} over the whole of the modeled region. HSM combines various environmental factors that define a species habitat into a single index to represent the relative quality of the habitat at a particular location. The environmental variables are categorized as having additive or, if they represent critical limiting factors, having multiplicative

effects on habitat quality. Additive effects from different factors are combined as a simple mean and multiplicative factors are combined as the geometric mean. In the model developed here the X_{ijk} are assumed to consist of both additive and multiplicative factors such that cumulative HSM weighting is given by:

$$X_{ijk} = \left(\frac{\sum_{l=1}^L A_{ijkl}}{L} \right) \left(\prod_{n=1}^N G_{ijkn} \right)^{1/N} \quad (2)$$

where A_{ijkl} and G_{ijkn} are the values of the additive factors (l) and critical factors (n), at location ijk , and L and N are the number of additive and critical factors, respectively. Assignment of the additive versus critical (multiplicative) attribute to an environmental variable is somewhat arbitrary. Critical factors are those whose negative effects cannot be ameliorated by positive effects of other environmental factors. An index value of zero for a single critical multiplicative factor propagates through the equation to make the habitat suitability for that time-space to be zero. In contrast, the cumulative effect of additive factors can be positive even when one of the included factors is zero. The numerical values of the A_{ijkl} and G_{ijkn} are the habitat suitability values at the magnitudes of the associated environmental variables at location ijk . For the blue marlin example here, DO is assumed to be a critical factor because I assume marlin could not survive hypoxia, and temperature effects are assumed to be additive. These assignments may be reconsidered as more information becomes available and other environmental features such as primary production and sea surface height are included. The magnitudes of the habitat suitability values range from 0.0 to 1.0. They can be derived from complicated fitted models or, as in the example presented here, they can be drawn from histogram representations of their respective cumulative distributions. The value of the indices (the A_{ijkl} or G_{ijkn}) at any point in time and space are estimated from the values of the corresponding environmental variables at that time and location.

I assume that 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:

$$R_{ijk} = X_{ijk} V_{ijk} / \sum_{i=1}^I \sum_{j=1}^J \sum_{k=1}^K X_{ijk} V_{ijk} \quad (3)$$

The product of R_{ijk} and population number can be used to calculate the absolute average density in time and space for any total number of fish in the population. Many pelagic species including blue marlin and other billfishes exhibit diurnal cycles in their vertical distribution, spending more time near the surface at night and are deeper in the water column during daylight hours (e.g., Goodyear et al., 2008; Braun et al., 2015; Lam et al., 2015). It may be important to capture this effect in the predicted species distributions. This pattern is probably a local accommodation to factors ultimately related to the diel cycle in ambient light intensity, though it may be mediated via a response to some other factor (e.g., prey distributions). No matter what the causative processes, the cyclic variation in habitat utilization causes the fish to spend different amounts of time in each layer of temperature that makes up the temperature-depth stratification. This makes it possible to predict depths from temperatures using information on the thermal stratification. The most common implementation of this approach has been to normalize the temperature measurement relative to the temperature in the surface mixed layer, termed Delta T (ΔT). This approach is commonly used to predict billfishes depth distributions from oceanographic temperature data (e.g., Hinton and Nakano, 1996;

Bigelow and Maunder, 2007; Lynch et al., 2012; Hoolihan et al., 2015). The blue marlin ΔT distributions may differ between night and day (Goodyear et al., 2008; Braun et al., 2015) and these data are exploited here to extend the HSM to capture the day-night vertical distribution pattern. This is done by first summing the predicted average abundance at depth for each latitude-longitude to give the relative number (N_{ij}) in the water column at that location:

$$N_{ij} = \sum_{k=1}^K R_{ijk} V_{ijk} \quad (4)$$

The resulting N_{ij} are repartitioned into the depth strata using P_{ijkt} , the proportions at ΔT in the k^{th} depth stratum for the time of day (t), again correcting for the critical HSI factors:

$$D_{ijkt} = (P_{ijkt}) \left(\prod_{n=1}^N G_{ijkn} \right)^{1/N} \quad (5)$$

The local vertical density fractions are 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:

$$Y_{ijkt} = N_{ij} D_{ijkt} V_{ijk} / \sum_{k=1}^K D_{ijkt} V_{ijk} \quad (6)$$

The Y_{ijkt} are proportional to the population densities in the habitat at the latitude, longitude, depth, and time of day given the distribution of oceanographic features existing for the time unit evaluated. This reaggregation does not modify the areal distribution of the population within each latitude-longitude stratum but shifts the local population densities vertically among depths to adjust for the strong diel changes in habitat depth utilization noted by Goodyear et al. (2008).

2.2. Data

2.2.1. Background

Application of the HSM approach to predict the spatial distribution of a species requires quantitative data about the physical environmental variables that are important determinants of its habitat. Temperature and dissolved oxygen concentrations are major factors shaping the pelagic marine environment. Temperature is perhaps the major feature of the pelagic ocean and is the environmental variable most frequently employed in habitat standardizations (Hinton and Nakano, 1996; Maunder et al., 2006). Dissolved oxygen is an important variable to include because at low levels it becomes a critical factor limiting habitat suitability for tropical species such as blue marlin (Prince and Goodyear, 2006). Together these two variables dominate the use of environmental data included in stock assessments. The 2013 World Ocean Atlas (WOA) provides spatially detailed temperature and oxygen estimates in a grid of 1° of latitude and 1° of longitude in 50 depth layers ranging from the surface down to 1200 m for each month (Boyer and Mishonov, 2013). Goodyear and Bigelow (2012) used annually-varying monthly temperature data from Ishii and Kimoto (2009) for a similar purpose but at a lesser depth resolution and without corresponding estimates for oxygen. Other temperature data sets exist, but estimates of oxygen are less readily available. Details about the WOA program including data validation and verification and associated research are provided by Boyer et al. (2013). These data are a focal point for climate analysis, serving as a benchmark against which climate studies judge improvements in methodology (e.g. Chang et al., 2009). The monthly WOA data also provide both temperature and oxygen at

the same high level of resolution. Consequently, these data were selected for this analysis. Also the seasonal variation in the month by month data was sufficient to evaluate the possible magnitude of time-varying changes in the density distribution that might be predicted by the model. The current modeling effort adopts this spatial detail (Table 1). By comparison, a typical longline deployment is about 100 km (FAO, 2003), a horizontal distance roughly equivalent to the length of the $1^\circ \times 1^\circ$ grid. Investigations of long-term trends in species distribution patterns will necessitate annual, seasonally-varying oceanographic data. Because of the attention to global warming in recent years, the extent and resolution of historical time series are constantly improving along with forecasts of future trends (Boyer and Mishonov, 2013; Saba et al., 2015).

2.2.2. Habitat suitability values

2.2.2.1. Background. Temperature related, habitat preference information used in this research was taken from a previous study of blue marlin (Goodyear et al., 2008). That study was based on information about the environment frequented by 51 individuals monitored with pop-up satellite archival tags (PSATs). The tags recorded depth, temperature, and light once every 30 or 60 s after being applied. They were designed to detach after a predetermined interval and transmit summaries of data through the ARGOS satellite system. However, all measurements taken during the deployment were retained in the tag's non-volatile memory. This feature allowed access to the complete set of archived data for six tags which were physically recovered. For satellite transmissions, depth and temperature records were binned at 3 or 6-h intervals. Temperature bins for most tags started with $\leq 12^\circ\text{C}$, each successive 2°C interval up to 32°C , and ended with $> 32^\circ\text{C}$. Depth bins included $\leq 1\text{ m}$, followed by successive intervals of 25 m, down to 250 m, then all depths $> 250\text{ m}$. Additionally, minimum and maximum temperatures, minimum and maximum depths, and temperatures at 6 additional depths between those points during each binning period were also transmitted.

Tagged fish ranged in estimated weight from about 36 kg to 363 kg with a mean of 89 kg. On average, tags successfully monitored about 40 days each (range 2–95 days) and contributed a cumulative total of 2036 days of data. The analyses estimated cumulative time spent at different temperatures, different depths, and ΔT . Average surface temperatures at the fish's location were determined from the values recorded where the depth was $\leq 1\text{ m}$ each day or were linearly interpolated from previous and subsequent day's temperatures if the fish failed to visit the surface on a particular day. Daytime and nighttime were differentiated using light intensity. Where the tags were not actually recovered, the temperature and depth distribution patterns were estimated using linear methods to interpolate the ARGOS-transmitted data to bins of 1°C for temperature and 10 m for depth. The interpolations used the time at temperature, time at depth, and the temperature-depth matrices estimated from the tags during each binning interval (Luo et al., 2006). The ΔT estimates were additionally conditioned on the probability density function derived from the high-resolution data from recovered tags prior to being assigned to bins of 1°C resolution (see Goodyear et al., 2008 for more detail). For the recovered tags, time at temperature, time at depth and ΔT were compiled directly from the high-resolution measurements.

2.2.2.2. Temperature. The overall average proportions of time spent at different temperature levels by the 51 marlin in that study were used as values for habitat suitability (Table 2). Likewise, the ΔT data used to evaluate the day-night vertical distribution of blue marlin abundance were drawn directly from the analyses presented in Goodyear et al. (2008) but omit the transitional crepuscular

Table 1
Areas and layer volumes for selected latitudes of the spatial grid. The HSM uses cells of 1° of latitude and longitude, partitioned into 50 depth layers (twenty 5-m layers from the surface to 100; sixteen 25-m layers from 100 to 500 m; and fourteen 50-m layers from 500 to 1200 m).

Latitude of midpoint of 1° cell	Area (km ²)	Volumes of the depth layers (km ³)		
		5 m layers 0–100 m	25 m layers 100–500 m	50 m layers 500–1200 m
0.5	12371	62	309	619
5.5	12314	62	308	616
10.5	12164	61	304	608
15.5	11921	60	298	596
20.5	11588	58	290	579
25.5	11166	56	279	558
30.5	10659	53	267	533
35.5	10072	50	252	504
40.5	9407	47	235	470
45.5	8671	43	217	434
50.5	7869	39	197	393
55.5	7007	35	175	350
60.5	6092	30	152	305

Table 2
Percent of time tagged blue marlin spent at temperature by time of day (from Goodyear et al., 2008). The values for the HSI for temperature used the array for the total normalized to the maximum (=28.68 for the bin 29 < 30 °C).

°C	Night	Day	Total	°C	Night	Day	Total
7	0.00	0.00	0.00	20	0.01	2.96	1.49
8	0.00	0.00	0.00	21	0.11	3.92	2.01
9	0.00	0.00	0.00	22	0.15	5.40	2.77
10	0.00	0.00	0.00	23	0.51	6.98	3.75
11	0.00	0.01	0.00	24	0.79	9.87	5.33
12	0.00	0.01	0.00	25	3.96	11.07	7.52
13	0.00	0.09	0.04	26	7.67	12.09	9.88
14	0.00	0.13	0.06	27	16.93	12.59	14.76
15	0.00	0.32	0.16	28	23.68	15.60	19.64
16	0.00	0.36	0.18	29	44.35	13.02	28.68
17	0.00	0.59	0.30	30	1.64	0.49	1.06
18	0.00	0.66	0.33	31	0.18	0.09	0.13
19	0.01	3.76	1.89	32	0.00	0.00	0.00

Table 3
Percent of time tagged blue marlin spent at temperature relative to the temperature in the surface mixed layer (ΔT) during hours of daylight and darkness (from Goodyear et al., 2008).

ΔT	Daylight	Darkness	ΔT	Daylight	Darkness
0	0.583	0.849	−8	0.019	0.001
−1	0.144	0.079	−9	0.020	0.001
−2	0.069	0.033	−10	0.012	0.000
−3	0.043	0.018	−11	0.003	0.000
−4	0.031	0.008	−12	0.003	0.000
−5	0.026	0.005	−13	0.001	0.000
−6	0.022	0.003	−14	0.001	0.000
−7	0.022	0.002	−15	0.000	0.000

period (Table 3). The pattern of day-night behavior employed is consistent with that exhibited by other istiophorid billfish species showing greater surface affinity during hours of darkness (e.g., Hoolihan, 2005; Hoolihan et al., 2011, 2015; Chang et al., 2013b).

2.2.2.3. Oxygen. No similar data exist to characterize the habitat suitability of the oxygen content of the water mass for blue marlin. Several authors have used 3.5 mL L^{−1} as an inflection point to partition unacceptable from acceptable levels of oxygenation for marlin (Prince and Goodyear, 2006; Prince et al., 2010; Stramma et al., 2012; Braun et al., 2015). This value was extrapolated from information about levels that induce symptoms of stress or that are lethal in some tropical pelagic tunas (Ingham et al., 1977; Evans et al., 1981; Gooding et al., 1981; Bushnell and Brill, 1991; Idrisi et al., 2002). Movement patterns of billfish inferred from data logged on

electronic tags also support this value as a useful threshold (Braun et al., 2015). I assume the schedule for oxygen suitability values (G_{oxygen}) to be: $DO < 3.25 \text{ mL L}^{-1}$, $G_{oxygen} = 0.0$; 3.25 mL L^{-1} to 3.75 mL L^{-1} , $G_{oxygen} = 0.5$; and $> 3.75 \text{ mL L}^{-1}$, $G_{oxygen} = 1.0$.

2.3. Model validation

The validity of the HSM was tested by comparing the predicted average distributions to the spatial distribution of blue marlin catches. Catch data were obtained from the 1956–2012 aggregate catch of blue marlin in 5° by 5° bins in the CATDIST data files maintained by ICCAT (available at <https://www.iccat.int/en/accessingdb.htm>, accessed April 2016) (Fig. 1). These data were compared to the HSM predicted areal abundances (N_{ij}) summed to the same level of resolution using the standard correlation coefficient (r). The two data sources are independent, but each is spatially autocorrelated raising concerns that tests of apparent significance of the observed correlation could be inflated by the spatial autocorrelation. To evaluate significance I employed (1) the standard test assuming independence, (2) the modified.ttest() function in R (R Core Team, 2015) that assumes r to be inflated by spatial autocorrelation, and (3) a model-derived empirical distribution for the correlation coefficient. Several authors have shown the latter procedure provides robust interpretation of the goodness-of-fit for model predictions (e.g., Dale and Fortin, 2002; Waller et al., 2003; Manly, 2007). Here I estimated the test distribution of r by computing 1000 Monte Carlo iterations that incorporated the full model structure and oceanographic data. Each iteration randomly varied the environmental affinity used to construct the X_{ijk} in Eq. (2). I arbitrarily chose the temperature suitability curve for this purpose and randomly selected a set of preference values within the range 15–30° for each iteration. This protocol provided a set of 1000 predictions of the spatial distribution of blue marlin. The correlation between each set of predicted distributions and the ICCAT catches provided the values used for the test distribution of r . This process compares the outcome using the best available information about temperature utilization to that of trials where temperature utilization is unknown.

3. Results

3.1. Predictions in the latitude-longitude plane

For brevity I make no distinction between the distribution of the species and the distribution of its habitat, and use the term abundance to refer to predicted values. The HSM computes a 3-D

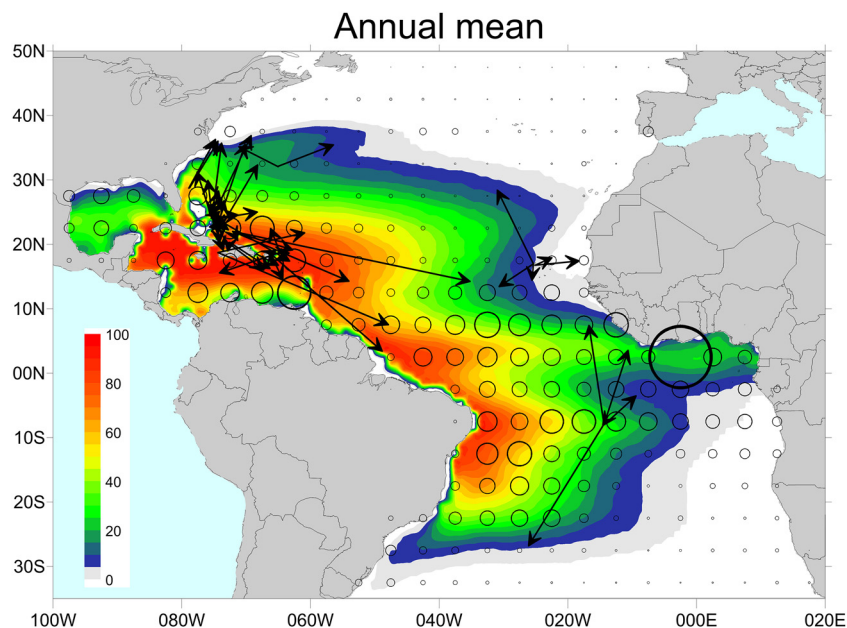


Fig. 1. The isopleths represent HSM-predicted areal distributions of blue marlin habitat averaged over all months. The contours depict the ratio of the abundance summed over depth at the geographic position to the average maximum abundance. Circles are the total 1956–2012 blue marlin catches on longlines by 5° by 5° latitude-longitude bins from the ICCAT CATDIST data files. The area of each circle is proportional to the catch in that bin. The vectors provide the starting and ending locations of blue marlin monitored with the PSAT tags that contributed to the time at temperature and depth data used in this study.

spatial distribution of the habitat as a function of oceanographic conditions. The result is expressed as a 4-dimensional array of the population relative density, Y_{ijkl} , for the latitude, longitude, depth, and time of day. The two-dimensional relative abundance in the latitude-longitude plane (the areal distribution) is a useful way to view the result. Day-night movements only affect the vertical position in the water column. Hence the examination of the predicted areal distribution neglects this feature and is based on the predicted relative abundance, N_{ij} . The annual average distributions are presented in Fig. 1 based on the oceanographic variables evaluated here. Month-by-month results are in Fig. 2. The concentration gradients in Figs. 1 and 2 depict the ratios of the N_{ij} to the maximum observed during each interval. The area of suitable habitat is a subset of the Atlantic that excludes broad regions of the northern and southern ocean. Maximum predicted abundance is on the western side of the ocean, centered about the tropics, but with seasonal shifts that follow summertime conditions in the northern and southern hemispheres. There is also a clear East to West shift in abundance in areas just offshore the Central West African coast from a peak around the March equinox to a minimum around the equinox the following September (Fig. 2). The broad equatorial region from the African coast westward toward South America exhibits moderate abundance for most months. However high surface densities in this area are moderated downward because the densities diminish quickly from the surface to uninhabitable environs just below, where a steep thermocline marks the beginning of an unsuitable hypoxic environment.

The 1956–2012 aggregate catch of blue marlin in 5° by 5° bins summarized in the CATDIST data files maintained by are positively correlated with annual average of the predicted areal abundances (N_{ij}) summed to the same level of resolution (Fig. 1). The exclusion of a single outlier off the African Coast just south of Ghana (Fig. 1) increased the correlation from $r = 0.35$ ($n = 237$) to $r = 0.62$ ($n = 236$). The outlier was from the inclusion of large catches from an artisanal gillnet fishery from Ghana and Côte d'Ivoire that only occurred in this sector. The value of $r = 0.62$ from the fully parameterized HSM exceeded the largest value of the test distribution from the

Monte Carlo procedure ($r = 0.36$), implying that the observed correlation between the HSM predictions and ICCAT catch was <0.001 by chance. This finding is in agreement with the interpretation that $P < 0.001$ from the standard test assuming sample independence (234 df, $P < 0.001$), as well as the result of the modified.ttest() function in R (R Core Team, 2015) that assumes the correlation is inflated by spatial autocorrelation (83 df, $P < 0.001$). Since the ICCAT catches were not involved in the parameterization of the HSM, these results constitute an assessment of the HSM performance with an independent data set, that Elith and Leathwick (2009) characterized as a desirable, but rarely-employed test of species distribution models.

3.2. Depth

The bottom of the habitat is a band of decreasing probability. Diving patterns monitored by tagged blue marlin show that the deepest occupied habitat involve infrequent, short-duration excursions (e.g., Goodyear et al., 2008). This behavior shows up as the long tails in the time-at-temperature and ΔT distributions in Tables 2 and 3. Though the absolute values of the volumes contributing to the individual elements of H_{ijk} are downweighted by these low probabilities, the spatial extent of the HSM includes large volumes of rarely-used space. The bottom margin of this habitat is both ill-defined and infrequently encountered. I picked an arbitrary density that would provide a more instructive boundary for the bottom geometry of the habitat space. The reference density was a value which along with all higher densities would include 99% of the predicted population abundance. The 3-D space occupied by the population is then represented by the volume between the ocean surface and the bottom of the deepest layer with a predicted relative density greater than or equal to this criterion. The lateral edges of the habitat are defined by either a shoreline or where the relative density of the shallowest depth does not meet this criterion. This convention takes advantage of the facts: (1) temperature declines with depth, (2) habitat suitability declines with temperature, and (3) hypoxic conditions increase with depth. The result of applying these rules is a matrix of the depths containing 99% of

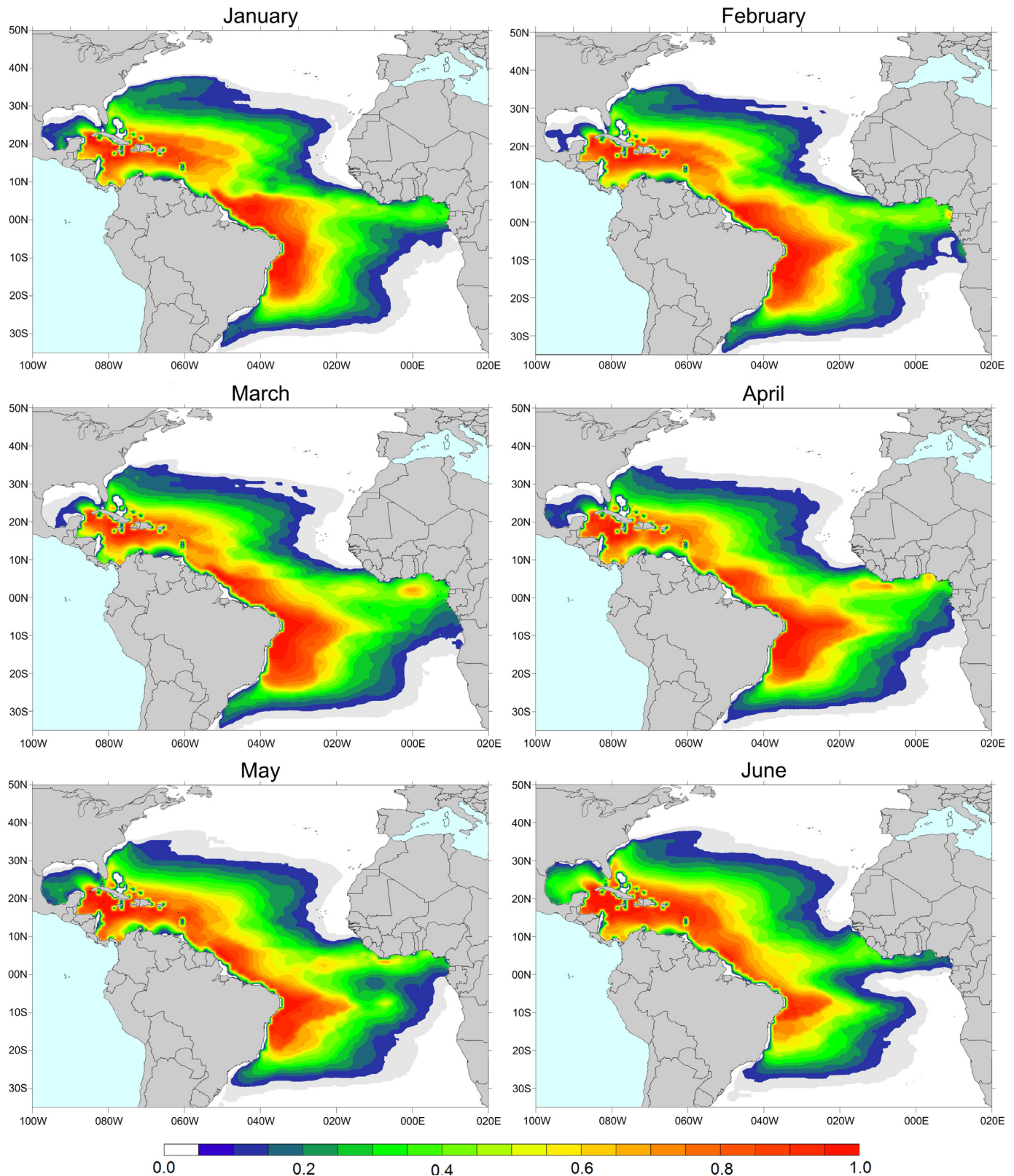


Fig. 2. HSM predicted areal distribution of blue marlin habitat by month. The scale depicts the ratio of the abundance summed over depth at the geographic position to the maximum abundance for the month.

the suitable habitat. Fig. 3 is the daytime HSM prediction of habitat bottom for May. The bottom of the distribution of acceptable habitat rises slowly from the south and west to a broad shallow band that extends northwest from the Central African Coast nearly

all of the way across the Atlantic. This shallow plateau reflects the influence of the tropical oxygen minimum zone (OMZ) and its associated shallow thermocline (Prince et al., 2010). This OMZ shelf drops sharply to the north at about 25° N latitude.

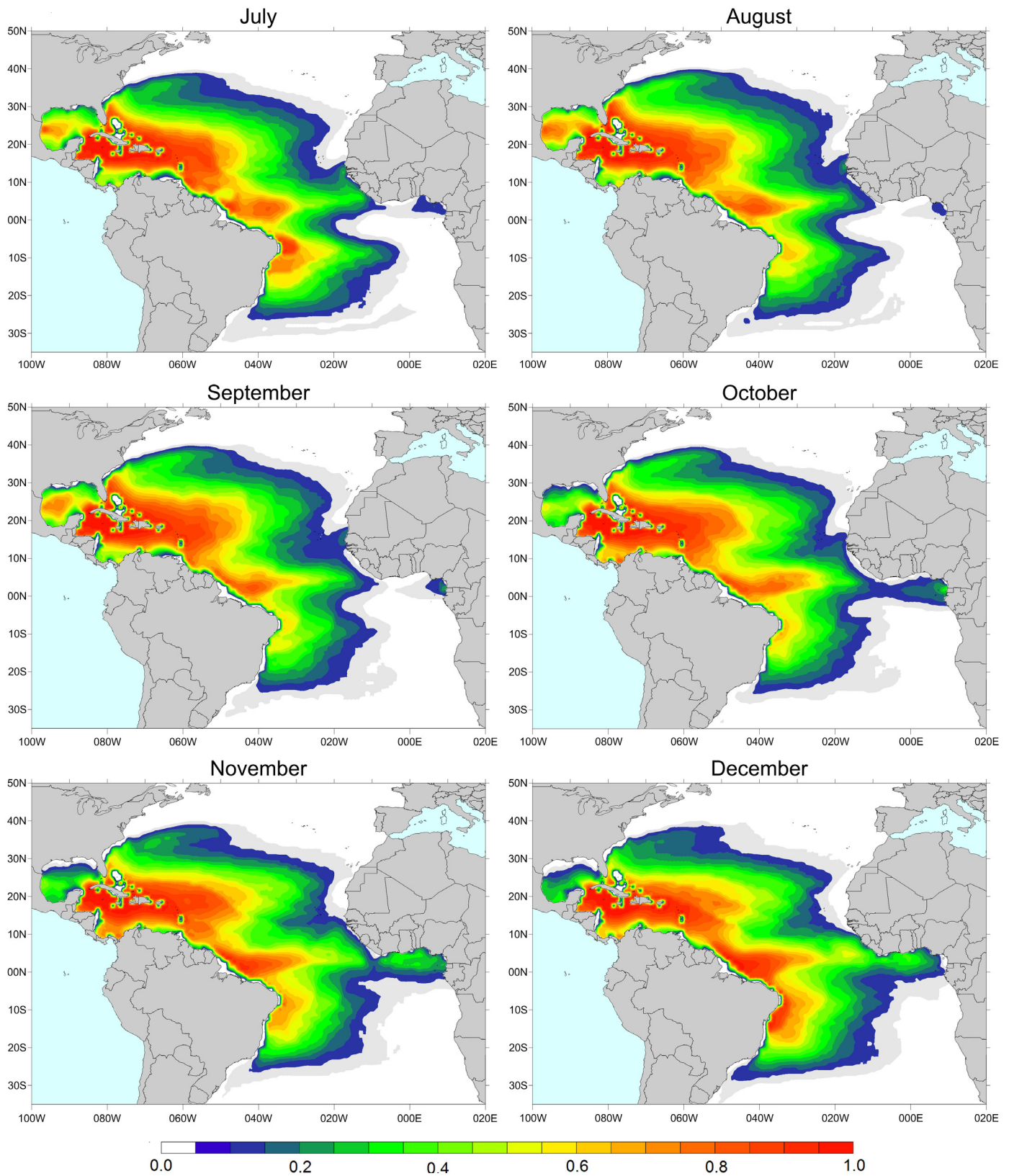


Fig. 2. (Continued)

A strong day vs. nighttime redistribution of the blue marlin population is implied by the temperatures utilization patterns (Tables 2 and 3). The HSM accommodates this behavior using the ΔT distributions from Table 3. The bottom of the environment con-

taining 99% of the suitable habitat along the north-south transect at the 29.5°W longitude (Fig. 3) for the average May oceanographic conditions is plotted in Fig. 4. The population extends much deeper during the daytime than at night. The difference is much reduced in

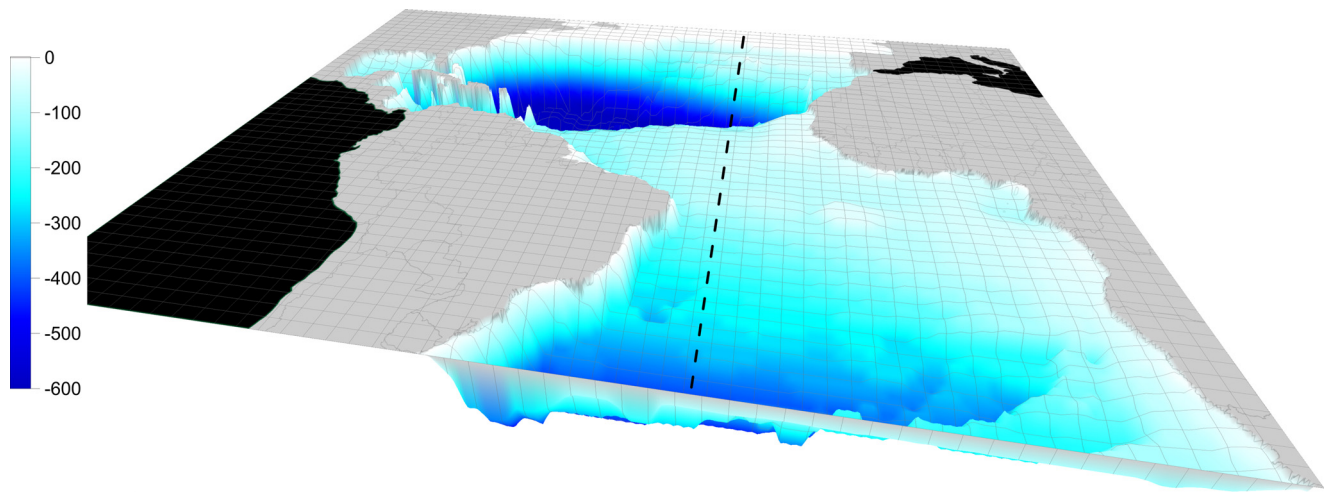


Fig. 3. Profile of the depth at the bottom of the Atlantic blue marlin habitat that includes 99% of the population during daylight hours based on World Ocean Atlas average oceanography for May. The dashed line at 29.5°W longitude shows the transect that connects the midpoints of the model cells plotted in Fig. 4.

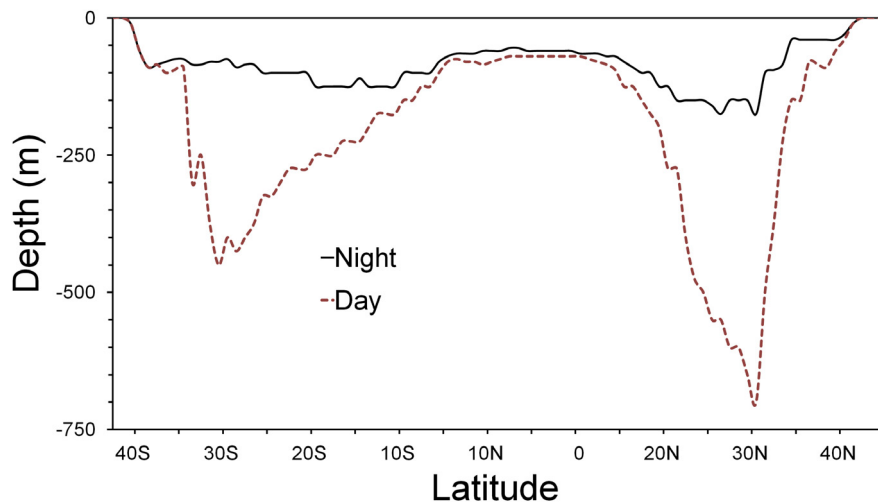


Fig. 4. Mid-ocean depths of the bottom of the Atlantic blue marlin habitat which include 99% of the population during hours of darkness and light based on the WOA average oceanography for May. The transect is for cells at 29.5°W longitude corresponding to the dashed line in Fig. 3.

the tropics where the oxygen-poor environment underlays a shallow thermocline, thereby limiting the depth of acceptable habitat. This behavior would clearly impact blue marlin vulnerability to surface longlines and other surface gears. The day-night differences increase from a near negligible magnitude in the tropics to very large differences in more temperate areas. Fig. 4 shows the potential importance of time-of-day interactions with fishing depths for only a single time and cross-section, but the pattern obviously exists for all other space-area configurations as well. One benefit of constructing the habitat model presented here is that it allows visualization of the species distributions implied by changes in physical oceanography.

3.3. Time-varying density

The cumulative habitat-weighted volume, H , is a measure of the magnitude and quality of the physical habitat that contains the population. In addition to the oceanography, the magnitude of the estimate is based on the schedule of indices used in the estimation, so its value cannot be easily compared across different HSM

implementations. However, variation in H arising from the same HSM with different physical oceanography reflects the variation in average density that would exist in the climate alternatives. Here, H varied by over 20% during the year, increasing from $8.8 \times 10^5 \text{ km}^3$ in January to about $11 \times 10^5 \text{ km}^3$ in September (Fig. 5). This change implies average density would vary by a similar proportion even in the absence of changes in abundance. Inspection revealed that this variation is the consequence of variation in the volume of the water mass contained between 26° and 30 °C. This variability highlights the need to evaluate the sensitivity of assuming that the habitat index value for temperature is adequately represented as a simple relative weighting. The relative utilization of habitat by temperature was inspected by dividing the average fraction of time blue marlin spent within a temperature interval (Table 2) by the annual average volume of the water mass within that interval from the WOA 2013 data. The result indicated exponentially increasing usage of the warmest available habitat that did not abate at the highest temperatures for which data exist (Fig. 6). The seasonal differences in the average volume of the water masses of different temperatures also becomes more pronounced as the tem-

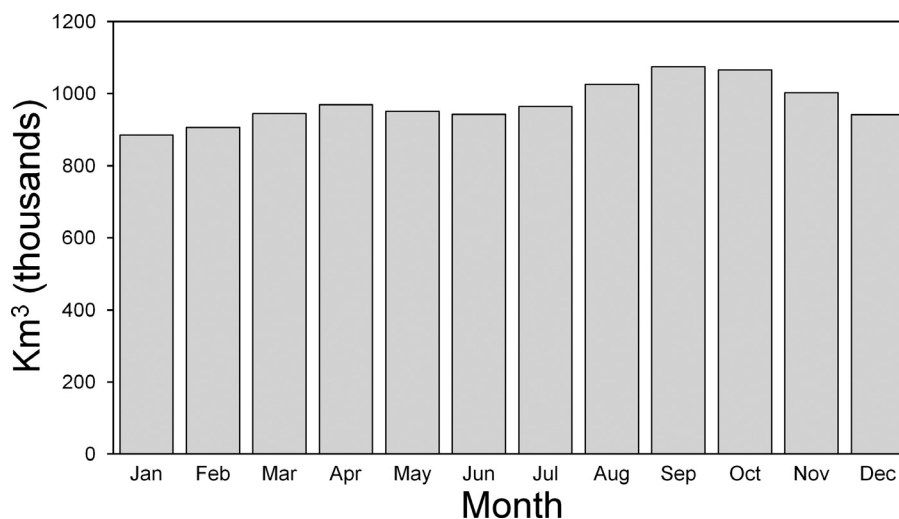


Fig. 5. Weighted habitat volumes for Atlantic blue marlin estimated by the HSM using monthly means of temperature and dissolved oxygen by 1° of latitude and longitude from the WOA average oceanography for each month.

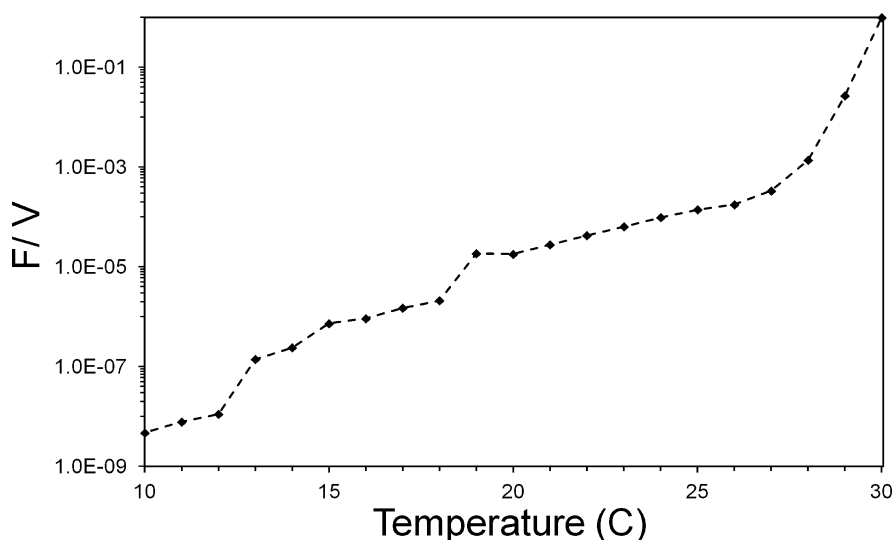


Fig. 6. Affinity of blue marlin for temperature estimated as the ratios of the fractions of time spent within each 1 °C bin from 15 °C to 31 °C to the annual average volumes of the Atlantic Ocean within that temperature bin. Affinity increased exponentially throughout the range and escalated as temperatures increase above 27 °C.

perature increases, with a variation of 1500% between January and September in the temperature range from 28° to <30 °C (Fig. 7).

4. Discussion

4.1. Distribution of habitat

4.1.1. Overview

Atlantic Blue marlin live within a thin film at the ocean surface. The dimensions of the physical habitat are in units of hundreds to thousands of kilometers in latitude and longitude but often just a small fraction of a kilometer in depth. The habitat is not fixed in location or size but rather is an amorphous 3-D space whose boundaries are constantly changing with seasonal and longer-term variations in climate. Except for the ocean surface and where its bottom intersects otherwise suitable conditions, the habitat boundary is best characterized as a nebulous band of increasing density in the direction of the habitat core. The HSM estimates the density distribution within this space and with respect to time of day (the Y_{ijkt}) without relying on spatial observations of the species or fishery-dependent data. I employed the WOA 2013 monthly means data for

the analysis here because its high resolution (1° of latitude by 1° of longitude and 50 depth layers) permitted relatively precise evaluations of the magnitude of seasonal variability in habitat space. The magnitude of that variability strengthens the view that the distribution of blue marlin habitat will be altered by a warming climate (Saba et al., 2015).

The seasonal areal distributions of the population in Figs. 1 and 2 agree favorably with general wisdom about the species in the Atlantic and broadly overlap the spatial distributions of the catch and CPUE (Goodyear 2003a; Anon., 2011, 2012). Formal statistical comparisons between model predictions and observed relative abundances are of limited value because of the same issues that limit catch or CPUE as measures of population abundance. Even so, there is a strong correlation between the spatial average catch and predicted abundances. HSM-predicted blue marlin habitat is clearly tropical but with south-north shifts that follow the seasonal progression of warm temperatures (Fig. 2), consistent with the pattern observed for the species in the Pacific (Su et al., 2008, 2011). The HSM also captures the effect of the OMZ in the Atlantic that has been identified as a primary feature limiting the scope of the habitat for istiophorid billfish in the area (Prince and Goodyear, 2006,

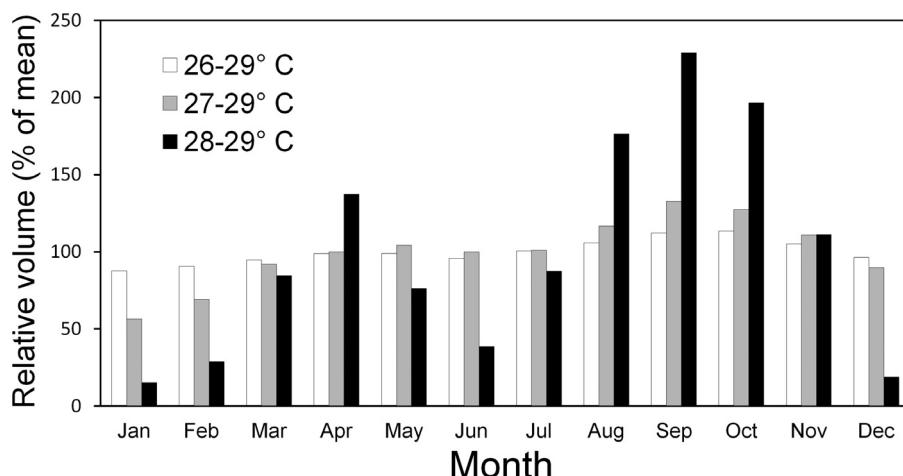


Fig. 7. Seasonal variation in relative volumes of the Atlantic Ocean within three temperature bands of increasingly preferred habitat based on the World Ocean Atlas 2013 monthly mean temperatures at depth. The volume of the water mass at and above 28 °C varied 15 fold between January and September. Monitored blue marlin spent an average of almost half of their time at temperatures within this range.

2007; Prince et al., 2010). The area is denoted by the broad, shallow habitat in the Central Atlantic between deeper regions to the north and south (Figs. 1–4). This is a permanent feature present in all months, but the shape and extent of the habitat affected by the OMZ varies with the season. Similarly, the proportions of the weighted total habitat that exist within the OMZ also vary seasonally, and the predicted depth of acceptable habitat is severely truncated by the shallow steep thermocline and the hypoxic conditions just below.

4.1.2. Distribution of marlin within the habitat

The probabilities that fish will actually be encountered in the field obviously increase with population size. The population density distribution can be estimated by multiplying the Y_{ijkt} by population abundance. For example, the most recent ICCAT assessment set the unfished population at 100,000 tons for one characterization of current stock status (Anon., 2012). The unfished average size of blue marlin available to the fishery is in the range of 215–235 cm lower jaw fork length (Goodyear, 2015) which, based on the length-weight conversions in Prager et al. (1995), corresponds to a value of about 100 kg. This would place one estimate of the unfished Atlantic Blue marlin population at about 1 million fish in the catchable stock and the yearly average density within the habitat space at just over 1 individual per km³. The HSM can provide estimates of the spatial densities and abundances for any population size from physical oceanography and can be used to investigate relationships that arise from interactions of real or hypothetical population trends and concurrent changes in the density distribution caused by trends in climatology.

The estimates represent expected averages over relatively large time-space scales, and cannot capture density effects from aggregations due to social behavior or local oceanographic features (e.g., eddies). The HSM also does not model species movement. Nonetheless, given their highly migratory life history, and the observed seasonal variations in the distribution of catch and CPUE (e.g., Goodyear, 2003a; Anon., 2011, 2012), it would be difficult to argue that the average temporal distribution of the population would differ from that of suitable habitat in any meaningful way. The monthly and year-specific oceanographic data necessary to address the effects of changing climate will also eliminate the smoothing caused by the multi-year averages used for the example. Also, The PSAT data which suggest marlin are preferentially attracted to the warmest areas may have been exacerbated by temperature anomalies within month-area strata. It seems likely that such anomalies are necessarily within regions with nearly the same oceanographic

conditions. For example, a short-term anomaly of 30 °C is more likely to be within a month-area stratum with an average temperature of 29 °C than some lower temperature. This process would minimize effects on the species distribution at the larger scale. Most discrepancies between the actual species distribution and the HSM estimates will likely be more the result of weakness in the HSM representation of habitat space than the species ability to redistribute themselves within available suitable habitat.

Changes in suitability of habitat at a location does not change the population overall, but rather shifts areal abundance from one place to another. If such changes represent persistent shifts in the suitable habitat as a whole, they may alter long-term average population size through processes integral to stock-recruitment and population renewal. These are longer-term processes beyond the scope of the current effort to predict the 3-D spatial distribution of a population from measurable oceanographic features

4.2. About data sufficiency

4.2.1. Sample size for preference information

Hobday et al. (2010) concluded their habitat model predictions were robust when the behavioral data were derived from at least 10 tags and 50 days of data, far fewer than the 51 tags and cumulative total of 2036 days of data in the Goodyear et al. (2008) study that provided the temperature preference data for this study. However, Goodyear et al. (2008) noted a potential weakness because of the clustering of tag deployments in both time and space caused by economics associated with the tagging operation (Fig. 1). Linear distances averaged 855 km (range 35–4007 km) from release to where the tags detached. The animals presumably covered greater distances representing larger areas during their wanderings. The tropical nature of the species and relatively large spatial displacements of monitored individuals may remove or reduce the potential bias from the spatial clustering. However, temperatures may still be underrepresented in the cooler tail of the frequency distribution because fish monitored near the OMZ had avoided the oxygen-deficient and colder parts of the water column. Examination of Fig. 1 reveals that only a few of the individuals tagged would have encountered these conditions. On the other hand, water temperatures below the range of the suitable temperatures described by Table 2 were present in the water column everywhere these marlin traveled. Consequently, Atlantic blue marlin probably do not visit environmental conditions cooler than estimated in Table 2 in great proportions. It is more likely that improvements in the informa-

tion about the temperature utilization will have greater effect at the upper end of the distribution.

The reliability of the HSI values used here for oxygen cannot be easily evaluated. The effect in the model is to exclude parts of the ocean within which the blue marlin could not survive, but most of these areas are also colder than areas included in the HSI distribution for temperature in Table 2. Changing the center of the 0.5 ml L⁻¹-width oxygen interval where $G_{\text{oxygen}} = 0.5$ by $\pm 10\%$ of its mid-value (≈ 3.5 ml L⁻¹) had an almost imperceptible effect on the predicted distributions. When the oxygen effect was completely removed, the correlation between predicted abundance in the ICCAT catches actually increased slightly from $r = 0.62$ for the complete model to $r = 0.63$ when oxygen was not limiting (outlier removed). This is probably the consequence of marlin avoiding unfavorable habitats as discussed in the next Section 4.2.2. (below), and may be unique to the Atlantic. The finding does, however, suggest that the temperature history of tagged fish may be sufficient to describe the distribution of their habitat.

4.2.2. Is the temperature HSI a preference or just a record of where they live?

The temperature data logged by the tags represented in Table 2 reflect not only thermal preferences but also the effects of all the other variables that influenced habitat selection by the monitored individuals. For example, areas avoided because of low dissolved oxygen also tend to be below the thermocline. Consequently, avoidance of areas of low oxygen would also affect the cumulative proportions of time occupied in the relatively cooler sub-thermocline environment. Since oxygen and temperature information may soon be co-monitored with electronic data-logging tag technology (Coffey and Holland, 2015), it may be possible to partition these effects in the future which will allow a more rigorous separation of their effects than possible here. However, many variables that can affect habitat utilization have more ephemeral characteristics and can neither be recorded on the tags nor are amenable to routine monitoring. These variables, which include such factors as prey availability, productivity, local current patterns, etc., would affect the amount of time marlin spend within the temperature envelope that constitutes acceptable habitat. Their combined effects would be integrated into the time-stream of temperature measurements recorded on the tags and ultimately into time-at-temperature data such as used here to quantify habitat suitability indices for temperature. This process actually maps where habitat is located within the temperature space of the ocean by integrating actual physiological preferences with the influence of other variables in the same space. It is clear that the patterns of time at ΔT seen in Table 3 also integrate the behavior of monitored fish with the effects of other features of the environment. The diel variability seen in Tables 2 and 3 is a common attribute of billfishes, but the magnitude of the effect varies (Kerstetter et al., 2003; Horodysky et al., 2007; Goodyear et al., 2008; Hoolihan et al., 2011, 2015; Chang et al., 2013b; Dewar et al., 2011).

The importance of the distinction can be illustrated by example. The variation in monthly habitat weighted volume (H) in Fig. 5 reveals that average density of the population is variable even when population abundance is not. The average density was about 20% greater in January than in September. Inspection of the data matrix revealed that abundance in otherwise similar spatial cells often varied by more than 30% because of the change in the overall habitat volume between seasons. In the current approach, the ratios of densities in two volumes is given by the ratios of the indices at the temperatures, and a change in volume at a temperature has only a moderate effect on predicted density through its weighted contribution to the total habitable volume. If however, marlin select habitat so that they maintain a fixed proportion of time within a temperature range irrespective of its volume, a large reduction

in the volume of favored temperature can greatly increase density therein. This outcome would result because the fish must spend the same proportion of time in the reduced volume. Seasonal variation in blue marlin density in optimum habitat could easily exceed an order of magnitude, consistent with this interpretation of the temperature utilization data. For example, the individuals monitored during the tagging studies spent about 48% of their time between 28 and 30 °C. The ocean volume within this temperature range varied 15 fold from 2.07×10^4 km³ in January to 3.09×10^5 km³ in August (Fig. 7). If the observed temperature distribution was strictly selected by fish preference, average densities in the optimal habitat would also fluctuate 15 fold, and would involve nearly half of the entire population. This interpretation of the available information is strongly favored by the apparently active selection of decreasingly abundant warmer environments seen in Fig. 6, and is an important feature to investigate in future studies.

The actual times spent within temperature bins between the extremes occupied by the species must represent some complex mix of true behavioral selection and chance encounters with thermal conditions within the core of acceptable habitat. This issue should be seen as a key topic for research. For the standard logistic surplus production model used to manage Atlantic blue marlin, the population is considered overfished when the population is reduced below half that of the unfished population (Anon., 2012). The assessment models are fit to longline CPUE which measure density not abundance. Active selection of water masses of preferred temperatures could cause CPUE to vary over ranges greater than those needed to spur significant restrictions of harvest with no concomitant change in abundance. This source of variability is not generally recognized, and it is not explicitly evaluated in current stock assessments. It may offset or exacerbate trends estimated with traditional methods. Partitioning these effects is an important research topic, but it is clear that large variations in population density unrelated to population abundance may result simply from fluctuations in the volume of preferred habitat.

4.3. Model uses

4.3.1. Habitat visualization

The HSM adds a research tool that is unavailable with routine analyses of catch and effort statistics. Though the bottom of the habitat is necessarily vague because it is best described as a band of decreasing probabilities, and uncertain because of limited knowledge of what actually determines habitat use, the location and shape of the HSM profiles are informative. For example, although the probability distribution of marlin within the habitat bounds estimated here may be subject to important revision, it is unlikely that the blue marlin habitat is very much larger or extends much deeper than the limits described. Also, the graphics presented in Figs. 1–4 only provide a hint of the predicted habitat detail. No small set of graphics can capture the scope of the information about the physical dimensions available with even a cursory inspection of the 3-D profiles at alternative orientations. This information brings physical oceanography and ecological niche to the forefront of stock assessment and will, at the very least, contribute to a richer pool of hypothesis.

4.3.2. Verification of methods to estimate abundance from longline catch and effort

4.3.2.1. Background. Fishing across spans of time and space and with gears with different characteristics causes catch rates to vary in ways unrelated to abundance or effort. Much of this variation is the result of changing interactions between gear and habitat. Innumerable alternative methods have been applied to derive indices of abundance from longline CPUE data (Punt et al., 2015). Maunder and Punt (2004) reviewed the use of GLMs which constitute per-

haps the most widely applied statistical method used to remove the influence of ancillary variables. Most alternative statistical approaches (e.g., GAMs, GLMMs) are variations on the intent of the basic theme of the analysis: to remove the effect of CPUE variation not related to stock-wide abundance (Mateo and Hanselman, 2014; Punt et al., 2015; Walsh and Brodziak, 2015). Many factors included in the models (month, location, hooks between floats, etc.) tend to be surrogates that represent different environmental conditions encountered by the gear, rather than environmental measurements themselves. Hinton and Nakano (1996) introduced a method (detHBS) to account for habitat effects using habitat preference data along with information about temperatures at depths fished by longline hooks. Maunday et al. (2006) integrated this approach into the GLM framework (called statHBS) to allow statistical estimation of the model parameters and a broader array of treatments of environmental variables. The best approach for any particular data set is often unclear, adding a degree of unquantifiable uncertainty to stock assessments. Additionally, these methods assume the total amount of habitat is constant. The average volume of the Atlantic within the range of temperature occupied by blue marlin about half the time varied by a factor of 15 between months. This finding supports the notion that global warming is probably changing both the amount and distribution of pelagic habitat used by blue marlin. Maunday et al. (2006) described a modification to statHBS that would address the problem of varying size of the habitat. It involves computing a total relative habitat derived by summing relative habitats computed for spatial strata weighted by habitat preferences, analogous to the model here.

4.3.2.2. Enlightened partitioning of catch-effort? Though beyond the scope of the current study, it is clear that the HSM described here provides the opportunity to explore new paradigms for estimating population abundance. The HSM may provide the vehicle to implement the improvement of statHBS which Maunday et al. (2006) suggested could address the problem of varying size of the habitat. However, an analysis using the spatial detail of the HSM may produce an impossibly complex statistical model. Simpler alternatives might exploit space-time stratifications where the spatiotemporal boundaries for data aggregations are conditioned on the HSM predictions of relative density or abundance. The most appropriate approach is not immediately clear.

4.3.2.3. Simulating “knowns” for testing methods. Simulated data are widely used to validate models and have been used to compare the performance of different methods of standardizing blue marlin longline CPUE (Goodyear, 2003b; Lynch et al., 2012; Chang et al., 2015). These analyses have been limited to specific comparisons that provide no guidance about the issue of changing habitat size and distribution as seen here. Goodyear (2006a,b) described a generic longline simulator that superimposes longline effort partitioned by latitude, longitude and gear type (hook-depth frequency) on species distribution using the same habitat geometry as the HSM. The longline simulator has been used to evaluate several CPUE methodological issues (Goodyear, 2006a,b; Schirripa and Goodyear, 2010; Goodyear and Bigelow, 2010, 2012), and is ideal to simulate longline CPUE data from HSM predictions. Application of these technologies can be used to produce series of knowns to investigate alternative CPUE standardization methods for removing the effects of habitat variability on indices of population abundance. HSM predictions using monthly-varying annual climatology will be ideally suited for testing the ability of alternative methods to reliably recover actual trends in population abundance from past and predicted future climatology.

4.4. Concluding thoughts

Blue marlin habitat is modeled here as a temperature-space phenomenon constrained to areas of acceptable dissolved oxygen. The need for such models is reflected by the development and application of similar models for near-term management and long-term planning based on short- and long-term oceanographic features (e.g., Hobday and Hartmann, 2006; Hobday et al., 2010; Robinson et al., 2015). The current approach can be applied with modification to other highly migratory species. Both the model and supporting data can be improved, which might involve additional habitat factors such as current, turbidity, salinity, nutrients, chlorophyll, the depth of the surface mixed layer, etc. These and other factors undoubtedly have important effects on the distribution of fish, but their combined effects have been mapped by the time-at-temperature histories of tagged individuals. Improvements will need to address this issue. Potential improvements aside, it clear that acceptable blue marlin habitat is continuously shifting in position and size within in the physical geometry we normally consider the ocean. The shifting habitat geometry is probably typical for most highly migratory species. It has important consequences for understanding population dynamics, interpreting population statistics, assessing population status and managing the fisheries. Although significant additional research is needed, sufficient oceanographic data exist to include habitat geometry as an explicit topic in stock assessments for pelagic species such as blue marlin. Fluctuations in habitat volume likely contribute to seasonal and longer-term fluctuations in CPUE that are independent of population abundance and add unrecognized uncertainty to estimates of population benchmarks. Climate change is altering seasonal patterns from historic norms and will change the distributions of the fish populations and their fisheries. These changes will confuse analyses of population abundance and confound all aspects of fish research and management that rely on accurate stock assessments until a rigorous accounting for habitat can be ensured.

Acknowledgments

This study was supported by The Billfish Foundation. I thank Michael Schirripa and Francesca Forrestal for their assistance, and several anonymous reviewers for their comments and helpful criticisms on earlier drafts.

References

- Anon. 2011. Report of the 2010 Blue Marlin Data Preparatory Meeting., Collect. Vol. Sci. Pap. ICCAT, 66 (4), 1554–1660. http://www.iccat.int/Documents/CVSP/CV066_2011/no.4/CV066041554.pdf (accessed 24.4.16).
- Anon., 2012. Report of the 2011 Blue Marlin stock assessment and white marlin data preparatory meeting., Collect. Vol. Sci. Pap. ICCAT, 68 (4), 1273–1386. http://www.iccat.int/Documents/CVSP/CV068_2012/no.4/CV068041273.pdf (accessed 24.4.16).
- Bigelow, K.A., Maunday, 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, In: Boyer, T., Mishonov, A., Technica (Eds.), 1–14. <http://www.nodc.noaa.gov/OC5/indprod.html>.
- Boyer, T.P., J.I. Antonov, O.K., Baranova, C., Coleman, H.E., Garcia, A., Grodsky, D.R., Johnson, R.A., Locarnini, A.V., Mishonov, T.D., O'Brien, C.R., Paver, J.R., Reagan, D., Seidov, I.V., Smolyar, M.M., Zweng, 2013. World Ocean Database 2013. In: Sydney, Levitus, Alexey, Mishonov, Technical (Eds.), NOAA Atlas NESDIS 72, 209 pp. http://data.nodc.noaa.gov/woa/WOD/DOC/wod_intro.pdf.
- Braun, C.D., Kaplan, M.B., Horodysky, A.Z., Llopiz, J.K., 2015. Satellite telemetry reveals physical processes driving billfish behavior. Anim. Biotelem. 3 (2), <http://dx.doi.org/10.1186/s40317-014-0020-9>.
- Bushnell, P.G., Brill, R.W., 1991. Responses of swimming skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) to acute hypoxia, and a model of their cardio respiratory function. Physiol. Zool. 64, 787–811.
- Chang, Y.-S., Rosati, A.J., Zhang, S., Harrison, M.J., 2009. Objective analysis of monthly temperature and salinity for the world ocean in the 21st century: comparison with World Ocean Atlas and application to assimilation validation. J. Geophys. Res. 114, C02014, <http://dx.doi.org/10.1029/2008JC004970>.

- Chang, Y.J., Sun, C.L., Chen, Y., Yeh, S.Z., DiNardo, G., 2012. Habitat suitability analysis and identification of potential fishing grounds for swordfish, *Xiphias gladius*, in the South Atlantic Ocean. *Int. J. Remote Sens.* 33 (23), 7523–7541.
- Chang, Y.J., Sun, C.L., Chen, Y., Yeh, S.Z., DiNardo, G., Su, N.-J., 2013a. Modelling the impacts of environmental variation on the habitat suitability of swordfish, *Xiphias gladius*, in the equatorial Atlantic Ocean. *ICES J. Mar. Sci.* 70, 1000–1012.
- Chang, Y.J., Kawabe, R., Musyl, M.K., Sun, C.L., Hung, H.M., Lin, H.C., Watanabe, S., et al., 2013b. Diel oscillations in sailfish vertical movement behavior in the East China Sea. *J. Mar. Sci. Technol.* TA 21, 267–273.
- Chang, Y.J., Brodziak, J., O'Malley, J., Lee, H.H., DiNardo, G., Sun, C.L., 2015. Model selection and multi-model inference for Bayesian surplus production models: a case study for Pacific blue and striped marlin. *Fish. Res.* 166, 129–139.
- Coffey, D.M., Holland, K.N., 2015. First autonomous recording of in situ dissolved oxygen from free-ranging fish. *Anim. Biotelem.* 3 (47), 1–9.
- Dale, M.R.T., Fortin, M.-J., 2002. Spatial autocorrelation and statistical tests in ecology. *Ecoscience* 9, 162–167.
- Dewar, H., Prince, E., Musyl, M., Brill, R., Sepulveda, C., Luo, J., et al., 2011. Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fish. Oceanogr.* 20, 219–241.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* 40, 677–697.
- Evans, R.H., McLain, R.A., Bauer, R.A., 1981. Atlantic skipjack tuna: influences of mean environmental conditions on their vulnerability to surface fishing gear. *Mar. Fish. Rev.* 43, 1–11.
- FAO, 2003. Fishing Techniques. Industrial tuna longlining. Technology Fact Sheets. In: FAO Fisheries and Aquaculture Department [online]. Rome. Updated 19 September 2003. <http://www.fao.org/fishery/fishtech/1010/en> (accessed 6.7.16).
- Gooding, R.M., Neill, W.H., Dizon, A.E., 1981. Respiration rates and low-oxygen tolerance in skipjack tuna, *Katsuwonus pelamis*. *Fish. Bull.* 79, 31–48.
- Goodyear, C.P., Bigelow, K.A., 2010. Preliminary explorations of CPUE standardization of the U.S. longline observer sailfish data using stathbs. *Collect. Vol. Sci. Pap. ICCAT* 65 (5), 1713–1724. http://www.iccat.int/Documents/CVSP/CV065_2010/no.5/CV065051713.pdf (accessed 24.4.16).
- Goodyear, C.P., Bigelow, K.A., 2012. Preliminary analyses of simulated longline Atlantic blue marlin CPUE with HBS and generalized linear models. *Collect. Vol. Sci. Pap. ICCAT* 68 (4), 1510–1523. http://www.iccat.int/Documents/CVSP/CV068_2012/no.4/CV068041510.pdf (accessed 24.4.16).
- Goodyear, C.P., Luo, J., Prince, E.D., Hoolihan, J.P., Snodgrass, D., Orbesen, E.S., Serafy, J.E., 2008. Vertical habitat use of Atlantic blue marlin (*Makaira nigricans*): interaction with pelagic longline gear. *Mar. Ecol. Prog. Ser.* 365, 233–245.
- Goodyear, C.P., 2003a. Spatio-temporal distribution of longline catch-per-unit-effort, sea surface temperature and Atlantic marlin. *Mar. Freshw. Res.* 54, 409–417.
- Goodyear, C.P., 2003b. Tests of the robustness of habitat-standardized abundance indices using simulated blue marlin catch-effort data. *Mar. Freshw. Res.* 54, 369–381.
- Goodyear, C.P., 2006a. Performance diagnostics for the longline CPUE simulator. *Collect. Vol. Sci. Pap. ICCAT* 59 (2), 615–626. http://www.iccat.int/Documents/CVSP/CV059_2006/no.2/CV059020615.pdf (accessed 24.4.16).
- Goodyear, C.P., 2006b. Simulated Japanese longline CPUE for blue marlin and white marlin. *Collect. Vol. Sci. Pap. ICCAT* 59 (1), 211–223. http://www.iccat.int/Documents/CVSP/CV059_2006/no.1/CV059010211.pdf (accessed 24.4.16).
- Goodyear, C.P., 2015. Understanding maximum size in the catch: atlantic blue marlin as an example. *Trans. Am. Fish. Soc.* 144, 274–282. <http://dx.doi.org/10.1080/00028487.2014.986339>.
- Hinton, M.G., Maunders, M.N., 2004. Methods for standardizing CPUE and how to select among them. *Collect. Vol. Sci. Pap. ICCAT* 56 (1), 169–177. http://www.iccat.int/Documents/CVSP/CV056_2004/no.1/CV056010169.pdf (accessed 24.4.16).
- Hinton, M.G., Nakano, H., 1996. Standardizing catch and effort statistics using physiological ecological, or behavioral constraints and environmental data, with an application to blue marlin (*Makaira nigricans*) catch and effort data from the Japanese longline fisheries in the Pacific. *Bull. Inter-Am. Trop. Tuna Comm.* 21, 171–200.
- Hirzel, A.H., Lay, G.L., 2008. Habitat suitability modelling and niche theory. *J. Appl. Ecol.* 45, 1372–1381.
- Hobday, A.J., Hartman, K., 2006. Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fish. Manag. Ecol.* 13, 365–380.
- Hobday, A.J., Jason, R., Hartog, J.R., Timmiss, T., Fielding, J., 2010. Dynamic spatial zoning to manage southern bluefin tuna (*Thunnus maccoyii*) capture in a multi-species longline fishery. *Fish. Oceanogr.* 19, 243–253.
- Hoolihan, J.P., Luo, J., Goodyear, C.P., Orbesen, E.S., Prince, E.D., 2011. Vertical habitat use of sailfish (*Istiophorus platypterus*) in the Atlantic and eastern Pacific, derived from pop-up satellite archival tag data. *Fish. Oceanogr.* 20, 192–205.
- Hoolihan, J.P., Luo, J., Snodgrass, D., Orbesen, E.S., Barse, A.M., Prince, E.D., 2015. Vertical and horizontal habitat use by white marlin *Kajikia albiga* (Poey, 1860) in the western North Atlantic Ocean. *ICES J. Mar. Sci.* 72, 2364–2373. <http://dx.doi.org/10.1093/icesjms/fsv082>.
- Hoolihan, J.P., 2005. Horizontal and vertical movements of sailfish (*Istiophorus platypterus*) in the Arabian Gulf, determined by ultrasonic and pop-up satellite tagging. *Mar. Biol.* 146, 1015–1029.
- Horodysky, A.Z., Kerstetter, D.W., Latour, R.J., Graves, J.E., 2007. Habitat utilization and vertical movements of white marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean: inferences from short duration pop-up archival satellite tags. *Fish. Oceanogr.* 16, 240–256.
- Idrisi, N., Capo, T.R., Luthy, S., Serafy, J.E., 2002. Behavior, oxygen consumption and survival of stressed juvenile sailfish (*Istiophorus platypterus*) in captivity. *Mar. Freshw. Behav. Physiol.* 36, 51–57.
- Ingham, M.C., Cook, S.K., Hausknecht, K.A., 1977. Oxycline characteristics and skipjack tuna distribution in the southeastern tropical Atlantic. *Fish. Bull.* 75, 857–865.
- Ishii, M., Kimoto, M., 2009. Reevaluation of historical ocean heat content variations with time-varying xbt and mbt depth bias corrections. *J. Oceanogr.* 65, 287–299.
- Kerstetter, D.W., Luckhurst, B.E., Prince, E.D., Graves, J.E., 2003. Use of pop-up satellite archival tags to demonstrate survival of blue marlin (*Makaira nigricans*) released from pelagic longline gear. *Fish. Bull.* 101, 939–948.
- Lam, C.H., Kiefer, D.A., Domeier, M.L., 2015. Habitat characterization for striped marlin in the Pacific Ocean. *Fish. Res.* 166, 80–91.
- Luo, J., Prince, E.D., Goodyear, C.P., Luckhurst, B.E., 2006. Vertical habitat utilization by large pelagic animals: a quantitative framework and numerical method for use with pop-up satellite tag data. *Fish. Oceanogr.* 15, 208–229.
- Lynch, P.D., Shertzer, K.W., Latour, R.J., 2012. Performance of methods used to estimate indices of abundance for highly migratory species. *Fish. Res.* 125–126, 27–39.
- Manly, B., 2007. Randomization, Bootstrap and Monte Carlo Methods in Biology, 3rd edition. Chapman & Hall/CRC, Boca Raton.
- Mateo, I., Hanselman, D.H., 2014. A Comparison of Statistical Methods to Standardize Catch-Per-Unit-Effort of the Alaska Longline Sablefish. United States Department of Commerce, NOAA Technical Memo, NMFS-AFSC-269, 71 p.
- Maunders, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* 70, 141–159.
- Maunders, M.N., Hinton, M.G., Bigelow, K.A., Langley, A.D., 2006. Developing indices of abundance using habitat data in a statistical framework. *Bull. Mar. Sci.* 79, 545–559.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Polacheck, T., 2006. Tuna longline catch rates in the Indian Ocean: did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? *Mar. Policy* 30, 470–482. <http://dx.doi.org/10.1016/j.marpol.2005.06.016>.
- Prager, M.H., Prince, E.D., Lee, D.W., 1995. Empirical length and weight conversion equations for Blue Marlin white marlin, and sailfish from the North Atlantic Ocean. *Bull. Mar. Sci.* 56, 201–210.
- Prince, E.D., Goodyear, C.P., 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fish. Oceanogr.* 15, 451–464.
- Prince, E.D., Goodyear, C.P., 2007. Consequences of ocean scale hypoxia constrained habitat for tropical pelagic fishes. *Gulf Caribb. Res.* 19, 17–20.
- Prince, E.D., Luo, J., Goodyear, C.P., Hoolihan, J.P., Snodgrass, D., Orbesen, E.S., Serafy, J.E., et al., 2010. Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. *Fish. Oceanogr.* 9, 448–462.
- Punt, A.E., Su, N.J., Sun, C.L., 2015. Assessing billfish stocks: a review of current methods and some future directions. *Fish. Res.* 166, 103–118.
- R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org> (accessed 24.4.16).
- Robinson, L.M., Hobday, A.J., Possingham, H.P., Richardson, A.J., 2015. Trailing edges projected to move faster than leading edges for large pelagic fish habitats under climate change. *Deep Sea Res. Part II* 113, 225–234.
- Saba, V.S., Griffies, S.M., Anderson, W.G., Winton, M., Alexander, M.A., Delworth, T.L., Hare, J.A., Harrison, M.J., Rosati, A., Vecchi, G.A., Zhang, R., 2015. Enhanced warming of the Northwest Atlantic Ocean under climate change. *J. Geophys. Res.* 120, 1–15. <http://dx.doi.org/10.1002/2015JC011346>.
- Schirripa, M.J., Goodyear, C.P., 2010. CPUE standardizations of species targeting in longline fisheries: initial investigations of the utility of simulated data for method verification. *Collect. Vol. Sci. Pap. ICCAT* 65 (6), 2351–2362. http://www.iccat.int/Documents/CVSP/CV065_2010/no.6/CV065062351.pdf (accessed 24.4.16).
- Stramma, L., Prince, E.D., Schmidtko, S., Luo, J.G., Hoolihan, J.P., Visbeck, M., Wallace, D.W.R., et al., 2012. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Change* 2, 33–37.
- Su, N.J., Sun, C.L., Punt, A.E., Yeh, S.Z., 2008. Environmental and spatial effects on the distribution of blue marlin (*Makaira nigricans*) as inferred from data for longline fisheries in the Pacific Ocean. *Fish. Oceanogr.* 17, 432–445.
- Su, N.J., Sun, C.L., Punt, A.E., Yeh, S.Z., DiNardo, G., 2011. Modelling the impacts of environmental variation on the distribution of blue marlin, *Makaira nigricans*, in the Pacific Ocean. *ICES J. Mar. Sci.* 68, 1072–1080.
- Waller, L.A., Smith, D., Childs, J.E., Real, L.A., 2003. Monte Carlo assessments of goodness-of-fit for ecological simulation models. *Ecol. Modell.* 164, 49–63.
- Walsh, W.A., Brodziak, J., 2015. Billfish CPUE standardization in the Hawaii longline fishery Model selection and multimodel inference. *Fish. Res.* 166, 151–162.