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

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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.

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

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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:

$$H_{ijk} = X_{ijk} V_{ijk} \tag{1}$$

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:

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

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 a 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:

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

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;