Modeling the dynamic habitats of mobile pelagic predators (*Makaira nigricans* and *Istiompax indica*) in the eastern Pacific Ocean

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ABSTRACT: Overexploitation and climate change can reduce the abundance and shift the spatial distribution of marine species. Determining the habitat suitability of a mobile pelagic species, such as blue marlin (BUM) *Makaira nigricans* and black marlin (BAM) *Istiompax indica*, can help describe their spatiotemporal distribution patterns over a broad spatial scale, which is crucial for fisheries management. We applied a species distribution model (MaxEnt) to model the dynamic suitable habitat of BUM and BAM using 14 yr (1997–2010) of Inter-American Tropical Tuna Commission occurrence data (n = 20 348) from purse-seine vessels in the eastern Pacific Ocean (EPO) and high-resolution remotely sensed oceanographic data. The spatial distribution of suitable habitat for both species varied seasonally and in response to El Niño–Southern Oscillation (ENSO), with BUM positively correlated with chlorophyll *a* (chl *a*) concentrations and sea surface temperature and BAM with chl *a* concentrations and sea surface height. The influence of these environmental variables shifted seasonally suitable habitat between coastal (winter and spring) and oceanic (summer and fall) waters. During La Niña events, suitable habitat was along the equator, while during El Niño, suitable habitat shifted to farther northern and southern waters of the EPO. Analyses on species' centers of suitable habitat (CSH) revealed that the strength of ENSO did not influence CSH; however, large displacements were observed during these events. The models applied in our study provide critical information on the spatiotemporal patterns of 2 mobile pelagic predators, which can potentially be used to forecast future distributions and develop effective management strategies in response to climate change.

KEY WORDS: Distribution shift · Black marlin · Blue marlin · Marine pelagic fish · Satellite remote sensing data · Incidental catch · MaxEnt · Species distribution model · Tuna purse-seine fishery

1. INTRODUCTION

Large predatory fish populations and communities have been significantly impacted by industrialized fisheries (Jackson et al. 2001, Myers & Worm 2003, Sibert et al. 2006, Worm et al. 2009). This, combined with climate change, pollution, and other anthropogenic activities, can put unprecedented pressure on higher trophic level predators, such as tunas, billfishes, or sharks, which may cascade downward through the food web and affect ecosystem function-

ality (Baum & Worm 2009). Overexploitation may reduce fish abundances (Jackson et al. 2001, Myers & Worm 2003, Coleman et al. 2004, Kitchell et al. 2006, Jensen et al. 2010), while climate change can cause shifts in spatial distribution of marine species (Pinsky et al. 2013, Hill et al. 2016). Currently, regional fishery management organizations are moving away from traditional fisheries objectives, e.g. achieving single-species maximum sustainable yield, to an ecosystem-based or dynamic management framework (Sinclair et al. 2002, Garcia & Cochrane 2005,

Maxwell et al. 2015). To improve the conservation and management of these apex predators, it is important to determine and understand their suitable habitat and spatial distribution (Pearce et al. 2001, Hoolihan et al. 2015, Hill et al. 2016). In this study, we used for the first time a presence-only species distribution model (SDM) to better understand habitat use patterns of blue marlin (BUM) *Makaira nigricans* and black marlin (BAM) *Istiompax indica* in the eastern Pacific Ocean (EPO; Fig. 1).

BUM and BAM are epipelagic species that are widely distributed throughout the tropical and subtropical waters of the Indo-Pacific Ocean (Nakamura 1985). In the Pacific, BUM are typically more tropical and densely distributed at low latitudes, whereas BAM have been observed to occasionally enter subtropical and temperate regions as far south as the Cape of Good Hope (Howard & Ueyanagi 1965, Nakamura 1985). Fisheries data suggest there is a single stock of BUM in the Pacific Ocean that migrates to the northwest and southeast Pacific Ocean in the boreal summer and winter months, respectively, which could be related to spawning regions (Howard & Ueyanagi 1965, Hinton 2001). The distribution of catches of BAM suggests a single stock centered off Australia, with the species widely

distributed but not consistently abundant elsewhere (Skillman 1988, Domeier & Speare 2012). Although previous studies on BUM and BAM demonstrated that both species are highly migratory and exhibit trans-basin and trans-oceanic movements (Squire Jr & Nielsen 1983, Hinton 2001, Carlisle et al. 2017), both species show affinity for continental margins and seamounts, increasing their accessibility to recreational anglers (Campbell et al. 2003, Gunn et al. 2003, Morato et al. 2010, Hill et al. 2016).

BUM and BAM are both highly important resources to commercial and recreational fisheries (Molony 2005, Chiang et al. 2015). Predominately caught in pelagic longline fisheries targeting tuna *Thunnus* spp. and swordfish *Xiphias gladius*, they are also taken in smaller numbers by purse-seine, harpoon, and gillnet fisheries (Hinton 2001, Chiang et al. 2015). Both species are prized targets of recreational anglers who fish relatively close to shore in various areas around the Pacific Basin (Kleiber et al. 2003, Pepperell 2011). The status of BUM in the Pacific Ocean remains unknown. One assessment concluded that the Pacific BUM stock is in healthy condition (Hinton 2001) though likely fully exploited (Kleiber et al. 2003). To date, there has not been an assessment of the BAM stock in the Pacific.
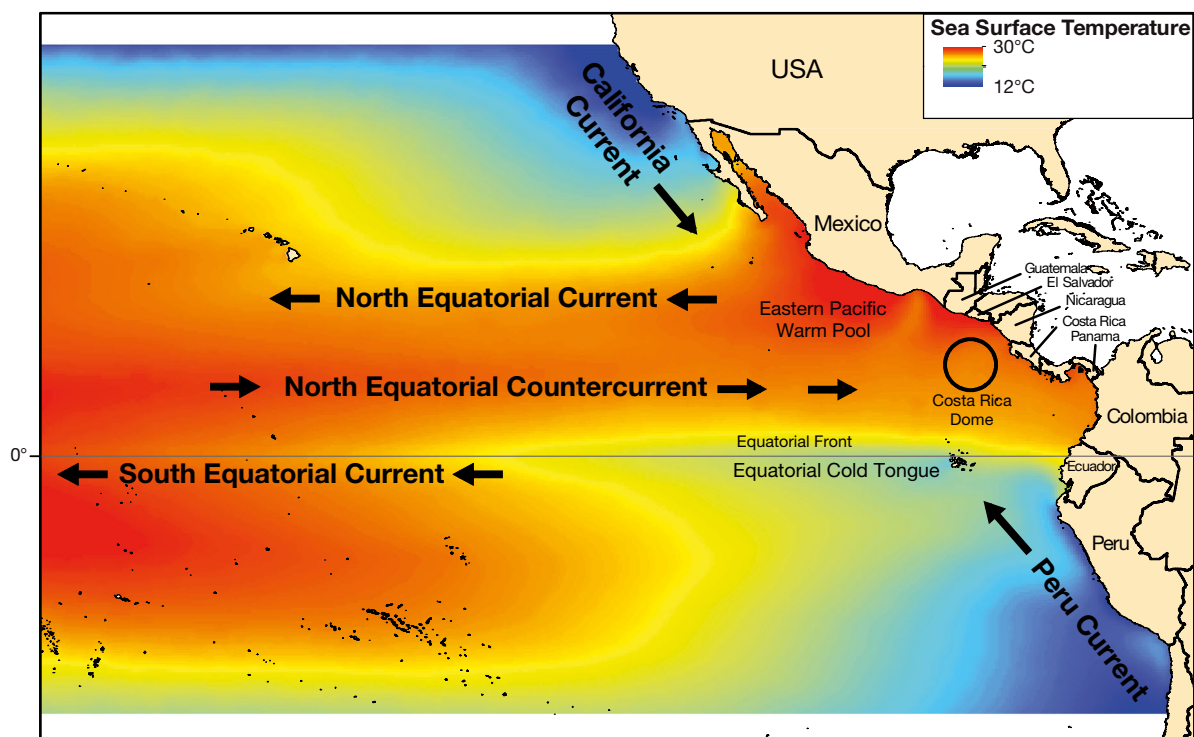

Fig. 1. Surface water currents and masses in the eastern Pacific Ocean. Color gradient represents mean sea surface temperature, for which data were derived from GHRSST L4 AVHRR (Reynolds et al. 2007), Optimum Interpolation and averaged for September–November between 1997 and 2010. Figure modified from Fiedler & Talley (2006)

Determining suitable habitat and spatial distribution is very important in the conservation and management of marine organisms (Pearce et al. 2001, Hoolihan et al. 2015, Hill et al. 2016). Acoustic and archival tags have been useful in understanding the spatiotemporal distribution of highly mobile species, such as BUM and BAM (Holland et al. 1990, Block et al. 1992, Graves et al. 2002, Chiang et al. 2015, Carlisle et al. 2017). However, in the absence of detailed tagging data, SDMs have been useful in predicting the spatial distribution of species relative to environmental variables. The most common SDMs are regression models, such as generalized additive or generalized linear models for binomial data; however, these statistical models require presence/absence data, which are not always readily available from fisheries-dependent samples (Phillips et al. 2006, Elith et al. 2011). In recent years, SDMs have been built that use presence-only data. The predictive performance of the presence-only SDMs are consistently comparable to presence/absence models (Ehrhardt & Fitchett 2006).

The environmental preferences and spatial distribution of BUM and BAM, inferred either from electronic tags or longline fisheries data, indicate that both species primarily inhabit oceanic waters of the Pacific Ocean, where sea surface temperatures (SSTs) are between 24 and 30°C (Graves et al. 2002, Boyce et al. 2008, Su et al. 2008, Chiang et al. 2015, Carlisle et al. 2017), chlorophyll a (chl a) concentrations are <1 mg m^{-3} (Su et al. 2008), and there is a deep mixed layer depth (Holland et al. 1990, Graves et al. 2002, Prince & Goodyear 2006, Su et al. 2008, Stramma et al. 2012, Chiang et al. 2015, Carlisle et al. 2017). Of these environmental factors, studies have suggested that SST has the most influence on the spatial distribution of both species (Holland et al. 1990, Graves et al. 2002, Prince & Goodyear 2006, Boyce et al. 2008, Su et al. 2008, Chiang et al. 2015, Carlisle et al. 2017). In contrast, a recent study using data from recreation fisheries concluded that chl a was the most influential environmental factor on BAM distribution in more nearshore regions (Hill et al. 2016). Given that such findings may be due to limitations in spatial distribution of effort and resolution of environmental variables, there is a glaring need to better discern the environmental factors that influence BUM and BAM distribution on a broad scale.

This study provides a unique opportunity to observe BUM and BAM habitat preferences, as we used incidental catch data from the tuna purse-seine fishery, which fishes in both coastal and oceanic waters throughout the EPO. In the EPO, habitat availability likely shifts over a variety of spatial and temporal scales due to the seasonal changes this region experiences (Ortega-García et al. 2015, Acosta-Pachón et al. 2017). Large-scale oceanographic changes during El Niño Southern Oscillation (ENSO) events may also impact habitat availability and distribution of BUM and BAM in the EPO (Su et al. 2011, Carlisle et al. 2017). The main objectives of this study were to describe the spatiotemporal patterns in habitat suitability of BUM and BAM in the EPO and to identify significant environmental factors influencing their spatial patterns, which can provide a basis for managing the fisheries that impact these species.

2. METHODS

2.1. BUM and BAM occurrence data

We used opportunistic occurrence data (incidental catch) of BUM and BAM collected by Inter-American Tropical Tuna Commission (IATTC) scientific observers aboard EPO tuna purse-seine fishing vessels (Fig. 2). We analyzed seasonal occurrence data collected between September 1997 and December 2010, because high-resolution, remotely sensed environmental data were available during this period. Catch data recorded by the scientific observers included: year, month, day, hour, location of capture, marlin species, set type, marlin length, and biomass (metric tons). In total, 12 680 BUM and 7668 BAM occurrence records were collected during this period within the region of 40° N to 25° S and 70–180° W.

2.2. Environmental variables

We evaluated whether satellite-derived measurement of SST, chl a, zonal current (U), meridional current (V), and sea surface height (SSH) affected BUM and BAM distributions (Table 1). All spatial layers were acquired using the Marine Geospatial Ecology Tool (MGET) in ArcGIS, developed at Duke University (http://mgel.env.duke.edu/mget) (Hill et al. 2016). Due to differences in spatial resolutions, all spatial layers were resampled to a common spatial resolution (0.1°) to satisfy modeling requirements. Spatial layers with clusters of no-data cells, possibly due to cloud cover, were interpolated using the 'del2a' method within MGET, which performs Laplacian interpolation and linear extrapolation. Depending on model criteria, environmental variables were averaged seasonally or climatologically.
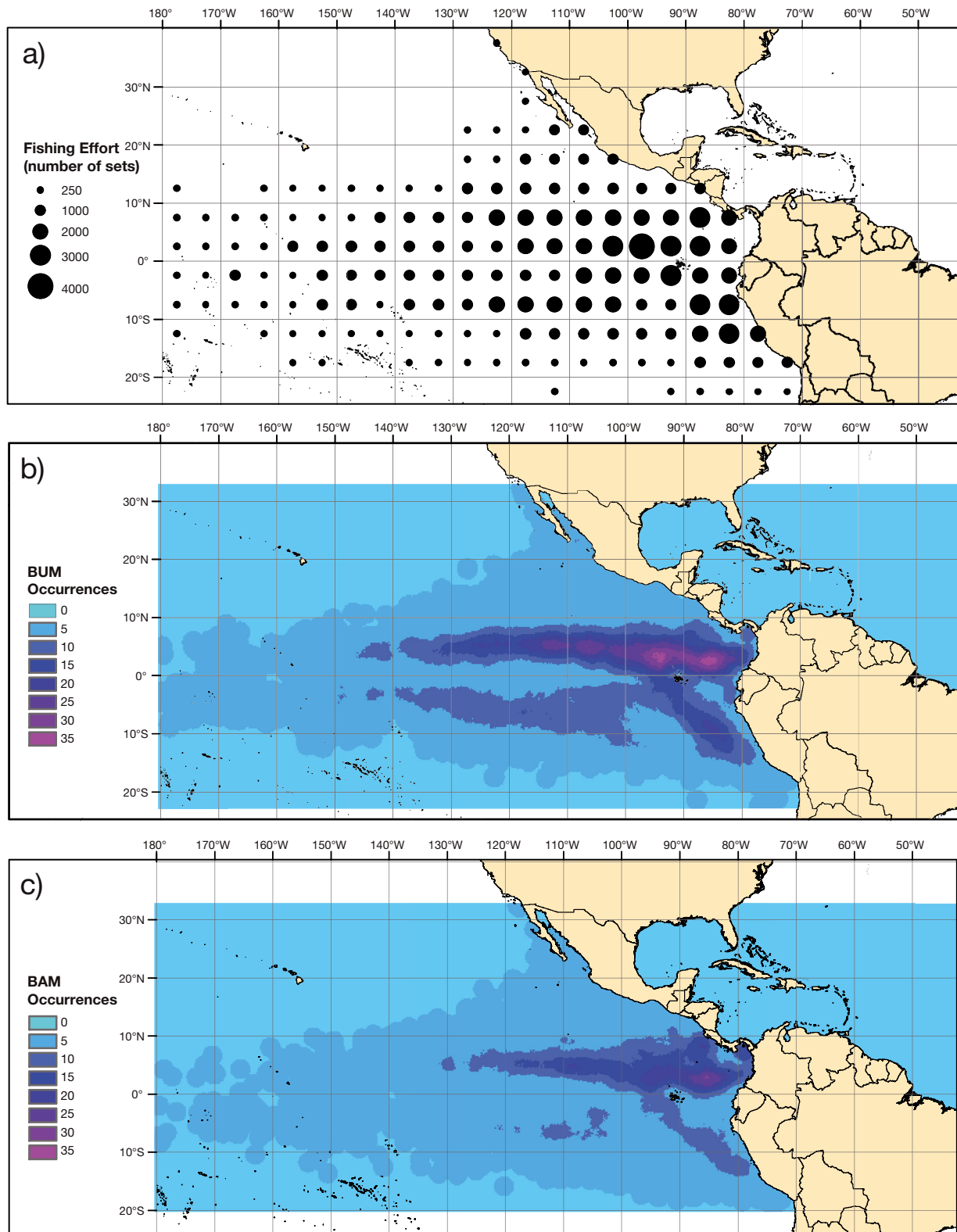
Fig. 2. (a) Spatial distribution of fishing effort of the tuna purse-seine fishery (number of sets), and spatial frequency plots of species occurrences for (b) blue marlin (BUM) and (c) black marlin (BAM) in the eastern Pacific Ocean during September 1997 to December 2010

Table 1. Environmental variables included in the MaxEnt models

Environmental variable	Product	Spatial resolution	Temporal resolution	Unit	Source
Chlorophyll *a* conc. (chl *a*)	SeaWIFS L3	0.1°	Monthly	mg m^{-3}	https://oceandata.sci.gsfc.nasa.gov/SeaWiFS/L3SMI/
Sea surface temperature (SST)	GHRSST L4 AVHRR, Optimum Interpolation Global	0.25°	Daily	°C	https://podaac.jpl.nasa.gov/dataset/AVHRR_OI-NCEI-L4-GLOB-v2.0
Sea surface height (SSH)	AVISO Absolute Dynamic Topography (MADT-H), DT all sat, Global	0.25°	Daily	cm	https://www.aviso.altimetry.fr/index.php?id=1271
Zonal current (*U*)	NOAA Ocean Surface Current Analyses – Real Time	0.33°	5 d	m s^{-1}	https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg
Meridional current (*V*)	NOAA Ocean Surface Current Analyses – Real Time	0.33°	5 d	m s^{-1}	https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg

2.3. Habitat modeling

We used the species distribution model MaxEnt, which estimates the probability distribution of a species, subject to a set of constraints of biologically relevant environmental factors (Phillips et al. 2006). MaxEnt is a general-purpose machine-learning method whose predictive performance is competitive with the highest preforming methods (Elith et al. 2006). Unlike commonly used techniques, such as generalized linear or generalized additive models, which require presence/absence data, MaxEnt is unique in that it uses presence-only data and is tolerant to small sample sizes (Elith et al. 2006, Phillips et al. 2006). MaxEnt produces a single continuous surface of habitat suitability values, ranging from 0 to 1, across a specified geographic space by determining a species distribution based on the environmental conditions at locations of known occurrence (Phillips et al. 2006). Additionally, the fine-scale catch data produced by purse-seine vessels are compatible with the requirements of MaxEnt. MaxEnt requires the input of fine-scale occurrence data, consisting of the latitude and longitude of where the species has been observed. Catch data from fisheries with lower spatial resolutions, such as from longlines or gillnets, would be inappropriate for MaxEnt. We built 60 simulations for each species with all possible combinations of the environmental variables.

We described the general seasonal suitable habitat of BUM and BAM in the EPO during September 1997 to December 2010 using seasonal climate. These simulations used 3 mo binned climatological averages of

each environmental variable matched with each observation of the species during that period. Each 3 mo bin was categorized by season: Fall (September–November), Winter (December–February), Spring (March–May), and Summer (June–August). For these seasonal climate simulations, the number of occurrence points inputted for BUM and BAM ranged from 2480 to 3354 and from 1413 to 2097, respectively. Additionally, ENSO climate simulations were constructed to describe the general suitable habitat in each ENSO state: Niño Neutral, El Niño, and La Niña. Similar to the seasonal climate simulations, these simulations included climatological averages from environmental variables for each ENSO state matched with occurrences of the species during each ENSO state. The ENSO states were determined by the Oceanic Niño Index (ONI) calculated by the NOAA NCEP Climate Prediction Center (http://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php).

ENSO events were defined as 5 consecutive overlapping 3 mo periods at or above the +0.5° anomaly for warm (El Niño) events and at or below the −0.5° anomaly for cold (La Niña) events. Additionally, events were classified as either weak or strong if they equaled or exceeded the threshold for at least 3 consecutive overlapping 3 mo periods. For these ENSO climate simulations, the number of occurrence points inputted for BUM and BAM ranged from 4042 to 6045 and from 2411 to 3774, respectively. Anomaly maps of habitat distribution were made relative to Niño Neutral distributions. Lastly, to capture the seasonal variability of suitable habitat each year from

September 1997 to December 2010, 'yearly' simulations included 3 mo averages (n = 53) of the environmental variables and all the occurrences of the species during that period in the EPO. For these 'yearly' simulations, the number of occurrence points inputted for BUM and BAM ranged from 107 to 360 and from 68 to 261, respectively. All simulations were run using the freely available MaxEnt software, version 3.4.1 (http://biodiversityinformatics.amnh.org/open_source/maxent/).

MaxEnt assumes an unbiased sampling of occurrence data within the study area; however, this is usually not the case. Sample selection bias can be problematic in presence-only models, such as MaxEnt, because background points may be selected in regions that are environmentally suitable but in which the species is never observed. This can increase false-absences, thereby producing a model that potentially models the sampling effort but not the species distribution (Phillips et al. 2009). Since our study has a large spatial extent, this can lead to the selection of a higher proportion of less informative background points (Barbet-Massin et al. 2012). To prevent this problem, many studies draw background points that are more regional to the occurrence data (Phillips et al. 2009, VanDerWal et al. 2009, Fourcade et al. 2014, Hill et al. 2016, Wang et al. 2018). To account for our occurrence data being biased towards areas of the tuna purse-seine fishery, we selected background data with equivalent spatiotemporal bias. Background points (n = 10 000) were randomly selected with a 100 nautical mile buffer of each occurrence per simulation. This buffer size was used as it most effectively balanced habitat sensitivity and specificity, offering the most biologically informative and logical results (VanDerWal et al. 2009).

Model performance was evaluated with a 5-fold cross-validation (500 iterations each), default regularization parameters, and a logistic output. To test model performance, 80% of the occurrence records were used to train the model and the remaining 20% were used for testing (Hill et al. 2016). All simulations produced an average output from the 5-folds and response plots showing the predicted probability of presence as a function of each environmental variable. Lastly, a jackknife test of environmental variable importance (Hill et al. 2016) was applied to each model to determine the training gain of each variable if the model was run in isolation, and these were compared to the training gain with all of the variables.

Model performance was evaluated using the area under the receiver operating characteristic curve (AUC). In presence-only modeling, the AUC represents the probability that the model fits better or worse than random occurrence (Phillips et al. 2006). An AUC value of 1 indicates a perfect fit of the data, a value of 0.5 indicates no better than random, and values approaching 0 indicate that the model performed worse than random (Phillips et al. 2006).

2.4. Center of suitable habitat analysis

To illustrate the effects of the factors on species distribution, the center of suitable habitat (CSH) for all simulations for each species was calculated using the 'mean_centre' function in the R package 'aspace' (Bui et al. 2012). This function computes the center of gravity from a set of grid points over the entire study area, weighted by the grid point's suitability values. Preliminary analysis on CSHs revealed variability among seasons and potentially an ENSO influence on their distribution (Fig. 3). Therefore, we used an ANCOVA (Whitlock & Schluter 2015) to test the effects of seasonality (a factor) and strength of ENSO (ONI value) and the interaction between seasonality and ONI on CSH in terms of (1) latitude and (2) longitude. Separate ANCOVAs were performed for both species using R v.3.3.2 (R Core Team 2016), and graphs were made using R package 'ggplot2' (Wickham 2016). To test for ANCOVA assumptions of normality and homogeneity of variances, residual plots and quantile-quantile plots were examined and suggested that both assumptions were met.

3. RESULTS

3.1. Model performance and variable contribution

All BUM and BAM simulations of suitable habitat produced AUC > 0.6 (Table 2), suggesting that the MaxEnt model performs well for predicting the distributions of these highly migratory species (Reside et al. 2011). No single environmental factor contributed the most across all simulations. Rather, seasonal and ENSO climate variable contributions demonstrated that the most influential factor towards BUM and BAM spatial distributions varied among chl *a*, SST, and SSH, excluding the BAM summer simulation (Table 2). Overall, chl *a* and SST had the greatest influence for BUM seasonal and ENSO distributions, while chl *a* and SSH had the greatest influence for BAM.
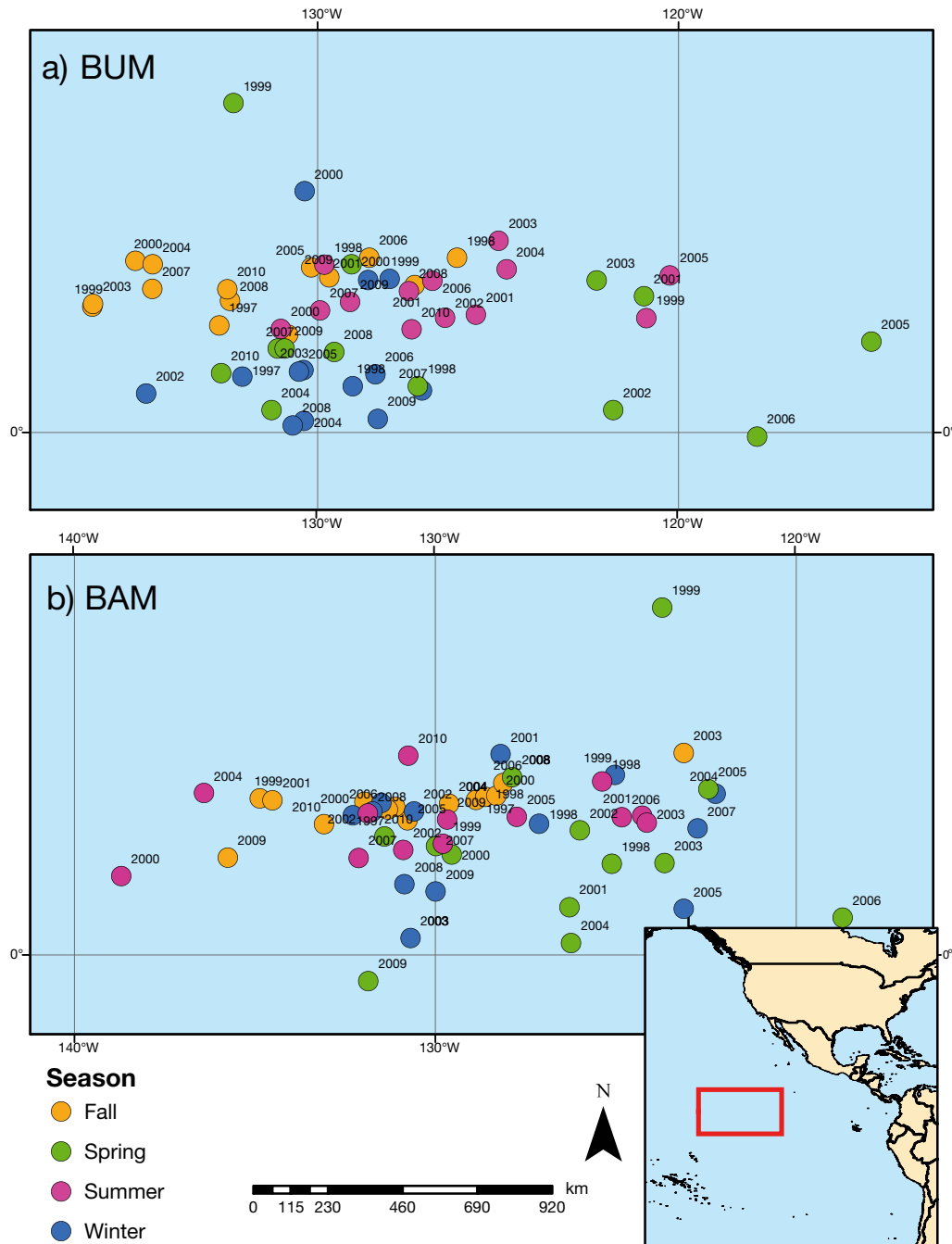
Fig. 3. Seasonal distribution of the center of suitable habitat (CSH) for (a) blue marlin (BUM) and (b) black marlin (BAM) in the eastern Pacific Ocean from 1997–2010 predicted by the yearly MaxEnt simulations

Chl *a* was the most influential variable for BUM winter, summer, Niño Neutral, and La Niña distributions, contributing >38% in model explanatory power (Table 2). In these simulations, SST was the second most influential variable for predicting BUM distributions, excluding winter distributions when SSH had a stronger influence on habitat suitability. Conversely, SST was the most influential variable

for predicting BUM fall and El Niño distributions (>55%), followed by chl *a*. SSH explained 4.9–52.2% of variation in habitat suitability across seasonal and ENSO climate simulations and was the most influential variable for BUM spring distribution. *U* and *V* were minor contributors (<14%) to the distributions of BUM across seasonal and ENSO climate simulations.

Table 2. Variable contributions (%) and area under curve (AUC) of the seasonal and El Niño-Southern Oscillation climate simulation for blue marlin and black marlin. The variables that contribute most to each simulation are highlighted in **bold**

AUC/variable	Winter	Spring	Summer	Fall	Niño Neutral	El Niño	La Niña
Blue marlin							
AUC	0.639	0.673	0.703	0.699	0.647	0.646	0.682
Chl *a* concentration	**38.8**	24.7	**39.2**	14.1	**55.3**	33.3	**49.1**
Sea surface temperature (SST)	13.7	15	24.1	**58.3**	20.7	**55.3**	28.9
Sea surface height (SSH)	24.1	**52.2**	22.9	12.8	18.7	4.9	13
Zonal current (*U*)	13.5	5.7	12.9	12	5.2	6	7.9
Meridional (*V*)	10	2.3	1	2.7	0.1	0.5	1.1
Black marlin							
AUC	0.657	0.680	0.695	0.694	0.667	0.651	0.713
Chl *a* concentration	22.7	**59.7**	25.5	12	37.3	29.3	**45.2**
Sea surface temperature (SST)	15.5	17.8	24.1	**39.3**	11.3	22.2	20.4
Sea surface height (SSH)	**43.5**	20	18.1	27.8	**39.7**	**39.3**	21.1
Zonal current (*U*)	11.1	1.4	**29.8**	19.1	11.3	4.9	13
Meridional (*V*)	7.2	1.1	2.4	1.8	0.4	4.2	0.4

BAM spatial distribution was most influenced by SSH, contributing >39% of model explanatory power for distributions during winter, Niño Neutral, and La Niña (Table 2). Chl *a* followed as the second most influential variable in these distributions as well as in the BAM summer distribution. Conversely, chl *a* was the most influential variable for predicting the distribution of BAM during spring and La Niña conditions, followed by SSH. SST and *U* had a strong influence on fall and summer distributions, respectively, but had less influence on all other seasonal and ENSO climate simulations (Table 2).

3.2. Response to environmental variables

BUM and BAM response plots for each environmental variable demonstrated slight variability among seasons and ENSO states (Fig. 4). Overall, responses to chl *a* showed that both species prefer waters with chl *a* >0.25 mg m^{-3} (Fig. 4). However, this relationship with chl *a* breaks down at low SST (see Section 4). Several simulations demonstrated probability of occurrence to decrease slightly at low chl *a* before plateauing as chl *a* increased. Specifically, BUM preferred higher chl *a* during the boreal winter, summer, and fall. However, in the boreal spring and during all 3 ENSO states, it appeared that their likelihood of inhabiting high chl *a* water diminished slightly. Similar trends were predicted for the BAM response to chl *a*, but the probability of BAM occurrence declined more rapidly during winter and spring.

Additionally, BUM and BAM had similar unimodal responses to SST. For both species, probability of occurrence rapidly increased as SSTs warmed and declined rapidly when SSTs exceeded 26–28°C. This indicates that both species prefer waters in the range of 23–28°C (Fig. 4). BUM and BAM also expressed a bimodal response to SSH, with higher probability of occurrence in low SSH waters (<0.5 cm) and high SSH waters (>1.25 cm). However, both species' spring and summer distributions and BAM Niño Neutral distributions showed low preference for high SSH waters. Excluding BAM summer distributions, *U* and *V* had negligible influences on these species' spatial distributions (Table 2). BUM and BAM were more likely to be present at higher velocities in the east–west (*U*) direction. BUM and BAM responded similarly to *V*, occurring at both negative and positive *V* velocities. However, during the boreal winter, probability of occurrence rapidly decreased with higher velocities for both species but increased for BAM during spring as *V* increased.

3.3. Seasonal variability

Seasonal climate simulations demonstrated shifts in suitable habitat between coastal and oceanic waters in the EPO (Fig. 5). In the winter and spring, suitable habitat for BUM and BAM was closer to the coasts between 20°N and 20°S of the EPO (Fig. 5a,b,e,f). Regions with high probability of occurrence (>50%) were the Costa Rica Dome and coastal stretches of Colombia, Ecuador, and Peru in the northern regions of the Peru Current (Fig. 5). The Eastern Pacific Warm Pool region, however, was highly unsuitable and decreased in suitability from
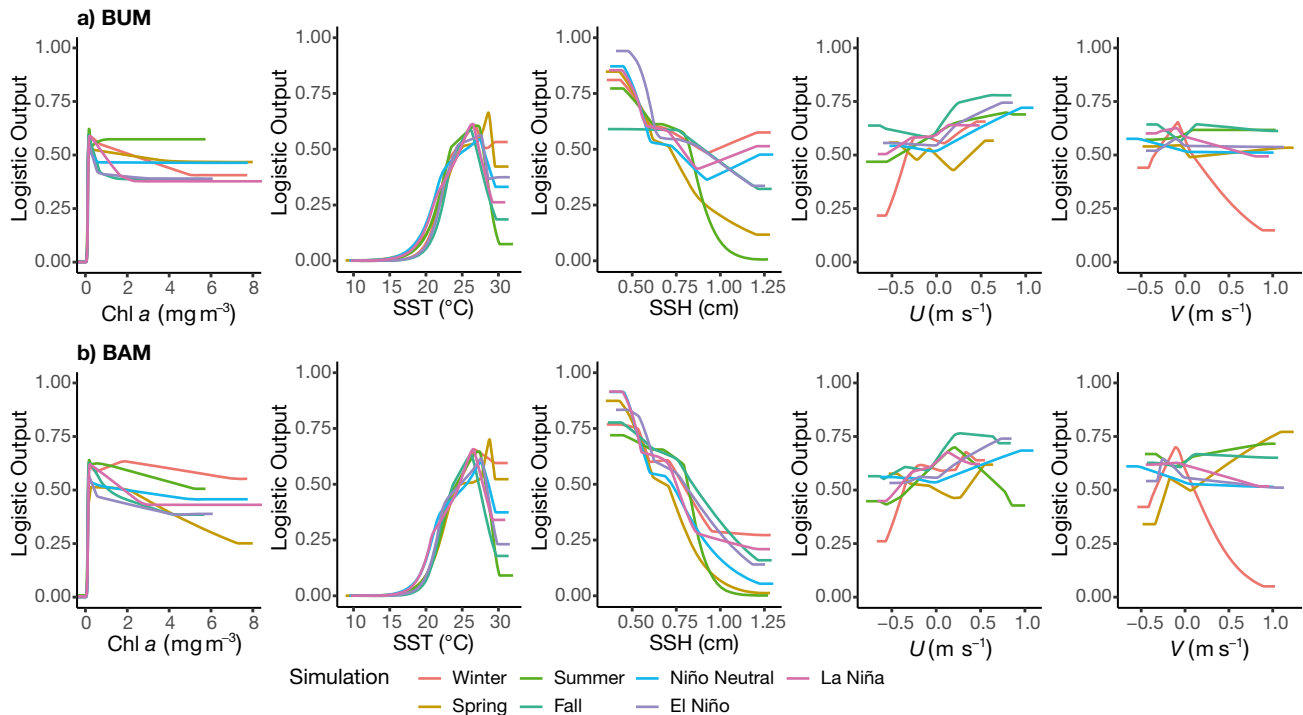
Fig. 4. Probability of presence of (a) blue marlin (BUM) and (b) black marlin (BAM) as a response to chlorophyll *a* (chl *a*), sea surface temperature (SST), sea surface height (SSH), zonal current (*U*), and meridional current (*V*) in the eastern Pacific Ocean under each season climate simulation (winter, spring, summer, fall) and El Niño-Southern Oscillation climate simulation (El Niño, La Niña, Niño Neutral)

the winter to the fall season for both species (Fig. 5). Moving westward, suitable waters appeared to extend into the Central Pacific Ocean (CPO; 180° W); however, suitability steadily diminished further from the coast and began to narrow between 10° N and 10° S. Simulations also predicted suitable habitat for both species to occur around the French Polynesian Islands during the boreal winter and fall. Regarding BUM, the waters south of the Equatorial Cold Tongue and west of Hawaii appeared to be more suitable during the winter (Fig. 5a). In the spring, distribution of suitable habitat became more coastal, with regions of highly suitable habitat only extending as far west as 120 and 110° W for BUM and BAM, respectively (Fig. 5b,f).

In the boreal summer and fall, suitable habitat shifted for both species to oceanic waters along the equator between 10° N and 10° S (Fig. 5c,d,g,h). During these months, high suitability ran along the front of the Equatorial Cold Tongue, extending out to 160° W in the waters of the North Equatorial Countercurrent and the Southern Equatorial Current. Although the spatial distribution of suitable habitat extended to waters offshore, the highest probability of occurrence was in waters off the coast of Colombia and Panama, and off the southern tip of Baja Califor-

nia, Mexico. During the boreal fall, suitable habitat for both species appeared to occur around the Hawaiian Islands and, for BAM, along the US coast as far north as the southern portion of the California Current.

3.4. ENSO variability

Between September 1997 and December 2010, considerable variability was observed among ENSO states (Niño Neutral, El Niño, and La Niña) (Fig. 6). When the system was Niño Neutral, the extent of suitable BUM and BAM habitat ranged westward from the coasts of Central and South America between 20° N and 20° S but narrowed latitudinally towards the CPO (Fig. 6a,d). Highly suitable regions were in and south of the Gulf of California, near the Costa Rica Dome, within the waters of the North Equatorial Countercurrent and South Equatorial Current adjacent to the Equatorial Cold Tongue, and north of the Peru Current. During El Niño conditions, both species moved to higher latitudes in both hemispheres, as the equatorial EPO became unsuitable (Fig. 6b,e). These shifts to higher latitudes were seen most prominently when El Niños
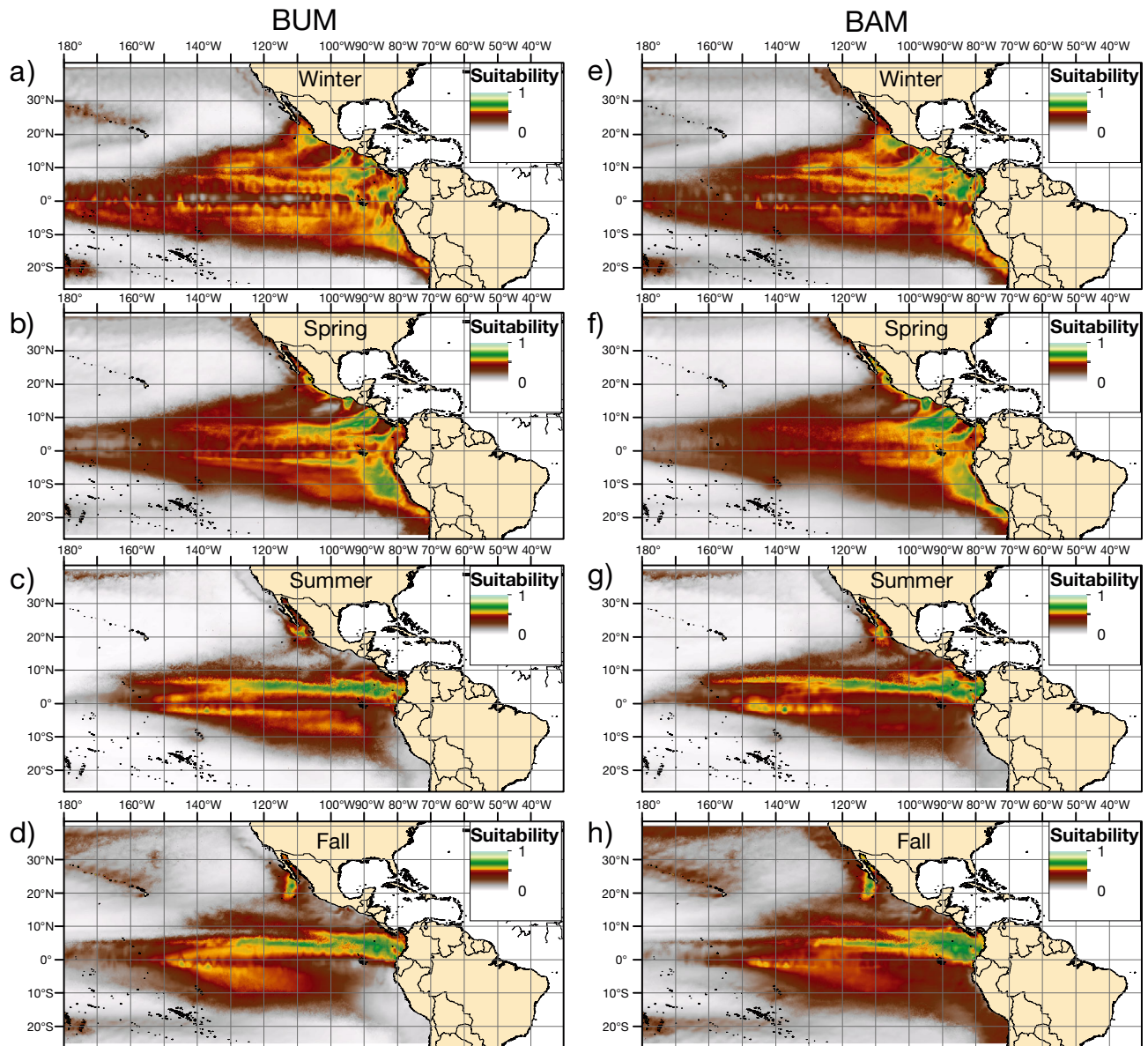
Fig. 5. Seasonal distribution of habitat suitability for (a–d) blue marlin (BUM) and (e–h) black marlin (BAM) in the eastern Pacific Ocean predicted by the seasonal climate MaxEnt simulations: (a,e) winter, (b,f) spring, (c,g) summer, and (d,h) fall. Color scale represents the probability of BUM and BAM presence

were 'strong,' such as in the Fall of 1997 (Fig. 7b,e). During this El Niño, suitable habitat for both species was found between 10 and 30°N in the waters of the North Equatorial Current and around the Hawaiian Islands, as well as between 0 and 20°S in the waters of the South Equatorial Current and around the islands of French Polynesia. When the system was in a La Niña state, suitable regions for BUM and BAM appeared in equatorial waters between 10°N and 10°S and in northern waters (>30°N) offshore of the USA (Fig. 6c,f). Differing from El Niño distributions, the waters of the South

Equatorial Current and northern Peru Current became unsuitable (Fig. 6c,f). This shift in spatial distribution is again more pronounced during a 'strong' La Niña (Fig. 7c,f), although each species' suitable habitat differs within this range. During a 'strong' La Niña, BUM suitable habitat extended further offshore to 120°W (Fig. 7c), whereas BAM probabilities of occurrence were highest in waters closer to the coast off southern Central America and northern South America (Fig. 7f). All 3 ENSO climate simulations commonly predicted the Eastern Pacific Warm Pool to be an unsuitable region.
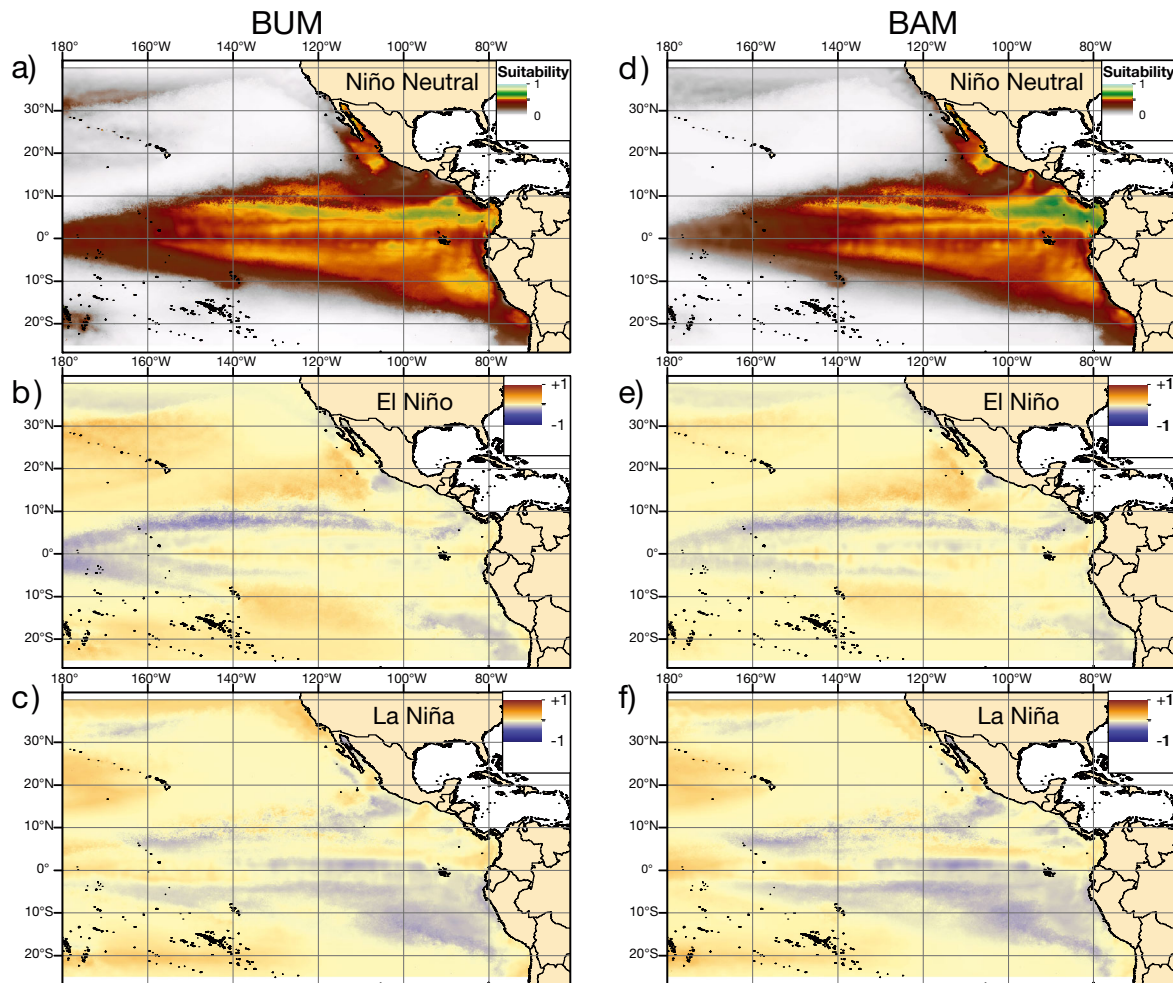
Fig. 6. El Niño-Southern Oscillation (ENSO) distribution of habitat suitability for (a–c) blue marlin (BUM) and (d–f) black marlin (BAM) in the eastern Pacific Ocean predicted by the ENSO climate MaxEnt simulations. Color scale represents the probability of presence of BUM and BAM during (a,d) Niño Neutral, (b,e) El Niño and (c,f) La Niña conditions

3.5. Center of suitable habitat

The effects of season and ENSO strength on the latitudinal and longitudinal position of the CSH differed between BUM and BAM (Fig. 8, Table 3). Despite the shifts in suitable habitat observed from both species' seasonal climate simulations, ANCOVA results indicated a longitudinal seasonal shift in BUM suitable habitat in the EPO (Table 3). The BUM CSH significantly differed between the spring and fall months, occupying waters eastward in the spring and waters farther west in the fall (Fig. 8, Table 3). CSHs for fall and summer also significantly differed from each other, with values for summer being near spring CSH distributions (Fig. 8, Table 3). However, winter and summer CSHs did not differ from each other (Table 3). Trend lines showed that during the winter and summer, the longitudinal position of the BUM CSH was most likely between 125 and 132° W, which falls within the spring and fall extremes (Fig. 8), suggesting that winter and summer act as the transitional phases between shifting from coastal to oceanic waters. BAM CSH also exhibited a seasonal shift in longitudinal position as spring significantly differed from the fall (Fig. 8, Table 3). BAM trendlines showed longitudinal position to be westward during the fall and summer, and eastward during the spring. However, during the winter, BAM CSH encompassed the entire longitudinal distribution (Fig. 8). Results indicated that the strength of ENSO events does not significantly affect the longitudinal position for either species (Fig. 8).

Latitudinal CSH distributions also differed between BUM and BAM (Fig. 8, Table 3). Similar to longitudinal analyses, BUM fall and spring CSHs significantly differed from one another and appeared to act as 2 extremes. Fall CSHs were distributed farther
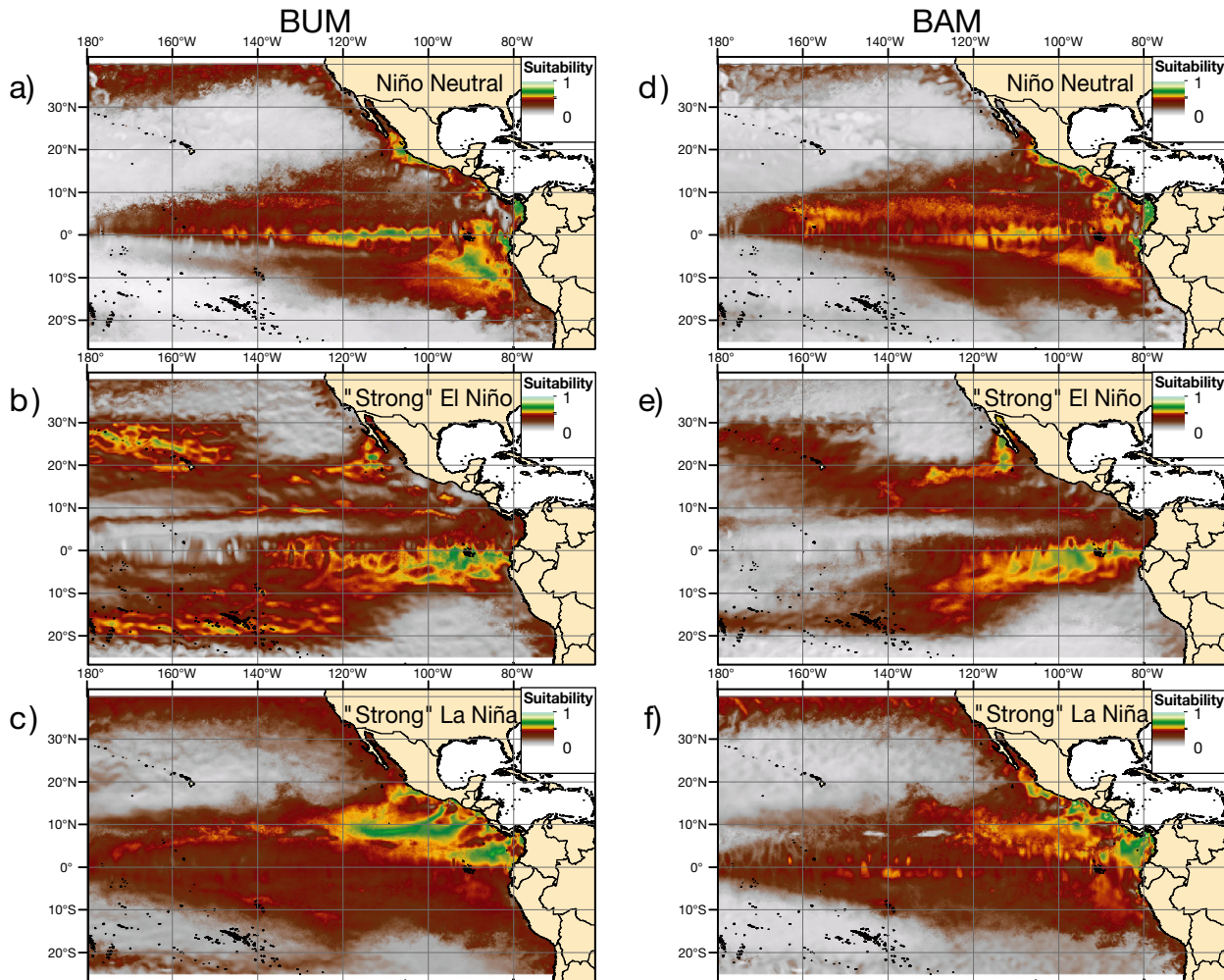
Fig. 7. El Niño-Southern Oscillation distribution of habitat suitability for (a–c) blue marlin (BUM) and (d–f) black marlin (BAM) in the eastern Pacific Ocean predicted by yearly MaxEnt simulations. El Niño and La Niña extremes according to Oceanic Niño Index (ONI) values between September 1997 and December 2010. Color scale represents the probability of BUM and BAM presence during (a,d) Niño Neutral spring 2003, (b,e) El Niño fall 1997, and (c,f) La Niña winter 1999–2000

north, above 4°N, whereas in spring and winter, CSH was in the southernmost latitudes (Fig. 8). Although summer and winter did not statistically differ from one another (Table 3), both seasons' CSH latitudinal positions fell between spring and fall, suggesting again that these seasons are transitional phases (Fig. 8). BUM analysis indicated an apparent interaction between ONI and spring latitudinal position. However, this interaction was the result of a single influential point in spring 1999, when CSH latitudinal position reached 9°N, and was not significant when this point was removed. BAM latitudinal position did not exhibit a seasonal shift, as neither of the seasons significantly differed from each other (Fig. 8, Table 3). There was no significant relationship between the strength of ENSO and the latitudinal position of either BUM or BAM CSHs (Table 3).

4. DISCUSSION

This species distribution model (SDM), using incidental catch data from the EPO tuna purse-seine fisheries and remotely sensed environmental data, provides a unique opportunity to identify the habitat preferences and effects a dynamic environment can have on the spatial distribution of BUM and BAM. Our results demonstrated that BUM and BAM are highly migratory species, shifting seasonally between oceanic and coastal waters; however, their distributions are driven by different factors. The primary drivers of the spatial distribution of BUM were chl a concentrations >0.25 mg m^{-3} and warm SST (23–28°C) waters. BAM preferred similar chl a concentrations (>0.25 mg m^{-3}); however, low SSH (0–0.5 cm) waters had a larger influence on their distribu-
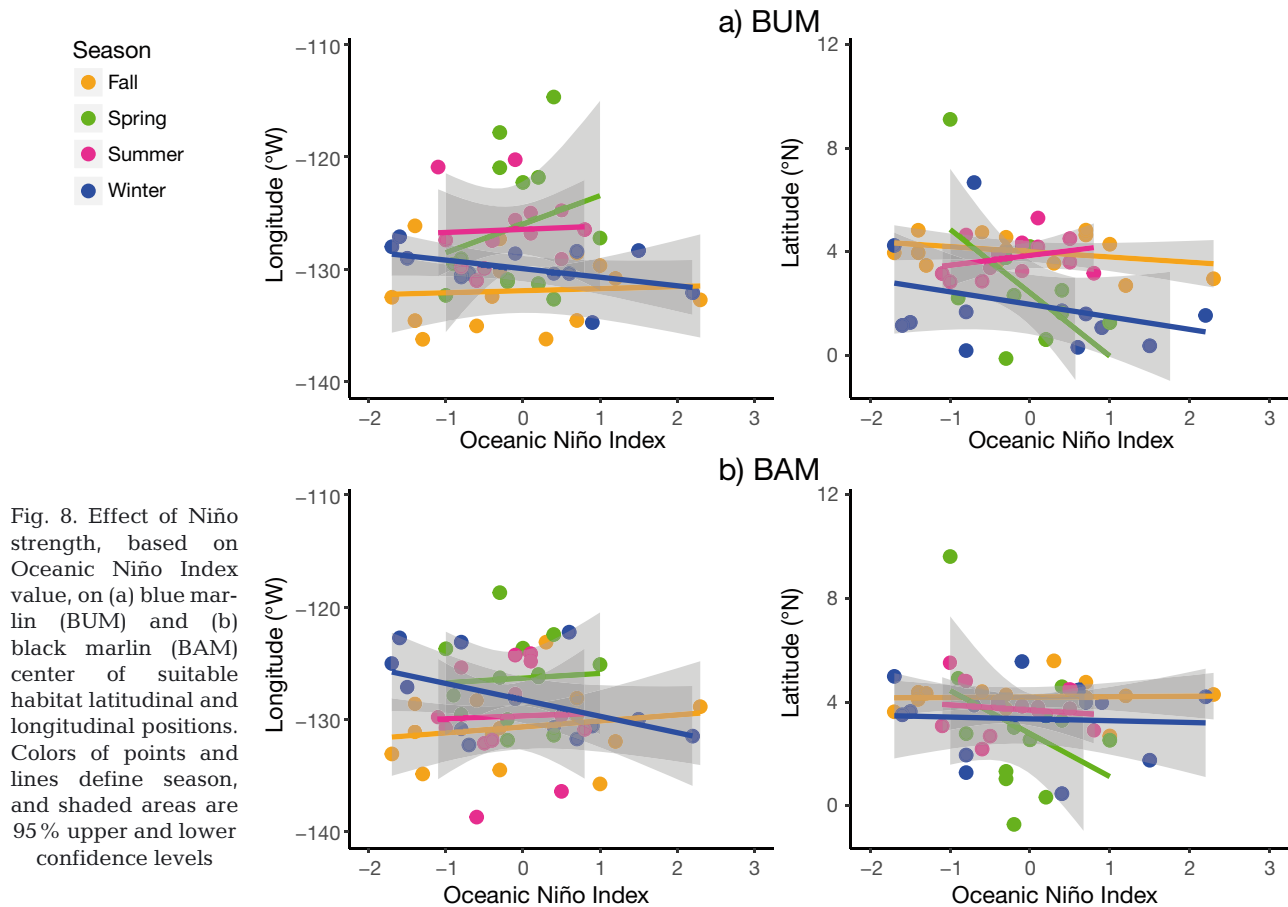
Fig. 8. Effect of Niño strength, based on Oceanic Niño Index value, on (a) blue marlin (BUM) and (b) black marlin (BAM) center of suitable habitat latitudinal and longitudinal positions. Colors of points and lines define season, and shaded areas are 95% upper and lower confidence levels

Table 3. ANCOVA of the effects of seasonality and strength of El Niño-Southern Oscillation (ENSO) and the interaction between seasonality and ENSO on the latitude and longitude of the center of suitable habitat. Oceanic Niño Index (ONI) values were used to represent strength of ENSO. Asterisks indicate significance: *$p < 0.10$, **$p < 0.05$, ***$p < 0.01$

| | ——— Longitude ——— | | | | ——— Latitude ——— | | |
Term	Parameter estimate	SE	t	Term	Parameter estimate	SE	t
Blue marlin							
Intercept	−131.91232	1.06840	−12 3.467***	Intercept	4.0068	0.3914	10.237***
ONI	0.18410	0.94224	0.195	ONI	−0.2008	0.3452	−0.582
Spring	5.92720	1.55483	3.812***	Spring	−1.5822	0.5696	−2.778**
Summer	5.46725	1.58501	3.449**	Summer	−0.1422	0.5807	−0.245
Winter	1.96419	1.53880	1.276	Winter	−2.0295	0.5638	−3.600***
ONI:Spring	2.35704	2.21897	1.062	ONI:Spring	−2.2443	0.8129	−2.761**
ONI:Summer	0.09604	2.14483	0.045	ONI:Summer	0.5774	0.7858	0.735
ONI:Winter	−0.94578	1.32468	−0.714	ONI:Winter	−0.2822	0.4853	−0.582
Overall model results: $F = 3.062$; $p < 0.05$; $r^2 = 0.2173$				Overall model results: $F = 4.326$; $p < 0.001$; $r^2 = 0.3092$			
Black marlin							
Intercept	−130.6737	1.0422	−125.385***	Intercept	4.19155	0.41891	10.006***
ONI	0.5334	0.9191	0.580	ONI	0.01580	0.36944	0.043
Spring	4.3457	1.5167	2.865**	Spring	−1.40769	0.60963	−2.309*
Summer	0.9821	1.5461	0.635	Summer	−0.49988	0.62146	−0.804
Winter	2.4084	1.5010	1.604	Winter	−0.84058	0.60334	−1.393
ONI:Spring	−0.1171	2.1645	−0.054	ONI:Spring	−1.67766	0.87003	−1.928
ONI:Summer	−0.2781	2.0922	−0.133	ONI:Summer	−0.21377	0.84096	−0.254
ONI:Winter	−1.9943	1.2922	−1.543	ONI:Winter	−0.08583	0.51939	−0.165
Overall model results: $F = 1.795$; $p > 0.1$; $r^2 = 0.09663$				Overall model results: $F = 1.289$; $p > 0.1$; $r^2 = 0.03749$			

tions compared to BUM. Our results are consistent with previous studies on the seasonal (Chiang et al. 2015, Hill et al. 2016, Carlisle et al. 2017) and ENSO (Hill et al. 2016, Carlisle et al. 2017) variability in spatial distribution of BUM and BAM in the Pacific Ocean.

4.1. Influence of environmental factors

Previous studies have acknowledged that SST (Holland et al. 1990, Graves et al. 2002, Goodyear et al. 2006, Su et al. 2008, Carlisle et al. 2017) or dissolved oxygen (Prince & Goodyear 2006, Carlisle et al. 2017) are generally the most influential environmental factors on the distributions of both species. However, these studies did not consider chl *a* to have a large influence on either species' distribution. This discrepancy in chl *a* influence between our results and these studies may be due to the limitations in spatial distribution of effort and resolution of environmental variables. Previously, data were obtained principally from BUM and BAM in oceanic waters where chl *a* has less signal and is less variable than in more coastal and highly productive environments. Thus, the power to identify an effect of chl *a* on BUM and BAM distributions was likely low. In contrast, the tuna purse-seine fishery obtains data from both nearshore and oceanic waters. Therefore, the BUM and BAM bycatch from this fishery was likely to be representative of their distributions in the entire EPO, which allowed us to contextualize previous results. Our simulations indicated that chl *a* contributed largely in determining BUM and BAM spatial distributions (Table 2), suggesting that both species choose to inhabit productive waters in the EPO. Brill & Lutcavage (2001) observed that chl *a* may be an indirect measure of forage abundance for large pelagic fishes. From our simulations, both species exhibited shifts in spatial distribution in relation to shifts in upwelling. For example, BUM and BAM simulations predicted high suitability in the north Peru Current, Costa Rica Dome, and southern portion of the California Current during the boreal winter and spring when the trade winds intensify and create favorable upwelling conditions in the coastal waters (Amador et al. 2006, Pennington et al. 2006). These shifts to upwelling regions fit with BUM and BAM high preference for low SSH waters (Fig. 4). This is particularly evident for BAM, as SSH was a highly influential predictor of suitable habitat in our results as well as in previous studies (Hill et al. 2016). Although BUM and BAM also indicated preferences for

high SSH (Fig. 4), this preference is possibly due to their association with fish aggregating devices, which attract prey and float towards high SSH, downwelling waters (Witherington 2002, Shimose et al. 2006). Suitability values were also rather low in the Eastern Pacific Warm Pool during the boreal winter and spring as the waters in this region are nutrient poor due to high stratification (Pennington et al. 2006). However, the BUM and BAM relationship with chl *a* breaks down in high chl *a*, low SST waters. For example, the waters in the California Current, off the coasts of California and northwest Mexico, are highly productive due to coastal upwelling (Pennington et al. 2006), but these waters are too cold (15–20°C) (Huyer 1983) for BUM and BAM preference.

BUM and BAM preferred warm tropical waters (23–28°C) (Fig. 4). These results are consistent with tagging studies (Chiang et al. 2015, Carlisle et al. 2017) and fishery-dependent studies (Howard & Ueyanagi 1965, Su et al. 2008) that documented BUM and BAM seasonal migrations between higher latitudes in the summer and lower latitudes in the winter. Due to their preferences for warm SST, both species exhibit seasonal migrations, which may be related to spawning and foraging (Howard & Ueyanagi 1965, Shimose et al. 2006, 2008, 2012, Domeier & Speare 2012). In the northern waters (10–30° N) of the western Pacific Ocean (WPO) and CPO, BUM are usually found in high densities from May through October (Howard & Ueyanagi 1965). Also in this region, female BUM undertake large foraging movements north after spawning and move to more productive waters to feed (Shimose et al. 2012). In contrast, the south/southeastern waters (south of 10° S) of the EPO generally have higher densities of BUM from November through March, with fish often moving across the equator, between 160° E and 170° W, towards French Polynesia (Howard & Ueyanagi 1965). This northwest–southeast migration in the Pacific Ocean likely indicates shifts of their habitats in accordance with the seasonal change of rising SSTs progressing from west to east, and is also thought to be related to spawning (Howard & Ueyanagi 1965). These known migrations are consistent with our results, as suitable habitats in fall and winter were observed around the Hawaiian Islands and French Polynesian Islands, respectively (Fig. 5). Each of these locations is recognized as a BUM spawning region during its respective season (Howard & Ueyanagi 1965, Hopper 1990). Currently, the only known spawning regions for BAM are in the WPO in the waters of the Coral Sea and the south China Sea

(Nakamura 1941, Domeier & Speare 2012). There-fore, seasonal migrations for BAM in the EPO may be related to foraging, considering our observation that chl *a* and SSH were the most influential factors affecting their distribution.

4.2. Seasonal distribution patterns

Our findings of BUM and BAM seasonal distribution shifts (Fig. 5) were similar to those in Acosta-Pachón et al. (2017) on the habitat preferences of striped marlin *Kajikia audax* in the EPO. Using SDMs, they found that the most suitable habitat for striped marlin was in the highly productive warm waters of the EPO, and that striped marlin distributions shifted seasonally between coastal waters in the boreal winter and oceanic waters in the boreal summer. The Inter-Tropical Convergence Zone (ITCZ) reaches its southernmost position, 5.3°S, during the boreal winter and much of the spring (Donohoe et al. 2013). During this time, the northeasterly trade winds intensify and the Tehuantepec, Papagayo, and Panama Jets strengthen (Amador et al. 2006). As a result, surface waters are advected westward, allowing deep nutrient-rich waters to be upwelled to the surface, particularly in more coastal regions, such as the Costa Rica Dome. BUM and BAM preferences for these productive waters were consistent with our seasonal climate simulations and ANCOVA, which showed suitable habitats to be more coastal in the boreal winter and spring (Figs. 5 & 8). In late fall and throughout winter, the Tehuantepec and Papagayo Jets produce both cyclonic and anticyclonic eddies in the region off Guatemala (Willett et al. 2006). These eddies significantly affect the distribution of highly migratory species (Seki et al. 2002, Kobayashi et al. 2008, Godø et al. 2012, Woodworth et al. 2012). These eddies are a retention mechanism for planktonic organisms, eggs, and larvae, which are sources of food for first-order consumers in the food chain (Ehrhardt & Fitchett 2006). As the eddies drift into the CPO, the BUM and BAM suitable habitat extends within them.

In the winter and spring, preferred habitat was found in the northern regions of the Peru Current (Fig. 5b,f). This region experiences strong seasonal upwelling with its highest levels of chl *a* and primary production occurring in the boreal winter (Kessler 2006, Pennington et al. 2006). In addition, drifting warm water from the equator may rest above upwelled cool waters, forming ideal conditions for BUM and BAM (Acosta-Pachón et al. 2017).

In the boreal summer and fall months, the ITCZ shifts to more northern latitudes, 7.2°N, weakening the upwelling winds and eddies that peak in the boreal winter and spring in the EPO (Pennington et al. 2006, Donohoe et al. 2013). As a result, waters that were favorable for BUM and BAM in the winter and spring (Costa Rica Dome, northern Peru Current, southern California Current) became unsuitable for both species. BUM and BAM distributions shifted to the open ocean along the front of the equatorial cold tongue (Fig. 5c,d,g,h). The cold tongue, a highly productive open oceanic upwelling region between the equator and 10°N, experiences moderate seasonal variability. Its coldest and most productive period is September, when upwelling is strongest (Pennington et al. 2006). In the summer and fall, phytoplankton and zooplankton biomass are maximal (Fernández-Álamo & Färber-Lorda 2006, Pennington et al. 2006). This biomass attracts smaller fish and thus creates areas with high prey concentration for BUM and BAM. The BUM and BAM distribution along the cold tongue are consistent with the finding of Olson et al. (1994) that billfish tend to aggregate along oceanic fronts (such as temperature fronts), that may be areas of increased productivity and relatively high prey abundance. BUM and BAM have been observed to dive into deep, colder waters during the day to forage (Holland et al. 1990, Block et al. 1992, Goodyear et al. 2008, Chiang et al. 2015). BUM and BAM cranial endothermy, counter-current heat exchangers, and thermogenic tissue allow for heat to be generated and retained in the brain and eye regions (Fritsches et al. 2003). This allows for better visual acuity in cold, deep waters while diving, which may be used for similar purposes if they forage in the cold surface waters of the Equatorial Cold Tongue.

4.3. Impact of ENSO on distribution patterns

The unique oceanography of the EPO is heavily influenced by ENSO, which is arguably the most significant source of temporal variability in the tropical waters of the EPO (Pennington et al. 2006). The El Niño events are triggered by weakening or reversal of the coastal trade winds in the WPO in response to the atmospheric pressure change across the Pacific Ocean. As a result, El Niño weakens the North Equatorial and South Equatorial Currents and deepens the thermocline and nutricline, thus suppressing primary production (Pennington et al. 2006). During El Niño, diminished primary production and the deepened thermocline have detrimental effects on sur-

vival and reproduction, and affect the distribution of higher trophic level organisms (Ballance et al. 2006). In our study, BUM and BAM habitat suitability diminished within equatorial and coastal upwelling areas during El Niño (Fig. 6b,e). Although upwelling continues in the Cold Tongue, the Costa Rica Dome, and off Peru, the upwelled waters come from the warm and nutrient-poor upper layer (Pennington et al. 2006) and consistently diminish the productivity in these areas. As the westward-moving North and South Equatorial Currents weaken or reverse during an El Niño, the North Equatorial Countercurrent strengthens and advects warm waters of the western CPO into the EPO (Kessler 2006). Therefore, the EPO currents that are normally just north of the equator move northward to 8–10°N and those starting around 8–10°N move to the east-northeast (Hinton 2015). In the Southern Hemisphere, the current structure shows similar patterns, but in the west-southwest direction (Hinton 2015). This likely explains why BUM and BAM suitable habitats branched off into 10–30°N and 0–20°S waters during El Niño (Figs. 6b,e & 7b,e). It is unknown what effect these current anomalies have on primary production, but the anomalies do advect warm waters to higher latitudes where these waters may normally be too cold for BUM or BAM.

During La Niña states, the BUM and BAM habitat suitability increased close to southern Central America near the equator as well as in northern regions off the USA (Fig. 6c,f). La Niña events are associated with a strengthened westward flow of the Southern Equatorial Current which leads to increased equatorial upwelling, shoaling of the thermocline and nutricline, and an overall extension of the equatorial cold tongue from the EPO into the CPO (Pennington et al. 2006, Carlisle et al. 2017). Therefore, these productive cold waters create oceanic fronts that extend westward and in which marlins aggregate (Olson et al. 1994). Considering BUM distributions are strongly influenced by chl *a* and SST, these oceanic fronts can be highly suitable waters for these fish as they will cross over into the colder waters to forage. Carlisle et al. (2017) observed BUM, tagged with pop-up satellite archival tags, near this westward extension of the cold tongue, yet the cold tongue appeared to act as a barrier that they did not cross. This extended cold tongue was also a barrier in our results, as BUM suitable habitat during a 'strong' La Nina was located just north of the cold tongue and did not cross to the southern hemisphere (Fig. 7c). BAM distribution of suitable habitat did not extend along the front of the Equatorial Cold Tongue. Rather, suitable habitat

occurred eastward in the waters off southern Central America and northern South America. BAM preference for low SSH waters (Fig. 4b), and the stronger influence of SSH on their suitable habitat compared to BUM (Table 2) may be a result of BAM staying closer to shore as amplified upwelling may occur in these waters during 'strong' La Niña events. From the 14 yr of occurrence data, we were able to capture the effects of each El Niño and La Niña on BUM and BAM spatial distributions. Our findings suggest that the strength of ENSO events did not significantly influence marlin distribution in the EPO. ANCOVA on CSH (Fig. 8) revealed that as El Niño and La Niña events get 'stronger' (higher or lower ONI values, respectively), marlin suitable habitats did not get displaced to a great extent, and seasonal differences in CSHs were typically larger than the apparent effects of ONI (Fig. 8). However, this is not to say that certain El Niño or La Niña events did not greatly influence their latitudinal or longitudinal positions. For example, during the 1998–2000 La Niña, both species' spring 1999 CSH were displaced to latitudes above 8°N, which was 3° north of any other CSH latitudes (Fig. 3). Longitudinally, BUM and BAM suitable habitat had a respective net displacement of 10° and 14° eastward during the 2004–2005 El Niño. Additionally, there were instances of both species' suitable habitat moving further west (past 135°W) during the 1998–2000 La Niña (Fig. 3). Su et al. (2008) also found an apparent shift in BUM distributions during ENSO, most notably an eastward movement along the equator during the 1997–1998 El Niño. Since our data began in September 1997, we were unable to quantify the full BUM and BAM displacement during the 1997–1998 El Niño; however, both species' CSH moved eastward as the El Niño ended. Better understanding of these anomalies in suitable habitat distribution during ENSO has important implications for the population dynamics and migration behavior of these species, especially if it hinders important feeding or reproductive migrations (Carlisle et al. 2017).

5. IMPLICATIONS FOR FISHERIES MANAGEMENT AND FUTURE DIRECTIONS

Determining the habitat suitability and distribution patterns of our marine resources is necessary for generating effective fishery management strategies. Shifts in spatial distribution have been observed for many marine species in response to the gradual rise in global SST, which can have effects on ecosystem

functionality and can cause economic strain on fishing ports and communities (Hazen et al. 2013, Pinsky et al. 2013, Pershing et al. 2015, Kleisner et al. 2017). Therefore, it is critical to understand how environmental conditions, such as SST, influence current and future distributions of resources in the ocean. The MaxEnt modeling framework applied in our study identified these relationships for BUM and BAM across seasons, which can provide useful information for stock assessment and the development of effective management for both species in the context of climate change (Wang et al. 2018).

Previous studies suggested that time-area closures are the best approach to manage the fisheries and reduce bycatch of billfish (Goodyear 1999). However, static approaches, such as these time-area closures, may be less effective in managing highly mobile organisms, which respond rapidly to shifting ocean conditions (Hyrenbach et al. 2006). A dynamic ocean management framework that uses near real-time data to support management responses that can change in space and time, at scales relevant for animal movement and human uses, may be more suited in managing these species (Maxwell et al. 2012, 2015, Hobday et al. 2013, Lewison et al. 2015). Because the oceans are in constant flux, the ability to accurately describe a species' habitat in near real-time would greatly increase management efficiency, by maintaining target catch within quota limits, reducing bycatch, and effectively assessing the amount of area to be closed (Lewison et al. 2015, Maxwell et al. 2015). If seasonal shifts in the suitable habitats of BUM and BAM can be determined accurately and provided to regulatory or resource management agencies, specific strategies can be formulated accordingly to manage these species in different seasons throughout the year.

Ecological information can be difficult to determine for highly migratory species, due to their naturally low population densities and patchy distributions (Hill et al. 2016), which may result in low spatial and temporal resolution data (Hobday & Evans 2013). While studies using data from tags (Squire & Nielsen 1983, Holland et al. 1990, Prince & Goodyear 2006, Chiang et al. 2015, Hoolihan et al. 2015, Carlisle et al. 2017) and industrialized fisheries, such as longline fisheries (Su et al. 2008, 2011, Shimose et al. 2010), provided useful information on species movements and habitat use, tagging studies can be expensive and spatiotemporally limited (Hobday & Evans 2013), and industrial fisheries do not cover all ecologically important species. Here, we used fine-scale BUM and BAM bycatch data from the EPO tuna purse-seine fishery to demonstrate the potential contribution of SDMs of highly migratory species to fisheries management. Future work should compare our SDM results, built upon remotely sensed datasets, with those built upon near real-time data assimilation ocean circulation models, as they avoid limitations of satellite remotely sensed data (e.g. cloud cover, variable resolution) and can potentially lead to superior predictive performance (Scales et al. 2017). Given the success of our models for 2 highly migratory species, methods presented here can be applied to other mobile marine species that may be affected by a changing climate.

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