

Seasonal and diel habitat use of blue marlin *Makaira nigricans* in the North Atlantic Ocean

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Knowledge of blue marlin, *Makaira nigricans*, movement patterns across a range of spatiotemporal scales is important for understanding the ecology of this epipelagic fish, informing responsible management strategies, and understanding the potential impacts of a changing ocean climate to the species. To gain insight into movement patterns, we analyzed data from 66 blue marlin satellite-tagged between 2001 and 2021 throughout the North Atlantic. We recorded migrations connecting west and east Atlantic tagging locations, as well as long-term residency within small sub-regions. Blue marlin showed a pattern of latitudinal migration, occupying lower latitudes during cooler months and higher latitudes in warmer months. Diving data indicate blue marlin primarily inhabited a shallow vertical habitat with deeper diving associated with higher sea surface temperatures and dissolved oxygen content. Consistent patterns in diel vertical habitat use support the hypothesis that these fish are visual hunters, diving deeper during the day, as well as dawn, dusk, and full moon periods. The wide-ranging movements of blue marlin indicate that traditional spatial management measures, such as static marine reserves, are unlikely to be effective in reducing the fishing mortality of this species. Longer tag deployment durations are required to delineate its annual and multi-annual migratory cycle.

Keywords: billfish, diel vertical movement, KUDs, migration, satellite telemetry.

Introduction

Over the past two decades, technological advances have transformed our ability to investigate aquatic animal behaviour and movement at a range of spatiotemporal scales (Block *et al.*, 2011; Hussey *et al.*, 2015). The use of satellite tags, such as pop-up satellite archival tags (PSATs), for instance, has enabled us to document vertical movement patterns at hourly scales (e.g. Merten *et al.*, 2014; Andrzejczek *et al.*, 2021), identify seasonal patterns in habitat use (e.g. Neilson *et al.*, 2009; Coffey *et al.*, 2017), and inform species distribution models across the entire global distribution of a species (e.g. Erauskin-Extramiana *et al.*, 2019; Dale *et al.*, 2022). This comprehensive understanding is important in distinguishing between the processes driving movement at different scales, especially in the context of understanding interactions between animals and anthropogenic activities (e.g. fishing) and the impact of a changing ocean.

The blue marlin, *Makaira nigricans*, is a highly migratory fish distributed circumglobally in primarily tropical and subtropical waters. It is one of the largest of the billfish species (maximum size >700 kg; Hill *et al.*, 1989), and highly adapted to long-distance travel and a pelagic mode of life (Long 1989, Block *et al.*, 1992). Genetic studies indicate significant divergence between Atlantic and Pacific populations (Finnerty & Block, 1992); however, no evidence of population structuring has been found within these oceans (Graves & McDowell, 2015; Williams *et al.*, 2020). Blue marlin are one of the most important targets of lucrative recreational sports fisheries that are based on catch-and-release of large pelagic fish species (Martinez-Escauriaza *et al.*, 2021), providing substantial economic input into the tourism sector in regions where game fishing is popular (Gentner, 2016). Though this species is not

directly targeted by commercial fisheries, significant bycatch from longline fisheries targeting tunas and swordfish has likely underpinned global declines in stock abundance (Mourato *et al.*, 2018), resulting in the species classification as “Vulnerable” on the IUCN Red List (Collette *et al.*, 2011). To inform strategies to reduce the fishing mortality of blue marlin, such as reducing its spatial and temporal overlap with commercial fleets, we need knowledge of its horizontal and vertical movement patterns across a range of spatiotemporal scales.

Satellite and conventional tagging in the Atlantic Ocean have revealed individual variation in the movements of blue marlin. Studies investigating horizontal movements have revealed patterns ranging from extensive cross-ocean migrations to high residency within subregions of the blue marlin range. For example, conventional tagging revealed the longest recorded single individual migration of ~15 000 km from the coastal waters of Delaware off the east coast of the USA to Mauritius, an island in the Indian Ocean (Orbesen *et al.*, 2003; Ortiz *et al.*, 2003). Alternatively, satellite tagging in the Gulf of Mexico recorded a range primarily restricted to the region (mean displacement distance = 588 km; Kraus *et al.*, 2011). Though predominately found in the epipelagic zone of the ocean (i.e. the top 200 m; Braun *et al.*, 2015), blue marlin are cranial endotherms, having modified extraocular muscle into a unique brain and eye heater (Block, 1986; Block & Franzini-Armstrong, 1988). This enables blue marlin and other billfishes to maintain elevated eye and brain temperatures when foraging in deeper, cooler waters (Carey, 1982; Fritsches *et al.*, 2003) and occasionally reach depths below 800 m (Goodyear *et al.*, 2008). Maximum depth may also increase with size class, reflecting ontogenetic differences in foraging behaviour and physiology, as observed in black marlin, *Istiompax indica*

Received: 17 August 2022; Revised: 12 January 2023; Accepted: 2 February 2023

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Table 1. Deployment summaries by region for PSATs deployed on blue marlin *M. nigricans* in the North Atlantic Ocean. See Supplementary Table 1 for deployment metadata from each individual.

Deployment region	Tags deployed	Mean deployment length (range) (days)	Mean distance deploy to pop-up (range) (km)	Estimated mass (kg)
Bahamas	11	74.2 ± 77.2 (5–203)	915.2 ± 1086.1 (14.8–3765.1)	96.6 ± 55.2
Bermuda	26	132.5 ± 103.0 (3–244)	2454.0 ± 2058.9 (66.7–7715.4)	119.5 ± 62.9
British Virgin Islands	1	180.0	2428	91.0
Canary Islands	6	63.7 ± 24.7 (33–102)	1386.5 ± 1228.5 (53.7–3478.1)	220.5 ± 58.6
Cape Verde	1	48.0	1664.9	130.0
Ghana	3	107.7 ± 77.4 (38–191)	201.9 ± 232.9 (55.6–470.4)	215.7 ± 69.0
Madeira	7	53.7 ± 26.1 (17–84)	1190.3 ± 1034.0 (87.0–2942.8)	363.4 ± 286.9
Puerto Rico	9	92.0 ± 41.1 (42–180)	1793.6 ± 2699.8 (326–8852.6)	112.0 ± 74.7
North Carolina	2	99.5 ± 113.8 (19–180)	2651.1 ± 2720.0 (727.8–4574.4)	72.5 ± 38.8
All	66	100.0 ± 82.1	1631.7 ± 805.4	152.4 ± 132.5

(Williams *et al.*, 2017). Although both prey size and trophic level have been found to increase with blue marlin size (Veiga *et al.*, 2011; Chang *et al.*, 2019), no study, to our knowledge, has explored changes in vertical habitat use with blue marlin size. Most tracking studies have also documented diel differences in depth use, with proportionally higher surface use during the night and deeper diving behaviours during the day (Kraus & Rooker, 2007; Goodyear *et al.*, 2008; Freitas *et al.*, 2022). Movement patterns appear to be consistently driven, at least in part, by temperature, dissolved oxygen, and light level (Braun *et al.*, 2015; Carlisle *et al.*, 2017; Dale *et al.*, 2022), though the extent to which marlin are reacting to their own physiological tolerances or dynamic prey distributions which are responding to these physical variables is less well resolved. Habitat suitability is also predicted to vary substantially between months (Dale *et al.*, 2022); however, the short attachment durations of externally placed tags have inhibited detailed insight into seasonal variation in both horizontal and vertical habitat use throughout the Atlantic Ocean.

In this study, we investigate the horizontal and vertical habitat use of 66 blue marlin satellite tagged in the North Atlantic. We explore connectivity throughout this region, seasonal patterns of movement, diel vertical movements and the underlying environmental drivers of movements. Finally, we discuss the potential consequences of changing ocean conditions and the conservation and management implications of our results.

Materials and methods

Data collection

We used two satellite tracking datasets resulting from the collaborative efforts of scientists and recreational fishers. The first data set was conducted initially with Stanford University and anglers (e.g. Mr Stewart Campbell and associates) in the Atlantic basin. More recently, tags were sponsored by the International Game Fish Association Great Marlin Race (IGMR; <https://igfa.org/the-great-marlin-race/>), involving tag sponsors (anglers) and fishing crews from over 10 years of billfish tournaments and sponsorships across the Atlantic Ocean. This IGMR partnership has grown into the world's largest citizen science program for satellite tagging of billfish.

Tags were deployed in multiple locations across the Atlantic Ocean (see Table 1, Figure 1, and Supplementary Table 1). For tags deployed from 2001 to 2010, the Stanford team worked directed in the field with the sponsors, anglers, and fishers. From 2011 onwards, tag deployments were guided by IGFA and Stanford personnel, and often anglers used a printout of

instructions to anglers and fishers on how to tag rod and reel captured fish. Specific angling and handling techniques varied by vessel and location. Fish were typically caught on rod and reel by trolling artificial lures (or a combination of artificial lure and dead bait) between 3 and 10 knots (1 knot = 1.85 km/hr). Once caught, fish were leaedered to the vessel and held alongside the boat for tagging, which most often took place in <1 minute. Tags were affixed to the dorsal musculature of the fish with a custom-built titanium dart using a 2 m aluminum tagging pole with a 13–15 cm stainless steel or titanium applicator tip. Following tag placement, the hook was, in most cases, removed and the fish released. Weight was estimated visually. Due to the inability to determine the age or sex of tagged animals, additional groupings were based on five arbitrary mass ranges that had sufficient sample sizes for downstream analysis. These were: small (30–50 kg), intermediate (50–100 kg), medium (100–150 kg), large (150–250 kg), and very large (>250 kg).

PSATs included in this study were deployed between 2001 and 2021 and included models from Wildlife Computers (versions PAT2, PAT4, MK10, miniPAT), Microwave Telemetry (X-Tag), and Lotek (PSATFLEX). PSATs were programmed to sample pressure, ambient light levels, ambient temperature, and to detach after periods ranging from 120 to 240 days. Depending upon tag manufacturer, tags would also detach if a constant depth reading (signifying mortality or shedding) was recorded for 24 hours or 3 days (prior to 2015). Depth and temperature data were summarised into 12- or 24-hour histograms and/or transmitted as time series at minute-hourly intervals. Full datasets sampled at 30 seconds or 1-minute intervals were downloaded from tags that were physically recovered.

All research was conducted under the Stanford University Administrative Panel on Laboratory Animal Care (APLAC) permit APLAC-10786.

Data processing

The program spanned several generations of algorithms used to process electronic tagging data. For this study, tags were all processed similarly, with daily geolocation estimates obtained from light levels and sea surface temperatures (SST) recorded from the tags and compared to remotely sensed SST (Teo *et al.*, 2004). The light-based geolocation tracks were interpolated into daily coordinates using a Bayesian state-space model (SSM), which also estimated the uncertainty around these daily estimates (Block *et al.*, 2011; Winship *et al.*, 2012). Known tag deployment and pop-up locations were also included as model inputs (Block *et al.*, 2011).

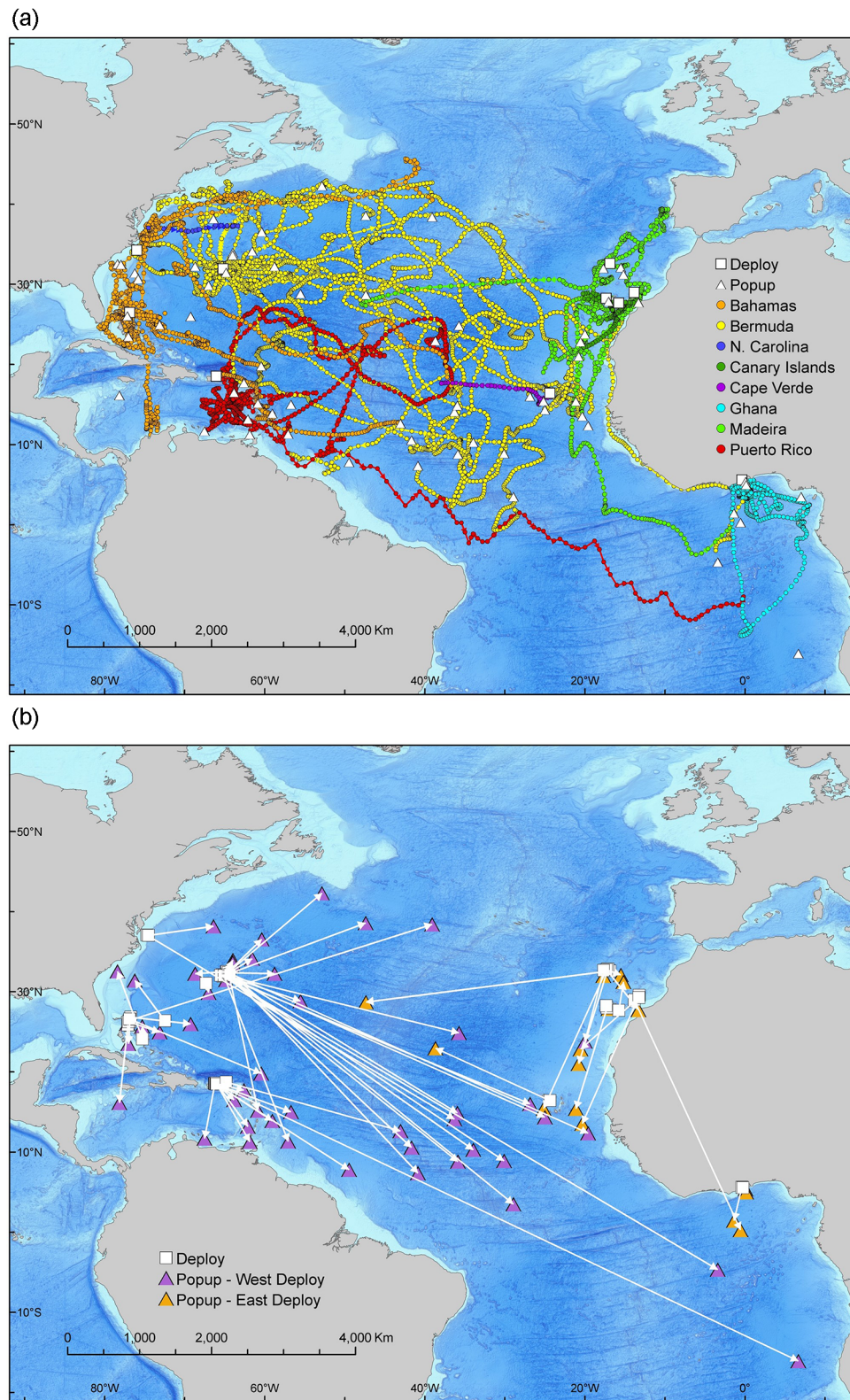


Figure 1. Map of horizontal positions of blue marlin in the North Atlantic. (a) Map of state-space-modelled blue marlin tracks ($n = 63$), coloured by region of deployment. (b) Deployment and popup positions of tracked blue marlin. White squares indicate deployment locations, and orange and purple triangles indicate pop-up locations for tags deployed on the east and west side of the Atlantic, respectively. Arrows link deployment and pop-up locations for individual deployments.

R 4.1 (R Core Team, 2020) was used for all further data processing and analyses, except where stated otherwise.

Track, depth, and temperature data were trimmed to the attachment period, with detachment from an individual identified by the depth time-series recording a constant near-zero depth for >12 hours, shortly followed by the initiation of Argos data transmissions. Seasons were delimited based on the lunar calendar for the northern hemisphere. The R package *suncalc* was used to obtain daily lunar illumination data, and to determine times of sunrise and sunset (Thieurmel & El-marhraoui, 2019) at the corresponding estimated track position, which were subsequently used to split the data into diel phases (day, night, dawn, and dusk). Daily mean SST was estimated by averaging the temperature in the uppermost 5 m of the water column for each day (Andrzejczek *et al.*, 2018).

Statistical analyses

Space use

Daily positions were used to calculate 50% (core use area) and 95% (home range) kernel utilization distributions (KUDs) (Worton, 1989) of Atlantic blue marlin using the R package *adehabitatHR* version 0.4.19 (Calenge, 2006). Kernel utilization distributions are a commonly used tool to describe the habitat use of marine animals from tracking data (Walli *et al.*, 2009; White *et al.*, 2017). The smoothing parameter (h) was estimated using the *ad hoc* method (“href”), which assumes a bivariate normal distribution. This estimation, which is recommended for animal movement data, is an extrapolation of where the animals spend their time, resulting in a wider distribution around each position than the animal’s actual location (Péron, 2019).

Core area and home range estimates were performed for all individuals (excepting three individuals that were removed due to inadequate position data) and in combined groupings based on tagging location and season. Kernel utilization distributions were calculated for eastern (Ghana, Cape Verde, Madeira, and the Canary Islands) and western (Bahamas, Bermuda, and Puerto Rico) Atlantic groupings, as well as for all fish tagged in Bermuda by season, defined by the lunar calendar. The 50% core area and 95% home range areas were calculated using the “kernel.area” function in *adehabitatHR*. For individuals with tracks >100 days in duration, core and home range area were also calculated for the first 100 days of the track alone to facilitate relative size comparisons.

Vertical habitat use

Where possible, each dataset was summarized into the percentage of time that an individual occupied a depth bin (with bins set at 0–2, 2–5, 5–10, 10–25, 25–50, 50–75, 75–100, and >100 m). For all individuals with time-series data, bin occupation was calculated for the overall track, as well as across each diel phase. For histogram data, these depth bins were also used to summarize histogram data, combining existing bins where necessary (e.g. combining 0- to 5-m and 5- to 10-m bins into a single 0- to 10-m bin). Where this was not possible for a particular bin size, a tag was excluded from the respective calculation.

Depth and temperature time-series data were also statistically summarised across diel phases for each individual, with computed variables including median, mean, minimum, maximum, and *SD*. Metrics were summarized across an entire track for each individual, then averaged across individuals

(placing each individual equal rather than weighting longer tracks higher to emphasize individual variation). As the data were strongly right-skewed, non-parametric paired Wilcoxon tests with significance set at $p < 0.05$ were used to compare the median and maximum day- and night-time depths as per Curnick *et al.*, (2020), both for each individual and across the entire dataset. Depth and temperature data from recovered tags were visualized in Igor Pro ver. 9.0.0.10 (WaveMetrics, Inc. Lake Oswego, USA).

Generalised additive mixed models

A suite of Generalized Additive Mixed Models (GAMMs) was constructed to test the response of biologically relevant vertical movement metrics to temporal and environmental variables. Due to distinct diel depth distributions, vertical metrics were modeled separately for “day” and “night” phases, and were therefore calculated for individuals with time-series data only. Calculated response metrics included (1) % time in the top 5 m (a metric of surface use), and (2) maximum depth and were summarized for each unique day of data for each individual marlin. Median depth was originally also modelled, however, due to lack of model fit both before and after transformation, was not included in the final analysis. Response metric (1) was logit transformed prior to analysis so that predicted values were not negative and did not exceed one, as well as to normalize the data, and was fitted with a Gaussian error distribution. Due to lack of model fit, the nighttime model was also removed from the final analysis. Response metric (2) was fitted with a gamma error distribution with a log link. The continuous predictor variables considered for all models were day of the year, tag-observed daily mean SST, dissolved oxygen concentration at 100 m depth, and fraction of the moon illuminated (0–1) (Table 2). Modelled oxygen data were obtained from the Copernicus Marine Environment Monitoring Service (CMEMS, <http://marine.copernicus.eu/>) global ocean biogeochemistry non-assimilative hindcast product (0.25° resolution). Dissolved oxygen concentration was extracted at 100 m depth for daily tag locations, with data averaged over a spatial area that matched the size of tag error estimates. Daily mean SST, time of year, and dissolved oxygen were included in our models due to their high relative importance in explaining marlin presence in recent models of global habitat suitability (Dale *et al.*, 2022). All continuous predictor variables were checked for potential correlation to ensure that collinearity was within acceptable levels, denoted by Pearson’s correlation coefficient values <0.28 (Graham, 2003). Region tagged and size class were also included as categorical factors. All models included blue marlin ID as a random effect to account for individual variation in movement patterns. We used the *corAR1* function to account for temporal auto-correlation in our datasets (Zuur *et al.*, 2009). Models were constructed using the *mgcv* package in R using maximum likelihood (Wood, 2017).

A full subsets approach was used to model all possible combinations of explanatory variables (70 possible combinations for each model) (Fisher *et al.*, 2018). Models within two AICc units of each other were considered to be equally ranked. When the difference in AICc values ($\Delta AICc$) between the top candidate models was <2, the model containing the lowest number of explanatory variables (i.e. the most parsimonious) was selected as the appropriate model for the data. As dissolved oxygen was only available for approximately one third of the data days, in cases where the chosen model did not

Table 2. Description of explanatory variables used in GAMM analysis of blue marlin vertical movement patterns in the North Atlantic Ocean.

Variable	Type of effect	Description
Day of year	Fixed: continuous, fitted with cyclic cubic regression splines ($k = 7$)	Day of the year
SST	Fixed: continuous, fitted with natural spline ($k = 5$)	Daily mean SST calculated from tag-derived temperature data
Dissolved oxygen	Fixed: continuous, fitted with natural spline ($k = 10$)	Dissolved oxygen concentration at 100 m depth. This modelled data were obtained from the CMEMS (http://marine.copernicus.eu/) global ocean biogeochemistry non-assimilative hindcast product (0.25° resolution).
Moon illumination	Fixed: continuous, fitted with natural spline ($k = 5$)	Fraction of the moon illuminated by the sun
Region	Fixed: categorical	Region in which blue marlin with time-series data were tagged (Virginia, Bahamas, Bermuda, Canary Islands, Madeira, and British Virgin Islands)
Size class	Fixed: categorical	Size classes based on mass of tagged blue marlin [small (30–50 kg), intermediate (50–100 kg), medium (100–150 kg), large (150–250 kg), and very large (>250 kg)]

include dissolved oxygen, the full subsets approach was repeated on the full dataset (i.e. without dissolved oxygen included as a potential explanatory variable). Residual plots of the final selected models were visually inspected to ensure models satisfied assumptions of homogeneity and normality (see Supplementary Figures S1–3).

Results

Data summary

Between 2001 and 2021, a total of 66 blue marlin were successfully tagged in the North Atlantic Ocean, with PSAT tags deployed in Bermuda ($n = 26$), the Bahamas ($n = 11$), Puerto Rico ($n = 9$), Madeira ($n = 7$), the Canary Islands ($n = 6$), Ghana ($n = 3$), North Carolina ($n = 2$), the British Virgin Islands ($n = 1$), and Cape Verde ($n = 1$) (Figure 1; Supplementary Table S1). Three of these tags were recovered and the full archived time series downloaded (two from the Canary Islands, and one from Madeira; Supplementary Table S1). One fish tagged in Bermuda suffered a likely predation event by an endothermic shark 28 days into tag deployment, with daily maximum depths increasing from ~100 to ~500 m and ambient temperature becoming relatively constant (between 24 and 26°C) after this point (Supplementary Figure S4). Marlin ranged in estimated mass from 32 to 454 kg, with a mean estimated mass of 144.1 ± 88.6 kg. Tags were primarily deployed in the boreal summer months ($n = 49$), with the remaining 17 tags deployed in the boreal spring (Supplementary Table S1). A total of 6681 days of tracking data were obtained, with a mean \pm SD deployment duration of 101 ± 82 days and a range of 4–244 days (Table 1). Tracking data were predominantly recorded during summer months (46.5%), followed by autumn (28.5%), winter (17.0%), and finally spring (8.1%). State-space models were unsuccessful for three tags, likely due to their short attachment duration (<8 days). Depth and temperature histogram data were transmitted from 22 tags and time-series data from 44 tags (Supplementary Table S1).

Horizontal distribution and movements

The blue marlin tracked in the North Atlantic displayed wide-ranging movements, with a mean straight-line distance between deployment and pop-up location of 954.5 ± 1016.5 km (Figure 1b) and a mean displacement distance per day of 19.4 ± 13.7 km/day (based on a conservative measure of

straight-line distance). The maximum recorded straight-line distance travelled between tag deployment and pop-up locations was 8853 km, recorded by a ~261 kg individual tracked for 120 days from Puerto Rico to ~550 km off the coast of Angola (Figure 1b). This marlin also recorded the highest displacement speed of 73.8 km/day.

State-space-modelled tracks revealed connectivity between tagging locations as well as broader regions throughout the North Atlantic (Figure 1a). For example, marlin tracked from the Bahamas moved northwest to the US coast, northeast into the mid-Atlantic, and further south into the Caribbean Sea. Of the 26 marlin tagged in Bermuda (mean deployment duration 132.5 ± 103.0 days), 14 displayed long distance displacements (>1500 km) to the southeast, with three individuals moving to the waters around Cape Verde and one individual ~1000 km south of Ghana (Figure 1). Notably, these four latter individuals had similar migration timings, crossing the Atlantic from the months of August through October. Two of the blue marlin were tagged within the same week in July 2015 and the other two were tagged in late July and August 2018 (Supplementary Table S1). From the Canary Islands, four blue marlin tracked south along the African coast, with one tag popping up ~500 km south of Ghana.

Kernel utilization distributions revealed extensive use of the North Atlantic from 60 tagged blue marlin, with overlap of both core use and home range habitat between marlin tagged in the east and west Atlantic (Figure 2). Core use areas largely centered around coastal deployment regions as well as some regions of offshore habitat (Figure 2). Core use area and home range area both showed moderate positive correlation with deployment duration ($r = 0.65$ and 0.68 , respectively). When considering only the first 100 days (for individuals with longer tracking durations), however, considerable individual variation in home range areas size was evident. For instance, one individual tracked from Bermuda to Cape Verde had an estimated core use area of 3 345 251 km² for the first 100 days, while another individual remained around the Bahamas for its entire 203-day track, with a core use area of 21 712 km² for the first 100 days.

When summarizing all Atlantic Ocean movement data, mean latitude changed across seasons, reaching its highest northern position in summer ($28.8 \pm 10.0^\circ$) and lowest in winter months ($14.0 \pm 7.2^\circ$), with core habitat use in winter also shifting into more offshore habitats (Supplementary Figure S5). Tag recorded temperature data indicated that the

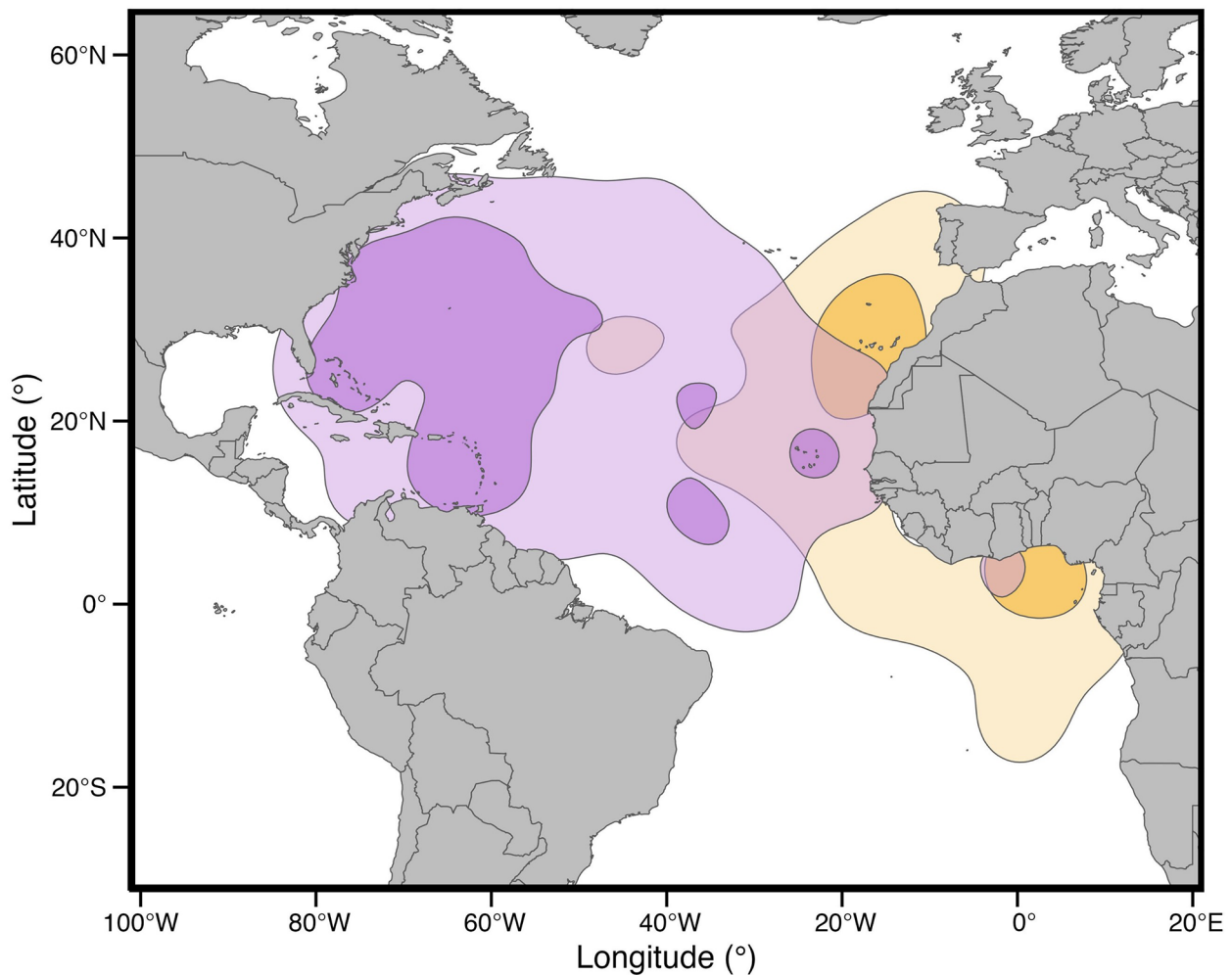


Figure 2. Kernel utilization distributions (KUDs) for 60 blue marlin *M. nigricans* tracked in the Atlantic Ocean between 2001 and 2021. Kernel utilization distributions were calculated separately for marlin tagged in the west (purple) and east (orange) Atlantic. Darker shades represent core use areas (50% KUD) and lighter shades the home range (95% KUD) of tracked marlin.

mean SST experienced by blue marlin in the Atlantic Ocean was $26.9 \pm 1.6^\circ\text{C}$ but varied by season (note that SST was not available for six of the earlier tags). The mean SST was warmest in the summer ($27.3 \pm 2.2^\circ\text{C}$) and coldest in the winter ($25.9 \pm 1.4^\circ\text{C}$) with intermediate temperatures in the spring and autumn ($26.4 \pm 2.5^\circ\text{C}$ and $26.7 \pm 2.3^\circ\text{C}$, respectively). For marlin tagged in Bermuda (the region with the highest sample size and seasonal spread of data), KUDs indicated a seasonal shift in core habitat use from higher latitude coastal habitat in summer (with mean daily latitudes centering around $33.3 \pm 4.8^\circ$), shifting offshore and further south from autumn through winter ($25.4 \pm 8.5^\circ$ in autumn, $13.1 \pm 6.9^\circ$ in winter; Figure 3). Seasonal mean SST for tags deployed in Bermuda were consistent to patterns in the overall dataset, with the highest SSTs in the summer ($27.5 \pm 1.7^\circ\text{C}$) and coolest in winter and autumn ($26.0 \pm 1.3^\circ\text{C}$ and $26.0 \pm 1.7^\circ\text{C}$, respectively) (Figure 3d).

Vertical distribution

Tagged blue marlin occupied a mean depth of 28.8 ± 12.3 m and a median depth of 10.3 m, reaching mean maximum depths of 430.7 ± 208.5 m (range 95–984 m; Figure 4). Depth

data revealed that blue marlin remained primarily in the top 100 m, spending $94.0 \pm 9.5\%$ of the time in this zone, with a majority of this being in the top 5 m ($53.6 \pm 22.6\%$ of the overall time). Marlin encountered ambient temperatures ranging from 3.9 – 31.2°C , with a mean of $25.7 \pm 1.4^\circ\text{C}$, spending $>50\%$ of the time between 26 and 30°C , and very rarely encountering temperatures $>30^\circ\text{C}$ (0.2% of the time; Figure 4c) or $<20^\circ\text{C}$ (3.2% of the time; Figure 4c).

Tagged blue marlin displayed strong patterns of normal diel vertical movement (nDVM; Figure 5). Recovered archival records ($n = 3$) revealed that blue marlin oscillated between warm surface waters and depths >100 m during the day, while primarily remaining in surface waters at night (Figure 5). Given the non-Gaussian distribution of the data, median depth was used to statistically summarize diel depth use, with marlin overall occupying a significantly deeper median depth during the day than the night (day: 41.9 ± 21.8 m (mean \pm SD); night: 5.1 ± 4.4 m; Wilcoxon paired rank sum test: $V = 79.054$, $p < 0.001$, 95% confidence interval: $-47.7, -46.0$; Figure 4). Mean maximum depths were also significantly deeper during the day than the night (day: 130.3 ± 48.4 m; night: 46.6 ± 24.4 m; Wilcoxon paired rank sum test: $V = 100.210$, $p < 0.001$, 95% confidence

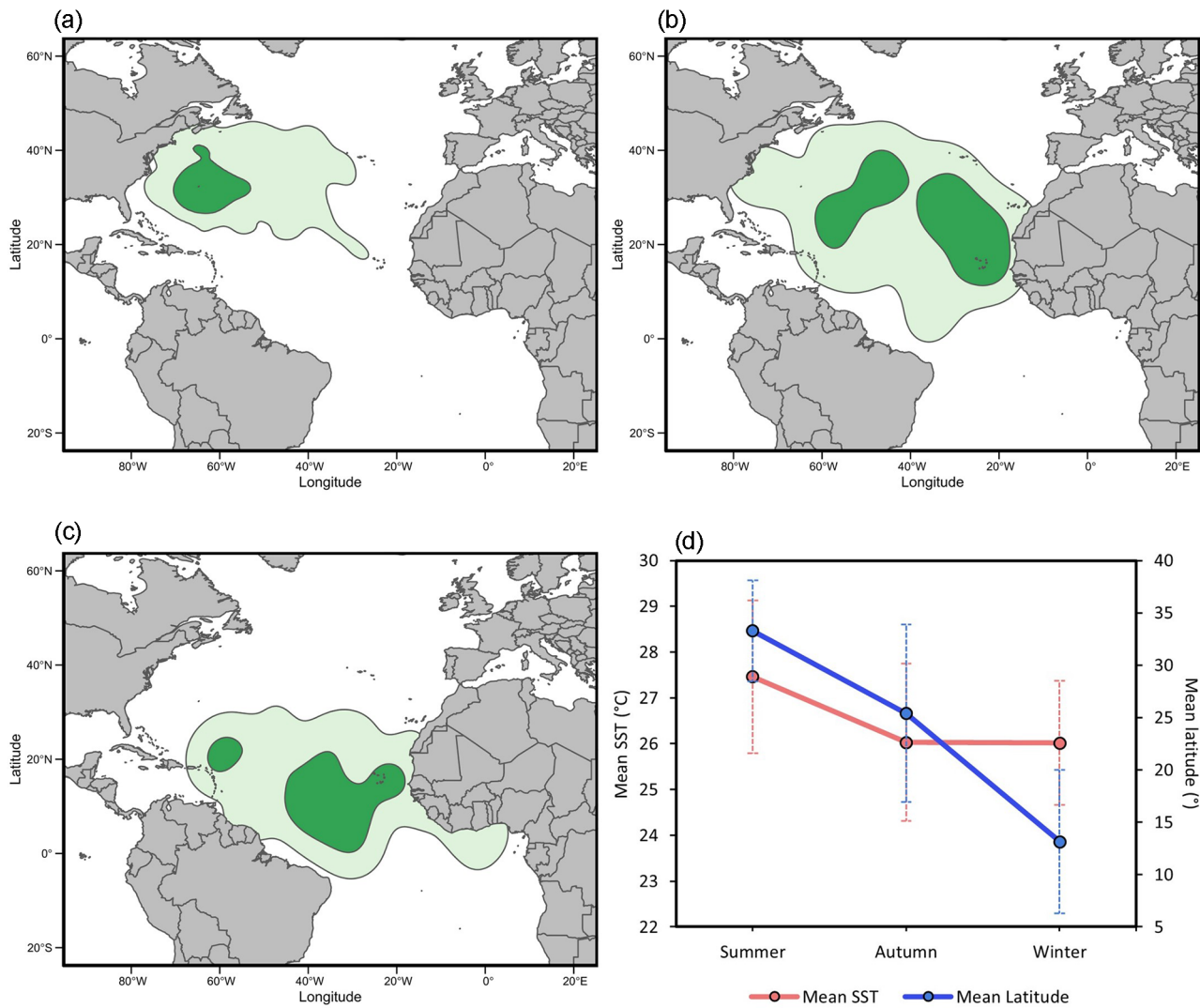


Figure 3. Seasonal movements of 23 blue marlin *M. nigricans* satellite-tagged in Bermuda between 2015 and 2020. (a–c) display KUDs for blue marlin in northern hemisphere (a) summer (1603 tracking days), (b) autumn (956 tracking days), and (c) winter (901 tracking days). Darker shades represent core use areas (50% KUD) and lighter shades the home range (95% KUD) of tracked marlin. (d) Daily mean \pm SD sea SSTs (SST, °C) and mean latitude (°) encountered by blue marlin tagged in Bermuda by season.

interval: $-92.8, -87.8$). On an individual basis, seven of the 40 individuals tested did not record significantly deeper median depths throughout the day, and three did not record significantly deeper maximum depths between diel periods. All individuals that did not record significant differences between day and nighttime depths (i.e. $p > 0.05$) had shorter than average tracks (24 ± 18 days versus an overall average 92 ± 68 days of depth time-series data).

At night, tagged blue marlin occupied the top 5 m $77.3 \pm 19.0\%$ of the time, with this proportion of shallow depth occupation more than halving during the day ($31.5 \pm 20.9\%$ of the time; Figure 4a). Conversely, during the day blue marlin spent much more time in depths >25 m (Figure 4a). We observed an overall decrease in the proportion of time spent in the top 100 m from day to night ($89.2 \pm 10.1\%$ in the day versus $99.6 \pm 0.6\%$ at night; Figure 4). This diel trend remained consistent among seasons, however, with a notable increase in time spent in the top 2 m during the night from $43.8 \pm 2.5\%$ in summer to $>65\%$ in other seasons (Supplementary Figure S6). Dusk and dawn

periods more closely resembled daytime depth distributions rather than night and revealed a deeper distribution during dawn than dusk (Figure 4b).

GAMM patterns

Generalized additive mixed models revealed temporal and environmental patterns in all modelled vertical movement metrics (Table 3 and Figure 6). The proportion of the variance explained (the adjusted R-squared) for the selected models ranged from 0.36 to 0.37, with the individual ID (the random effect) explaining more than half of this when modelled alone (Table 3). Day of the year and mean SST were retained in every model, and fish size class and region were not retained in any model. For a list of all model subsets considered in the selection process, see the Supplementary spreadsheet.

% top 5 m

The probability of being in surface waters (the top 5 m) during the day peaked in the middle of the year in summer months, steadily declining to a minimum in winter (Figure 6).

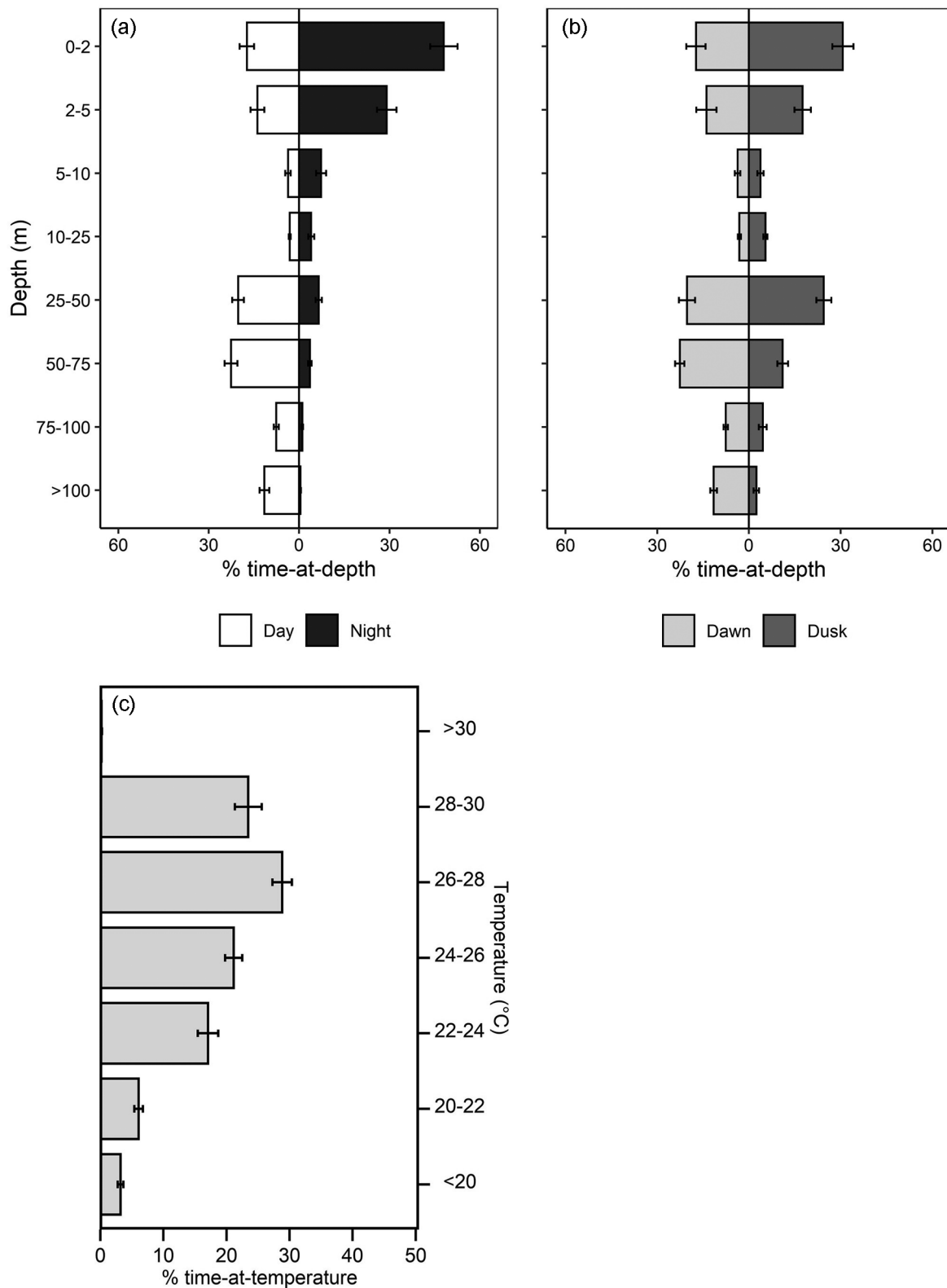


Figure 4. Summarised depth and temperature data from transmitted and recovered PSATs deployed on blue marlin *M. nigricans* in the North Atlantic Ocean. (a) Percent time-at-depth for day and night periods. (b) Percent time-at-depth for dawn and dusk periods. (c) Percent time-at-temperature. Note that bin size is not equal between depth categories.

Increasing mean SST reduced the probability of marlin being present in surface waters during the day (Figure 6; Table 3). Dissolved oxygen levels at 100 m and lunar illumination were not retained in this model.

Maximum depth

Maximum depths during the day were predicted to be deepest in winter months and shallowest in summer, while at night, the deepest depths were predicted to occur in spring

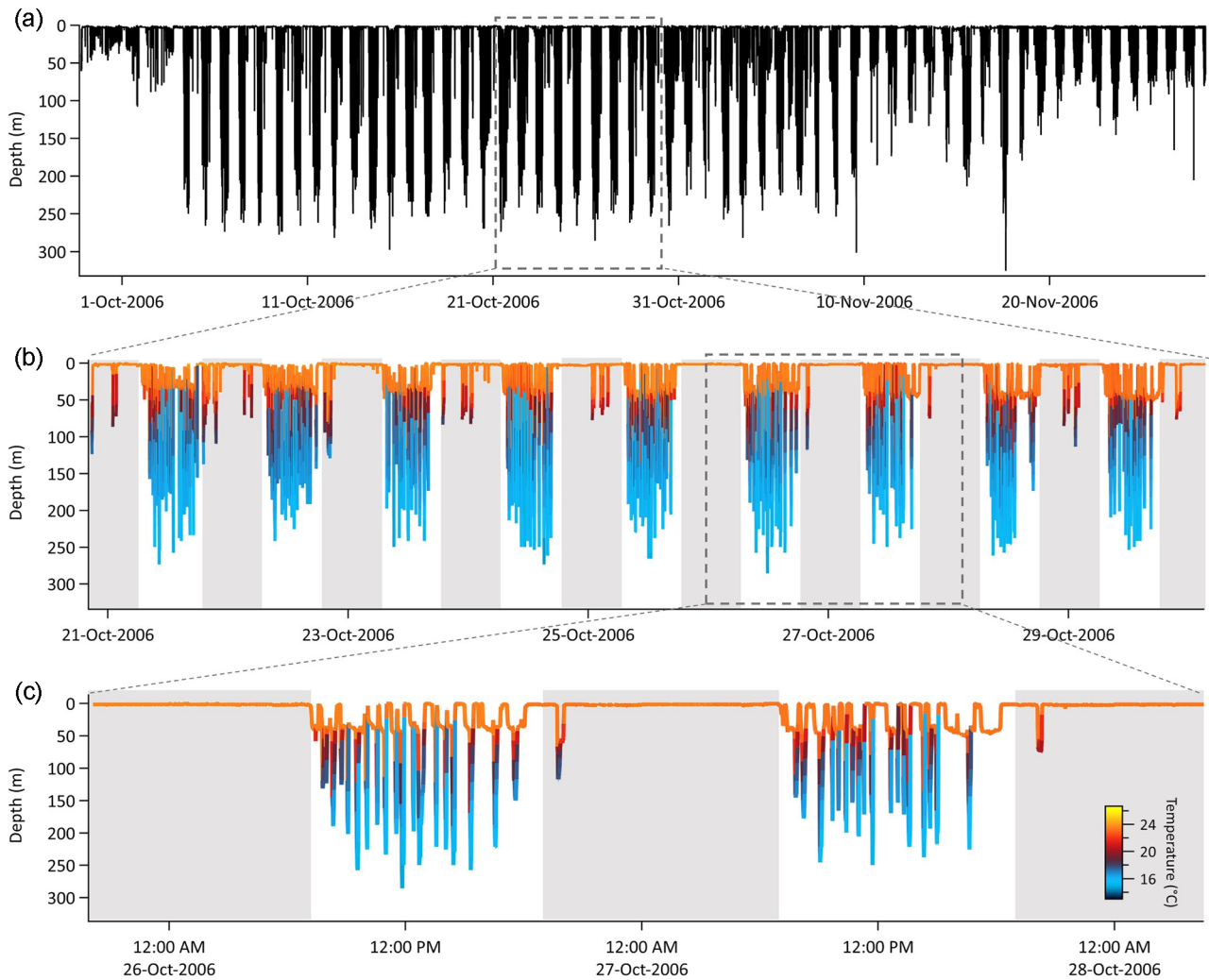


Figure 5. Representative raw archived depth time-series from one blue marlin at increasing resolution from (a) to (c). The blue marlin was tagged in the Canary Islands in September 2006. Depth traces are shaded by temperature (°C). Depth time-series are displayed for periods of (a) the entire track (61 days), (b) nine days, and (c) two days.

Table 3. Summary of the GAMMs selected by the model selection process (for full set of models included in the model selection process, see Supplementary Spreadsheet).

Selected models	Adjusted R-squared (full model/random effect)		Smoother	Estimated DF smoother	Significance of smoother
	Full model	Random effect only			
1a. Day % top 5 m ~ day of year + mean SST + BMID	0.398	0.298	Day of year	4.0	<0.001*
			Mean SST	2.3	<0.001*
2a. Day maximum depth ~ day of year + mean SST + O ₂ at 100 m + BMID	0.361	0.305	BMID	32.4	<0.001*
			Day of year	2.3	<0.001*
2b. Night maximum depth ~ day of year + mean SST + O ₂ at 100 m + moon fraction + BMID	0.369	0.352	Mean SST	1.0	<0.001*
			O ₂ at 100 m	1.0	0.005
			BMID	28.6	<0.001*
			Day of year	4.0	<0.001*
			Mean SST	1.0	0.003*
			O ₂ at 100 m	1.0	0.1
			Fraction of the moon illuminated	1.9	0.04*
			BMID	25.7	<0.001*

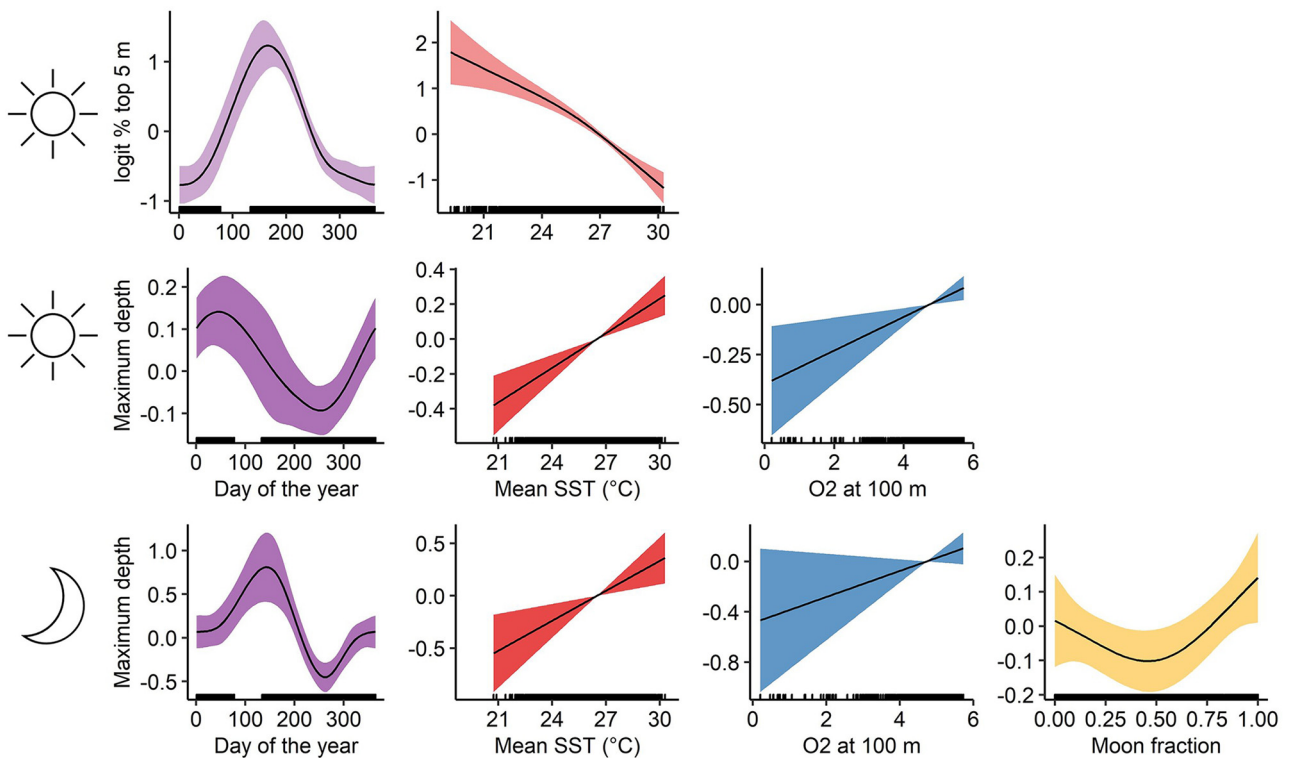


Figure 6. Marginal effects plots from top-ranked GAMMs indicating the effects, from left to right, of: day of the year, mean SST°C, dissolved oxygen at 100 m depth, and lunar illumination, on vertical movement metrics. The response variables for each model are, from top to bottom, % time in the top 5 m during the day (logit transformed), maximum depth during the day and maximum depth during the night. Note that scales on the y-axes differ among plots.

(Figure 6). For both diel periods, maximum depths were predicted to increase with increasing mean SST (Figure 6, Table 3). Increasing levels of dissolved oxygen at 100 m increased the probability of deeper maximum depths during the day, while the smoother for dissolved oxygen was not significant at night (Figure 6, Table 3). Maximum depths at night were also predicted to be deeper during the full moon period (i.e. highest lunar illumination; Figure 6).

Discussion

In this study, we used a large satellite telemetry dataset to examine the horizontal and vertical habitat use of blue marlin in the Atlantic Ocean. Our data found temporal patterns at diel, lunar, and seasonal scales that are likely to influence interaction rates with anthropogenic activities and individual variation in the extent of movements throughout the region. Variability in movement patterns with environmental parameters, specifically mean SST and dissolved oxygen, facilitated insight into how these physical variables may influence blue marlin movements and therefore how such patterns may be affected by a changing ocean climate.

Diel vertical movement patterns

Blue marlin primarily resided in warm epipelagic waters and displayed strong patterns of nDVM, recording a deeper distribution during the day than night, conforming to patterns observed in previous tagging studies in the Atlantic (Kraus & Rooker, 2007; Goodyear *et al.*, 2008), as well as the

Pacific (Carlisle *et al.*, 2017). Though primarily remaining in the top 100 m, blue marlin also dove for brief periods into the mesopelagic, with an individual tracked from the Bahamas expanding the known depth range of this species, diving to a maximum depth of 984 m. Deeper diving during the day is predicted to be a foraging strategy for these visual hunters, who predominantly feed on pelagic fishes (Veiga *et al.*, 2011; Young *et al.*, 2018; Guillemin *et al.*, 2022), though brief deep dives into twilight zone waters may be motivated by other drivers, such as predator avoidance (Braun *et al.*, 2021). In between daytime dives into cooler waters, marlin returned to surface waters, presumably to rewarm, and reoxygenate (Goodyear *et al.*, 2008). At night, marlin remained in warm surface waters, potentially in a “quiescent” or resting swimming phase (Carlisle *et al.*, 2017). Given that tracked marlin continued to exhibit deeper distributions during dusk and dawn, we suspect marlin continued to forage in the deep scattering layer during this period, exploiting vision adapted to low light conditions (Block & Finnerty, 1994). Similarly, while lunar illumination did not affect the primary vertical habitat of the tagged marlin, maximum depths at night were predicted to increase during the full moon, a pattern that has also been observed in the Gulf of Mexico and in the South Atlantic (Kraus & Rooker, 2007; Madigan *et al.*, 2020), and one we suspect is related to light-based foraging. Individual variation in diel patterns of vertical habitat use was recorded, with seven of the 40 individuals with time-series data having no evidence for nDVM, but we suspect this deviation was primarily due to the shorter sampling intervals for these individuals. Other possible drivers of the observed variation to individual vertical movement patterns could include season, geographic region,

and physical variables such as mean SST and dissolved oxygen.

Seasonal patterns in habitat use

Seasonal patterns were observed in vertical and horizontal distributions throughout the Atlantic, likely linked to seasonal variation in environmental conditions and/or prey distributions. While the overall nDVM pattern remained consistent among seasons and environmental conditions, depth distributions within diel periods varied. In winter, daytime maximum depths were predicted to be the deepest, which may be related to bathymetry, and/or changing prey distributions as marlin tracked offshore during these periods. It is also possible that shallower daytime distributions may be driven in part by spawning behaviours, with spawning in the North Atlantic regions presumed to be occurring in late spring and summer months (Luckhurst *et al.*, 2006; Richardson *et al.*, 2009; Kraus *et al.*, 2011). Higher mean SSTs increased the likelihood of deeper daily maximum depths, suggesting that warmer surface temperatures may facilitate behavioural thermoregulation, enabling longer and/or more frequent dives into deeper, cooler waters to forage, or alternatively, that prey were distributed deeper in warmer waters. Increased levels of dissolved oxygen at 100 m also increased maximum daytime depths.

Surprisingly, marlin size class was not retained in any model, with no evidence of larger fish spending more time in deeper waters. This could be due to the inaccuracy of visual size estimates, the choice of size classes not being biologically relevant, and/or size not being a limiting factor for time spent in cooler, deeper waters. It is also important to acknowledge that a high amount of the variability in vertical distribution remained unexplained in the final GAMMS, and that a majority of that explained was due to the individual ID. Such variability could be due to a number of unmeasured variables, including physical variables that could not be quantified at the appropriate resolution as well as biological traits that could not be determined for live fish (e.g. sex, maturity status). Collectively, our data support the notion that blue marlin vertical habitat is a continuum consisting of a near-surface core area with elastic depth limits dictated by physiological tolerances and prey distributions in a dynamic local environment, a pattern also reported in the Pacific for both blue marlin (Carlisle *et al.*, 2017) and black marlin (Chiang *et al.*, 2015).

Horizontal distributions shifted offshore and to lower latitudes from summer to winter, tracking relatively consistent warm SSTs between seasons. SST has previously been found to be one of the most likely drivers of variation in habitat use by marlin with strong preference for surface temperatures $>22.9^{\circ}\text{C}$ (Braun *et al.*, 2015; Dale *et al.*, 2022), so it may be that the marlin tracked in this study were tracking preferred thermal environments between seasons, though temperatures recorded here were somewhat warmer, with an overall mean of $25.6 \pm 1.3^{\circ}\text{C}$. The shift into offshore regions in winter may be related to prey distributions, spawning activity, and/or complex water mixing (e.g. fronts and eddies) (Braun *et al.*, 2015), but we note that this result is somewhat biased by tagging, with more of our deployments occurring in coastal regions during summer months.

Connectivity in the Atlantic Ocean

Consistent with past studies, blue marlin in this study moved widely throughout the Atlantic, demonstrating connectivity

between the east and west, as well as temperate and tropical regions (Orbesen *et al.*, 2003; Ortiz *et al.*, 2003; Goodyear *et al.*, 2008; Prince *et al.*, 2010). While several marlin tagged at western sites migrated to the east Atlantic, none tagged in the east crossed to the west. This may be an artefact of the reduced sample size and tagging durations of eastern fish, with one marlin tagged in Madeira tracking towards the central Atlantic over its 71-day track duration. Blue marlin tracked for longer durations typically displayed larger displacements and home ranges; however, some individuals remained in their tagging region for long periods (i.e. >100 days). One small individual (~ 45 kg), for instance, remained around the Bahamas for its entire 203-day track and had a much smaller estimated home range size relative to other marlin tracked for similar periods, suggesting that suitable conditions persisted here throughout this period. In contrast, several individuals crossed the Atlantic, moving between tagging areas and exhibiting relatively large home ranges. Notably, several individuals tagged in Bermuda and ranging in size ~ 68 – 136 kg, recorded similar migration timings, moving towards Cape Verde and the African coast in late summer, indicating that this may be a regular migration pattern. Such movements may be driven by the need to follow favorable environmental conditions and/or regions of high productivity. Larger sample sizes and longer tracking durations are required to test the commonality of this migration pattern throughout the population. Collectively, the extensive movements recorded both here and previously and the lack of spatial partitioning in genetic variation provide further evidence for an Atlantic-wide population of blue marlin (Graves & McDowell, 2015).

Management and conservation implications

The largest threat to blue marlin populations, as well as a majority of other billfish taxa, is bycatch from drifting commercial longlines that are set in epipelagic waters, primarily targeting tunas, and swordfish (Cramer, 2003). The increased use of electronic tag technology has revealed the majority of what we know about billfish biology and life history (Braun *et al.*, 2015). Specifically, in data-poor regions and species, data from electronic tags has been instrumental to filling gaps on species-specific behaviour that is relevant to population modelling and bycatch reduction (Lam *et al.*, 2022).

Because of their wide-ranging movement behaviours, traditional spatial management measures, such as the designation of static marine reserves, will be of little benefit in reducing the commercial bycatch of these vulnerable species (Dunn *et al.*, 2016). For example, Filous *et al.*, (2022) found that in Palau, the size of the national marine sanctuary was not large enough to encompass the distributions of tagged blue marlin, with calculated home ranges being up to four times larger than the Palau EEZ, and two of the tagged fish being caught by fishing operations occurring outside of Palau waters. Instead, focused efforts to identify commercial fleet overlap with identified blue marlin habitat are of key importance in management controls at ICCAT (the International Commission for the Conservation of Atlantic Tunas). In addition, dynamic time-area controls that take advantage of variation in the catchability between target and bycatch species may be of greater utility in reducing marlin bycatch rates (Goodyear, 2003). As marlin are likely foraging in the day, we predict that they may be more vulnerable to baited hooks during this period (Graves *et al.*, 2003). Seasonal distribution data could therefore be paired

with knowledge of diel vertical distributions to understand the hours of the day and times of year that a marlin may be most vulnerable to a baited hook at a given depth and region. When paired with knowledge of a target species movements, such dynamic ocean management strategies can provide effective bycatch reduction while maintaining fishing opportunities (Hazen *et al.*, 2018). Larger sample sizes and tracking durations, especially for under-sampled seasons (i.e. spring), will facilitate further understanding of temporal and spatial variability in marlin capture vulnerability.

Given the available data, we were unable to conclude if changes in movement patterns with mean SST and dissolved oxygen at 100 m were primarily due to the physiology of the tagged individual or that of its prey. As differences in physiological thresholds between marlin and their prey are likely, mismatches in distributions may develop as taxa adjust to available environmental conditions. For blue marlin, modelling has demonstrated that core habitat suitability has shifted poleward and decreased in equatorial regions (Dale *et al.*, 2022). As movements to equatorial latitudes in the North Atlantic largely took place during winter months, such shifts in suitability may influence seasonal migration patterns, and the resulting effects will depend on how spawning sites are affected as well as how primary prey respond to changes in their preferred habitat. Alternatively, in eastern boundary currents, the shoaling of oxygen minimum zones is predicted to increase interaction rates between marlin and their prey, restricting both to higher oxygenated surface waters and potentially increasing marlin bycatch by longlines (Prince & Goodyear, 2006; Prince *et al.*, 2010). Collectively, we predict that climate change will drive a complex shift in the three-dimensional distribution of blue marlin because of both marlin physiology and the distribution of their prey. An important next step will be to utilize other technologies, such as oxygen sensor tags, to tease apart these drivers.

Acknowledgements

We thank the captain, crews, anglers, and scientists who collaborated to tag blue marlin in the Atlantic with Stanford, TAG and the International Great Marlin Race. We dedicate this paper to the memory of Stewart N. Campbell, a remarkable angler, engineer, and billfish supporter. Captain Barkey Garnsey and first mate Charles Perry made it all happen as a team aboard the F/V. Chunda. We are also grateful for the critical comments of three anonymous reviewers that improved the draft manuscript.

Supplementary data

[Supplementary material](#) is available at the *ICESJMS* online version of the manuscript.

Conflict of interest

The authors have no conflicts of interest to declare.

Funding

Funding was made possible through small direct sponsorships of tags. We thank all who sponsored tags for this work, including Frank Rodriguez, Jim Jensen, Jose Luis Beistegui, Lainey Jones, Laura & Byron Russell, Mike Bozzuto and Roy

W. Cronacher Jr. We thank the late Stuart Campbell, Mr. Jose Luis Bestigui, and Mr. Wayne Whippen, who supported eastern Atlantic tagging. From 2011–2018, funding was organized with the International Great Marlin Race by Mr. Jason Schratwieser, who also helped deploy tags. We also thank anonymous donors to Stanford for billfish research and Pure Edge for supporting postdoctoral researchers working on billfish tagging research in our lab. We thank Dr. Bruce Pohlot of IGFA for more recent efforts in Bermuda. We thank Dr. Randy Kochevar for his help early on in organizing and transitioning the Stanford blue marlin program to the IGMR, and the technical staff (James Ganong and Alan Swithenbank), former postdocs and technicians at Stanford, and the Tuna Research and Conservation Center, who through the past 20 years have helped to prepare and ship tags for billfish deployments. Jonathan Dale was funded in part by NOAA grant NA22NMF4720376.

Author contributions

BB and SA conceived the study. BB and MC assisted with fieldwork and data collection. SA, CM, JD, and MC performed data analysis, and SA and BB interpreted the data. SA led the writing of the manuscript, and all authors read and approved the final manuscript.

Data availability

All raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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Handling Editor: Kylie Scales