Animal Biotelemetry

TELEMETRY CASE REPORT

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First insights into the movements and vertical habitat use of blue marlin (*Makaira nigricans*) in the eastern North Atlantic

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Abstract

Background: The blue marlin (*Makaira nigricans*) is a vulnerable migratory fish inhabiting tropical and subtropical pelagic waters of the Atlantic, Pacific and Indian Oceans. The biology and spatial ecology of the species in the eastern North Atlantic is poorly understood, despite being exploited in the region by recreational and commercial fisheries. Here, we present results of the first study to use pop-up satellite archival tags to track blue marlin off Madeira, Portugal ($n = 3$) and obtain insights into the movements and habitat use of the species within the eastern North Atlantic.

Results: Blue marlin were tracked for 24 to 83 days, moving from Madeira to pelagic waters off the Canary Islands, Cape Verde Islands, as well as along the continental shelf brake of Europe and Africa. Blue marlin spent 71% of their time in the upper 5 m and 89% in the upper 50 m, though all individuals dived to depths over 200 m (maximum: 336 m). Temperature at depth ranged from 12 to 28.6 °C, but the greatest proportion of time was spent in waters between 20 and 26 °C. Detailed depth and temperature time-series data were obtained from a tag recovered eight years later. These data show clear diel differences in depth use, involving consistent use of the surface at night and deeper dive activity during the day, predominately to depths greater than 50 m.

Conclusions: The highly migratory patterns of this vulnerable species in the eastern North Atlantic highlights the need for both local and international conservation measures. Depth-use patterns, particularly the high usage of the upper 5 m of the water column, make them susceptible to surface longline fisheries.

Keywords: Billfish, Istiophoridae, Telemetry, Satellite tags, Spatial behaviour

Background

Marine top predators provide important functions and services in oceanic and coastal ecosystems, including regulating food webs, cycling nutrients and supporting fisheries and tourism [1, 2]. Such species are commonly characterized by large body size and late sexual maturity, making them vulnerable to demographic perturbations [3]. Despite their important ecological, economic, and cultural value, numerous marine top predators have been threatened by overexploitation in industrial fisheries, incidental catches in artisanal and local fisheries, climate change, pollution and habitat loss, which together have caused population declines and local extinctions [4, 5]. Because anthropogenic pressure and climate shifts vary both spatially and temporally, improved understanding of the spatial ecology of marine top predators is crucial for ensuring their conservation and preventing loss of biodiversity and ecosystem services.

The blue marlin (*Makaira nigricans*), a billfish of the family Istiophoridae, is a large pelagic fish inhabiting tropical and subtropical waters of the Atlantic, Pacific

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and Indian Oceans [6]. The species is highly migratory [7, 8], forming a single Atlantic-wide genetic stock [9, 10], as well as a single genetic population throughout the Pacific Ocean [11]. The blue marlin has been exploited extensively by recreational and commercial fisheries throughout their range [12–16]. Population assessments indicate that the Atlantic stock is overfished, and biomass levels are 40% below the level that would support a maximum sustained yield [17, 18]. The species is currently classified as 'Vulnerable' on the IUCN (International Union for Conservation of Nature) Red List of threatened species, with a declining population trend [19].

Despite ocean-wide connectivity, mark-recapture records and satellite tagging suggest that blue marlins may spend a high proportion of time in subregions of their stock range [8, 20, 21]. The biology and spatial ecology of blue marlin in the eastern north (NE) Atlantic is poorly understood, particularly in the waters surrounding Madeira, Portugal, where the species has been fished by recreational fishermen since the 1970s [22]. The fishing season for blue marlin in Madeira and nearby regions of the Azores, Southern Portugal, Canary Islands and Cape Verde Islands spans from May to September [23–25]. The distribution of the species outside the summer fishing season is unknown, but is likely to include tropical areas further south, given the affinity of the species to warm water above 24 °C [21, 26–29]. Recreational fisheries in Madeira and other regions are primarily based on catch and release [25] and post-release mortality is generally low (~5%) [30]. Conversely, incidental catches on longline fisheries, targeting tuna and swordfish, account for the majority of the fishing mortality of Atlantic blue marlin [18, 31]. Recent development of a surface drifting longline fishery, targeting the swordfish *Xiphias gladius* and other pelagic fish in some areas of the NE Atlantic [32], has generated concerns about potential interactions with vulnerable pelagic species, such as sea turtles [33, 34] and blue marlin. Studies from other regions show that blue marlin spend most of the time in the first few meters of the water column [21, 26, 27], therefore, increasing their susceptibility to bycatch by surface-based fishing gears [18]. Individuals have also been recorded to perform diel vertical movement patterns, remaining very close to the surface at night, while oscillating between the surface and deeper waters (>100 m) during the day, presumably driven by a visually based foraging strategy [26, 28, 35]. These patterns, however, can be highly variable between individuals and vary depending on the temperature and dissolved oxygen levels of the surface mixed layer [21, 36–38]. So far, no telemetry studies have tracked the movements and vertical habitat use of blue marlin in the NE Atlantic. Filling this knowledge gap is crucial to understand blue marlin ecology and evaluate potential interactions with fisheries or other anthropogenic activities. In this study we used pop-up satellite archival tags to monitor the movements and patterns of depth and temperature utilization of blue marlin off Madeira and adjacent regions, obtaining the first insights into their spatial ecology in the region.

Methods

Biotelemetry

Three blue marlin were tagged with pop-up satellite archival tags (PSATs) off the south coast of Madeira Island, Portugal in August 2012 (Table 1, Fig. 1). PSATs were of type MK10 from Wildlife Computers (Redmond, WA, USA), leadered with 18–20 cm monofilament fishing line (136 kg test), which was protected by a layer of braided Kevlar surrounded by shrink-wrap to prevent abrasion. One end of the leader was affixed to the tag and the other end had a 6 × 1.3-cm titanium dart attached with stainless steel crimps.

Tagging was performed by sportfish anglers as part of the International Great Marlin Race (IGMR) organized by the International Game Fish Association (IGFA) in collaboration with Stanford University (https://igfa.org/the-great-marlin-race/). Blue marlin were caught on rod and reel with artificial baits, trolled in spreads of four or five lures off sport fishing vessels at 7—10 knots. Once a blue marlin was caught on hook and line, the fish was brought alongside the boat for tagging. Using an aluminum tagging pole, the tag was inserted into the dorsal musculature of the marlin just below and behind the leading edge of the dorsal fin. Once the tag was affixed, the hook was removed from the blue marlin's mouth and the fish released. Fish weight was visually estimated during tagging by experienced recreational anglers.

Table 1 Summary of tracking records of three blue marlin (*Makaira nigricans*) tagged in Madeira, Portugal in August 2012

Fish ID	Tag ID	Weight (kg)	Deployment date	Pop-up date	Track duration (days)	Max depth (m)	Min temp (°C)	Max temp (°C)
BM1	11A0721	320	2012–08-03	2012–08-27	24	224	15	25.2
BM2	11A0717	227	2012–08-10	2012–11-01	83	302.7	14.3	28.6
BM3	11A0724	272	2012–08-23	2012–11-07	76	336	12	27.0

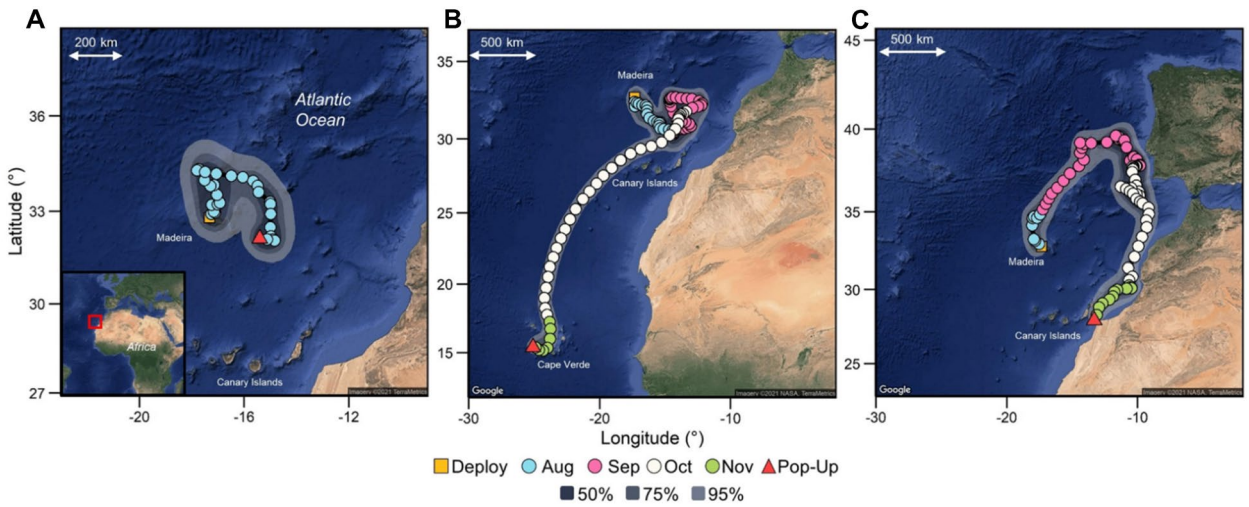

Fig. 1 Estimated most probable tracks for three blue marlin, BM1 (**A**), BM2 (**B**) and BM3 (**C**), equipped with pop-up satellite archival tags off Madeira, Portugal in August 2012. Circles are daily estimates of location derived from transmitted light, depth and temperature data and are coloured by month and deployment and pop-up locations. Inset map indicates location of study region. Polygons represent the merged probability density surfaces for each PSAT, with light to dark shades representing 95%, 75% and 50% probability contours. Note that the horizontal scale differs between maps

The tags were programmed to record temperature, depth and light at 1-min intervals. Data were recorded on the tag until either the tag reached its programmed 120-day deployment period, or it detected no change in depth greater than ± 2.5 m for a period of 96 h, indicating that the tag had either pulled free from the fish or that the fish had ceased all activity. Once one of these conditions was met, the tag passed an electric current through the corroding pin attaching it to the leader, causing it to be released and brought to the surface. Upon surfacing, the tag transmitted for a period of 7–10 days, relaying the tag location and a summary of its stored data through the Argos satellite system. Summary data were provided for daily (24 h) blocks that included: (i) time-at depth (TAD), i.e., the proportion of time spent within 12 depth bins (0–5, 5–10, 10–25, 25–50, 50–100, 100–150, 150–200, 200–250, 250–300, 300–500, 500–1000 and > 1000 m); (ii) time-at-temperature (TAT), i.e., the proportion of time spent within 12 temperature bins (< 8, 8–10, 10–12, 12–14, 14–16, 16–18, 18–20, 20–22, 22–24, 24–26, 26–28 and > 28 °C), (iii) maximum depth, (iv) mean sea surface temperature (SST), i.e., temperature at 1 m depth; and (v) light levels. One tag was physically recovered, allowing the whole archival data set (1-min sampling interval) to be downloaded.

Data analysis

Data received from the PSATs were processed using the Wildlife Computers software (DAP Processor; Wildlife Computers, Redmond, WA, USA), which provided daily summaries of time-at-depth, time-at-temperature, max depth, mean SST and light level. Daily geolocation estimates were generated for each individual using the Wildlife Computers GPE3 software, a discretized hidden Markov model that requires observations of light level, SST, and maximum swimming depth as inputs [39]. Pop-up locations were estimated by the Argos System using Doppler shift. Only Argos messages with location classes 2 and 3 (accuracy 500 and 250 m, respectively) were used to determine the pop-up location of each fish. The straight-line distance between tagging and pop-up locations were determined using great circle distance. Probability density surfaces of 50%, 75% and 95% were also calculated for each individual by averaging the 24-h probability density surfaces generated by GPE3 and resampling the 0.25° GPE3 grid at a resolution of 0.0125° with bilinear interpolation using the packages 'ncdf' and 'raster' in the R statistical environment [40]. The resulting tracks and probability density surfaces were subsequently plotted using the R packages 'ggmap' and 'ggplot2'.

Depth and temperature data were used to investigate the vertical distribution and thermal preference of blue marlin in the NE Atlantic. The proportion of time spent in each depth and temperature bin was plotted using ggplot2. For fine-scale data recovered from a physical tag, the R package 'suncalc' was used to split the data into diel phases by determining times of sunrise and sunset at each daily geolocation estimate [41]. Igor Pro ver.

8.0.3.3 software (Wavemetrics, Inc. Lake Oswego, USA) was used to plot depth profiles and ambient temperature data.

Results

Tagged blue marlin were tracked for 24 to 83 days and together collected 183 days of tracking data (Table 1). All three individuals were tagged in the same year and month (August 2012) and in the same site located off the south coast of Madeira (Table 1). Pop-up locations were determined with accuracies of 250 m, 500 m and 250 m for individuals BM1, BM2 and BM3, respectively. Most-probable tracks, probability surfaces and pop-up locations indicated that the tracked fish used pelagic waters off the archipelagos of Madeira, Canary Islands and Cape Verde, all located outside the northwestern coast of Africa, as well as along the continental shelf brake of Europe and Africa (Fig. 1). Individuals tended to move southwards in autumn, notably in October and November (Fig. 1). The maximum straight-line distance from tagging to pop-up location was recorded by BM2, with 2050 km moved in 83 days, representing an average displacement of 24.7 km/day (Fig. 1). The tag from this individual popped up near Cape Verde in November 2012, and was found on a beach in Eleuthera, Bahamas, in February 2021, enabling the full archival record to be downloaded.

All three tagged blue marlin spent the majority of their time (89%) in the top 50 m of the water column, but 71.6% of that time was in the top 5 m (Fig. 2). Individuals spent a small proportion of time in mesopelagic waters (>200 m), with a maximum depth of 336 m recorded by BM3 (Table 1). Ambient temperatures ranged from 12 to 28.6 °C (Table 1, Fig. 3), but the majority of time was spent in water ranging from 20 to 26 °C (Fig. 2). BM3 spent more time in the lower temperature range at 20–22 °C (29.8%) than the other two fish (BM1: 7.24%, BM2: 1.9%), coinciding with its movements into higher latitude waters (Figs. 1, 2, 3).

The PSAT tag from BM2, recovered in the Bahamas in 2021, provided access to the entire fine-scale data set, i.e., depth and temperature time-series at a 1-min frequency. These data revealed fine-scale patterns of diel vertical migration (DVM) throughout the deployment record for this individual (Figs. 4, 5). Mean depths (±SD) at day and night were 22.2 ± 43.6 and 3.0 ± 10.1 m, respectively. Notably, median depths did not differ between diel periods (day = 1.4 m, night = 0.8 m). During the night, this individual spent > 90% of the time in surface waters < 5 m with limited vertical movements, while during the day, surface movements were interspersed with deeper dives to depths > 50 m (Figs. 4, 5). As autumn progressed and BM2 moved southwards (Fig. 1), SST increased from ~ 24 to 28 °C (Fig. 5). Median daytime depth remained < 2 m until the last four days of the deployment, where median depths of 10.3, 19.3, 22.33 and 27.3 m were recorded, coinciding with increased ambient water temperature both at the surface and at depth (Fig. 5).

Discussion

This study collected valuable information on the movements and habitat use of blue marlin in the NE Atlantic. Despite the low number of deployments, the tracked individuals accumulated 183 days of movement data in an Atlantic region which has not been previously studied. Blue marlin were tracked from Madeira to pelagic areas off the Canary Islands, Cape Verde and within the productive eastern boundary current off the African and European continental shelves. Individuals moved southwards in autumn, i.e., October and November, possibly reflecting a seasonal southward migration as a response to cooling sea temperatures further north. Our results demonstrate high mobility of the species across international borders in the NE Atlantic during a period of less than 3 months, supporting the highly migratory nature of this species [7–9]. Animals moved up to 24.7 km/day, which aligns with displacement rates reported in previous studies in the Pacific and west Atlantic [27, 29, 42].

Diving behavior and water temperature preferences off Madeira were similar to those of blue marlin previously tagged with satellite and acoustic tags, demonstrating a preference for shallow (0–5 m) and warm (20–26 °C) waters [21, 26–29]. Blue marlin tagged in this study spent more than 70% of their time in the upper 5 m of the water column. The substantial use of surface waters is common to blue marlin in the western Atlantic and Pacific [26, 35, 43] and is also common to other billfish species [36, 44]. This makes these fish particularly susceptible to incidental catches on surface-based fishing gear [26]. In the offshore banks around Madeira, surface longline fisheries that target swordfish operate mostly during autumn and winter [32]. This is well timed, as blue marlin are likely absent from these waters during winter. Still, catch statistics report dozen to hundreds of blue marlin catches by Portuguese and other European surface fishing fleets [18]. Time-series data downloaded from the recovered tag (BM2) revealed patterns of DVM, involving consistent use of the surface at night and deeper dive activity during the day, predominately to depths greater than 50 m. This may result in increased susceptibility to surface fishing gear at night, particularly because surface longline fisheries off Madeira also concentrate their effort during the night [32].

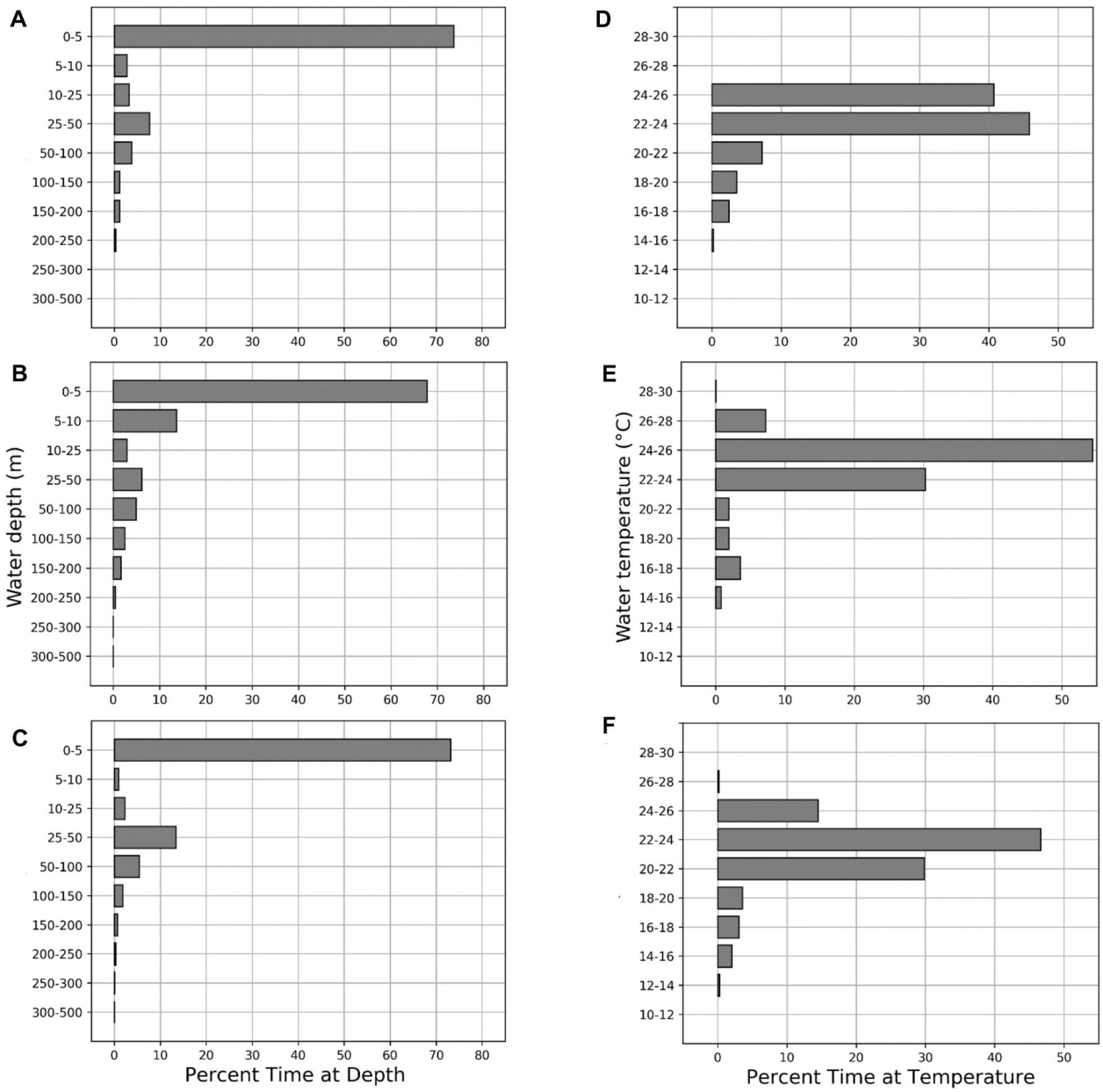

Fig. 2 Percent time at depth (**A**–**C**) and percent time at temperature (**D**–**F**) for blue marlin BM1 (**A**, **D**), BM2 (**B**, **E**), and BM3 (**C**, **F**), tagged off Madeira in August 2012. Histograms for BM2 were made using 1-min time-series data retrieved from the recovered tag

Fine-scale dive data from BM2 also showed deeper diving activity during the day, a pattern previously reported for blue marlin in the west Atlantic and Pacific [26, 28, 35]. These predators are likely using ambient light available during the day to locate prey at light-limited depths, where their morphological and physiological visual adaptations allow them to forage successfully [26, 45, 46]. As temperatures at depth are much cooler than at the surface, however, fish may need to swim back to the surface to rewarm between dives, resulting in a pattern of oscillatory diving during the day. Ambient sea temperature is important for the maintenance of muscle activity in blue marlin, as they lack heat exchangers in the vascular system supplying blood to the swimming muscles and, therefore, do not have the ability to sustain swimming muscle temperature significantly above water temperature, as do tunas [43]. Over the course of its track, BM2 moved approximately 2050 km SSW to

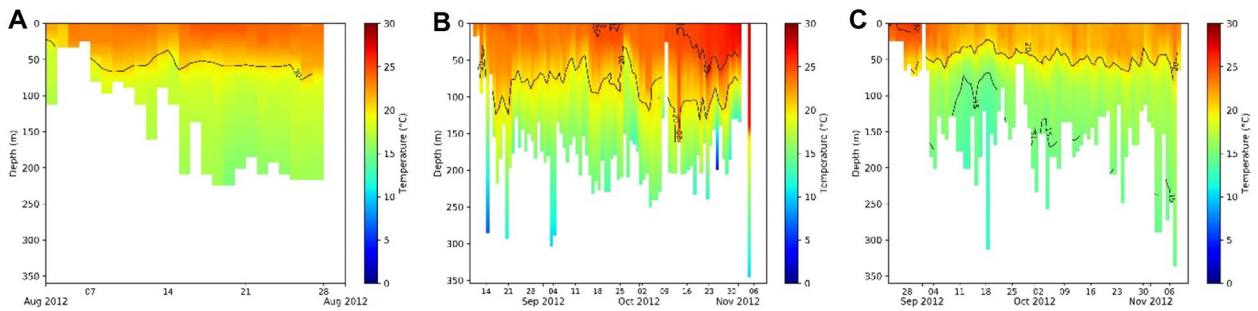

Fig. 3 Temperature and depth profiles for three blue marlin, BM1 (**A**), BM2 (**B**) and BM3 (**C**), tagged off Madeira in August 2012. Data for BM2 from archival data set. Black solid lines display isotherms

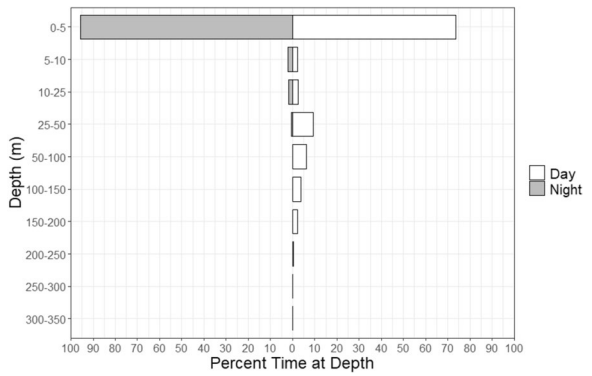

Fig. 4 Percent time at depth for blue marlin BM2 during day and night summarized from recovered archival tag data

Cape Verde. Movements in this southern location coincided with increasing daytime depths and warmer SSTs. The processes underlying this changed vertical behavior are difficult to disentangle but may be due to more suitable ambient temperatures at depth, so that this ectothermic fish did not need to swim back to the surface to rewarm between deep dives. Alternatively, changes in diving behavior may have been driven by local prey availability. This generalist species is known to prey on a variety of epipelagic and demersal fish and cephalopods [47]. Increased sample size of satellite tag deployments is required to further investigate these hypotheses.

In addition to ambient temperature, other factors such as mixed-layer depths and dissolved oxygen availability can limit the vertical and horizontal distribution of blue marlins [21, 36–38]. For instance, blue marlin in the eastern tropical Atlantic (south of Cape Verde) spend a greater proportion of time in near-surface waters when dissolved oxygen is limited at depth, likely increasing their vulnerability to overexploitation by surface gears [37, 38]. Dissolved oxygen levels are generally higher in waters around Madeira and Azores [37]; however, climate change may expand oxygen-limited zones. Understanding environmental drivers of movements and habitat use is vital to predicting where and when a species is vulnerable to fishing pressure, and how patterns may change with a changing climate, both of which are critical for effective management [43] and are, therefore, important factors to be investigated in future studies in this region.

Conclusions

This study provided important initial insights into the movements, depth use and environmental preference of blue marlin in the NE Atlantic. This type of information is vital to understanding the biology and ecology of this apex predator, evaluating their vulnerability to fishing pressure and climate change, and generating effective management strategies [48–50]. Southward movements during autumn are likely to reflect seasonal migration to avoid unfavorable cooling waters further north. Future climate change may allow the species to use the waters off Madeira year-round. The highly migratory behavior of the species in the NE Atlantic suggests the need for local and international management cooperation. Depth use patterns, namely, the high usage of the upper 5 m of the water column, make blue marlin susceptible to surface longline fisheries in the region. Future research, including an increase in tagging effort, with more tags and longer deployments, is needed to obtain a clearer picture of spatial distribution and connectivity between areas within the NE Atlantic, and to identify areas of special conservation interest, such as foraging hotspots, spawning areas and migration corridors.

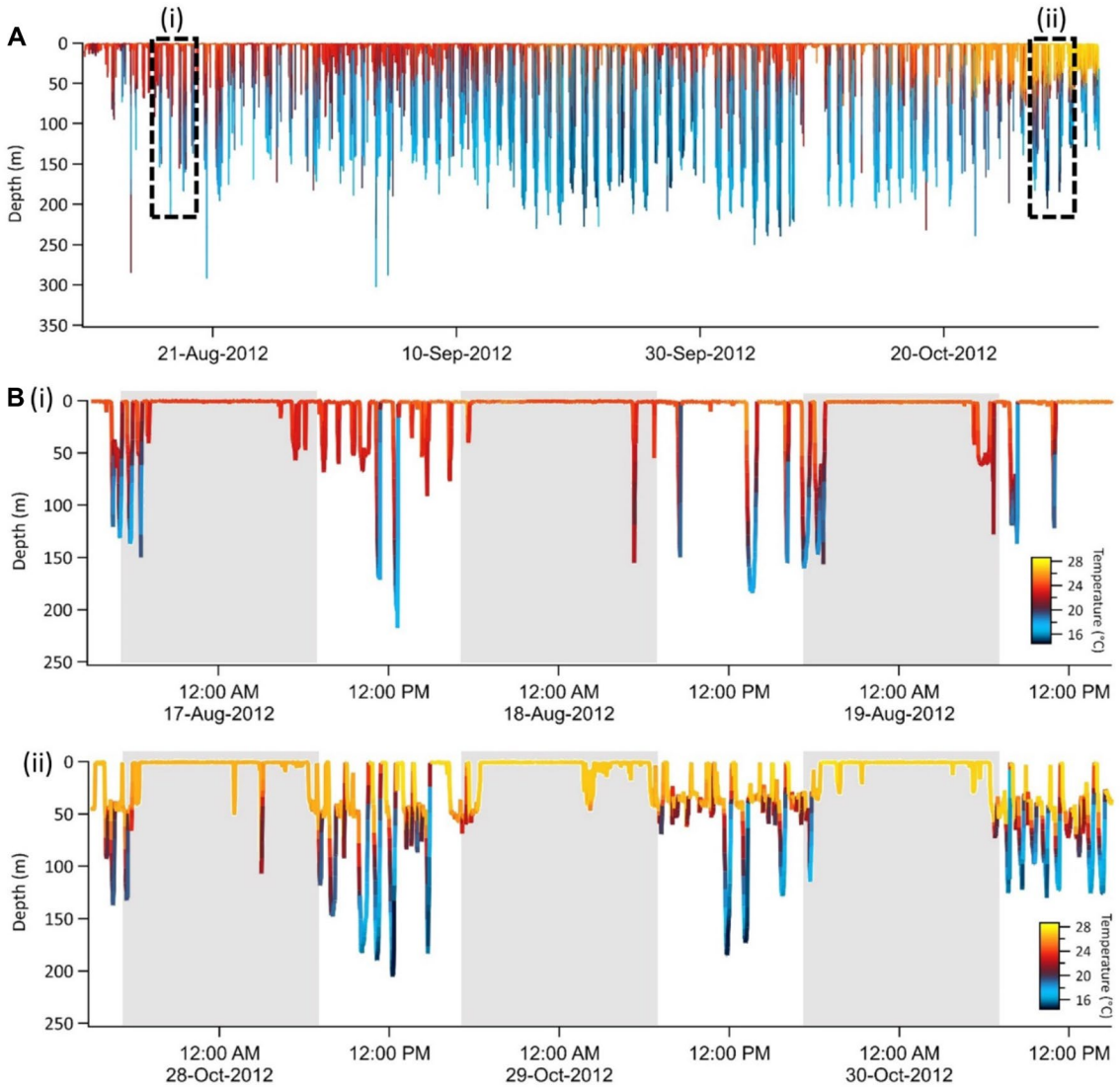

Fig. 5 Raw archived depth time-series data from a blue marlin tagged off Madeira (BM2). Depth traces are shaded by temperature (°C) and are displayed for **A** the full deployment period and **B** three day periods from near the (i) start and (ii) end of the track. Grey areas in panel B correspond to nighttime and white areas to daytime

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Author contributions
Idea conception: WW, MF, BAB. Data collection: WW. Data analyses: CF, SA, JJD. Writing: CF, MF, SA, JJD, BAB. All authors read and approved the final manuscript.

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Availability of data and materials
The data sets used during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
All research was conducted under the Stanford University Administrative Panel on Laboratory Animal Care (APLAC) permit APLAC-10786.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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