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Movement and habitat use of striped marlin *Kajikia audax* in the Western Indian Ocean

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Abstract

Striped marlin *Kajikia audax* are globally Near Threatened and their stock in the Indian Ocean was last assessed as "overfished and subject to overfishing". Significant gaps in our understanding of their ecology remain, hampering the efforts of fisheries managers to ensure stock sustainability. There is a particular lack of fisheries-independent data. Here we present the results from the first large-scale satellite tracking study of *K. audax* in the Indian Ocean. We tagged 49 *K. audax* with pop-up archival satellite-linked tags off the Kenyan coast from 2015 to 2019. Individuals were highly mobile, covering horizontal distances of up to 9187 km over periods ranging up to 183 days, with a mean daily distance of ~48 km. Long-distance movements were recorded to the east and north of East Africa, with the most distant tracks extending north to the Arabian Sea and east to near the Maldives. None of the *K. audax* swam south of East Africa. Kernel utilization distributions of fish locations demonstrated their shifting seasonal activity hotspots. Over the sport-fishing season (and tagging period) in Kenya, from December to March, *K. audax* typically stayed off the East African coast. After March, the activity hotspot shifted north to a region close to the Horn of Africa and Socotra Island. Remotely sensed sea surface temperature and chlorophyll-*a* maps indicated that this seasonal movement could be driven by a shift in prey availability. Our results show the high mobility of *K. audax* in the Western Indian Ocean, and that individuals seasonally range between two major fishing areas.

KEYWORDS

billfish, biotelemetry, movement ecology, satellite tag, Somalia

1 | INTRODUCTION

The striped marlin *Kajikia audax* (Philippi 1887) is a widely distributed istiophorid billfish species in tropical and temperate waters through the Indo-Pacific region. *K. audax* feed largely on epipelagic fishes, such as scombrids (Loor-Andrade *et al*., 2017; Shimose *et al*., 2010), carangids (Young *et al*., 2018) and molids (Shimose *et al*., 2010), but also on cephalopods (Evans & Wares, 1972; Young *et al*., 2018). They reach up to 224 kg in weight and live to at least 11 years old (Collette *et al*., 2011; Hinton & Maunder, 2009). *K. audax* are primarily caught as by-catch in commercial long-line tuna fisheries, but they also provide livelihood support to coastal communities, being harvested in small-scale artisanal fisheries, and the species is an important and valuable target in sports fisheries (Collette *et al*., 2011). Catch data from commercial fisheries has linked their distribution to environmental variables, particularly sea surface temperature, indicating a preferred temperature range of 23–26°C in the North Pacific Ocean (Lien *et al*., 2014). Other studies reported a preferred temperature range of 20–25°C in the Pacific (Howard & Ueyanagi, 1965) and 22–24°C in Mexico (Ortega-García *et al*., 2003).

K. audax are highly mobile, but stocks appear to be regional rather than transoceanic. Several genetically distinct populations exist through the Indo-Pacific, including eastern and western populations within the Indian Ocean (Mamoozadeh *et al*., 2018). The Western Indian Ocean population is the most distinct and therefore isolated (Mamoozadeh *et al*., 2018). Extensive satellite tracking in the Pacific Ocean showed that *K. audax* in Australia, Ecuador, Mexico, California and Hawaii stayed within an ~2000 km radius of their tagging sites and within an ~3500 km radius from New Zealand (Domeier, 2006). Longer movements were generally recorded at the temperate extremes of the species' distribution (Domeier, 2006). Satellite tracks of individual *K. audax* have typically covered short time-scales, with a mean retention of pop-up archival tags of 65 days (*n* = 15; Sippel *et al*., 2011), 49 days (*n* = 24; Domeier, 2006) and 40 days (*n* = 5; Sippel *et al*., 2007). Despite tracking results from most billfishes being limited by similarly short tag retention times (Domeier *et al*., 2019), individual fish have commonly demonstrated rapid dispersal from tagging areas.

No satellite tracking data of *K. audax* exist from the Indian Ocean. Conventional tags deployed off Kenya since the 1950s have recorded only two large-scale movements among the recaptured individuals, with one caught north-east of the Seychelles after 39 days at liberty and another caught off Perth, Australia, after 195 days (Kadagi *et al*., 2011). Since conventional tags only provide the start and end positions of a track, there is limited information on individual movements of *K. audax* within the Indian Ocean. Fisheries-dependent data from commercial catches have suggested that there is a seasonal north–south shift in abundance in the Western Indian Ocean, with higher catch rates in the Arabian Sea and the Gulf of Bengal from March to June, and peak abundance further south, off Kenya, from November to March (Pillai & Ueyandagi, 1978). It is unclear whether these patterns reflect individual movements or region-specific seasonal variations in catchability.

K. audax are classified as Near Threatened on the IUCN Red List with an estimated decline of 20–25% globally over their last three generations based on the species' overall stock assessment in 2011 (Collette *et al*. 2011). The most recent Indian Ocean stock assessments still classify *K. audax* as "overfished and experiencing overfishing" (Parker *et al*., 2018; Wang, 2018b). These assessments used a variety of different models that provided similar results to previous assessments, indicating that the stock has been subject to overfishing for at least the past two decades. Fisheries management and conservation assessment of *K. audax* have been hampered by a lack of data on their biology, ecology and catches within multiple fisheries (Collette *et al*., 2011). Fundamentally, even species identification by fisheries observers has proven to lack reliability (Williams *et al*., 2018). While modern fisheries management principles call for a precautionary approach to managing harvests from the species in the face of such uncertainty, species-specific catch limits for billfishes are yet to be implemented in the Indian Ocean.

Here, we report the results of the first satellite-tracking study of *K. audax* in the Indian Ocean, with the objective to improve understanding of the movement ecology and stock structure of the species. We tracked the movements of 40 of 49 tagged *K. audax* using pop-up archival tags deployed off the Kenyan coast. We aimed to (1) examine whether they disperse from the Kenyan coast; (2) identify their activity hotspots; (3) determine whether they display seasonal patterns in habitat use; and (4) identify the environmental conditions that may drive their movements.

2 | MATERIALS AND METHODS

2.1 | Tagging location

K. audax were tagged off the Kenyan coast. Watamu was the main tagging location, with 34 tags deployed, followed by Shimoni on the southern coast of Kenya (13 tags; Figure 1). Two tags were deployed between these two sites, off Mombasa. The Kenyan coast is a hub for sport fishers targeting billfish, with over 30 recreational fishing boats operating during the peak season. *K. audax*, black marlin *Istiompax indica* (Cuvier 1832), blue marlin *Makaira nigricans* Lacepède 1802, broadbill swordfish *Xiphias gladius* L. 1758 and sailfish *Istiophorus platypterus* (Shaw 1792) are all regularly caught during the main fishing season between October and April. Fishing locations varied depending on the target species, but boats typically searched for *K. audax* from ~25–45 km offshore, with water depths at tag deployment locations ranging from 140 to 610 m (mean 330.3 m). All *K. audax* were tagged in daylight hours between 6:00 h and 15:30 h, with 76% of tags deployed between 8:00 h and 13:00 h. Fish weights were estimated by experienced skippers.

2.2 | Tagging procedures

Satellite tags were deployed on *K. audax* from recreational fishing boats by experienced skippers, scientists or trained crew members. Four Desert Star SMOD_C tags were deployed on *K. audax* in 2015. Only two of those tags reported data, which were of limited utility, and hence these tags were not used in further analyses. Thereafter, 49 miniPAT tags from Wildlife Computers were deployed on *K. audax* across four consecutive local fishing seasons: 17 tags in December to February 2015–2016, eight tags in January to February 2017, 17 tags in December to March 2017–2018 and seven tags in December to January 2018–2019 (Table 1). Tags were programmed to always generate light level and sea surface temperature (SST) geolocation data products. They were set to detach from the animal and start transmitting data after a 180-day deployment period or, as a failsafe, to prematurely detach and transmit if the tag either descended past 1700 m depth or stayed at a constant depth for a period of >24 h, indicating either tag shedding (and floating at the surface) or sinking to the bottom in a presumed mortality event. Five tags detached from the fish and floated at the surface, but did not start transmitting data on time due to a clock error not initiating the constant depth release and transmission sequence (Wildlife Computers, pers. comm.). In those cases we used the tags' depth data to identify when the tag detached from the fish and ended the horizontal track at that point accordingly.

The tagging procedure comprised three stages, and the duration of each stage was recorded in a logbook that was submitted as a record. Fish were kept in the water at all times. The first stage was from hooking the fish to bringing it alongside the boat as quickly as feasible ("fight time"). Only fish that were deemed strong and healthy after being caught and reeled in were tagged. During the second stage of the tagging procedure ("handling time"), one crew member held the bill to control and orientate the fish to ensure its gills received good water flow, while another crew member inserted the tag anchor between the dorsal pterygiophores using a handheld applicator with a 14 cm long pin. Holding the fish by its bill allowed an assessment of its condition to be made, facilitated hook removal and allowed confirmation that the tag was properly attached and well-positioned before the individual was released. Most *K. audax* (84%) were revived after tagging and before release during the third stage ("revive time"). This process involved maintaining the fish alongside the boat as it slowly motored forward until the fish could independently orientate itself and swim away strongly.

Specific tag attachment techniques differed among the fishing seasons as we experimented in an effort to improve tag attachment and retention based on feedback from colleagues, fishers and reported tag data. The tagging procedure itself remained the same throughout the study. Tags deployed in the first season (2015–2016) were attached to a single large "Domeier" umbrella dart using a 300 lb monofilament line. The line was later covered with heat shrink to thicken its diameter. Used alone, we hypothesised that the "naked" monofilament line may have cut into the fish's dorsal tissue, promoting tag shedding. Tags deployed in the second season (2016–2017) had a double tether anchored with two darts. However, tag retention further reduced in 2016–2017, potentially because the double darts hampered tag hydrodynamics and increased handling time. We replaced the umbrella darts with a single surgical grade nylon "flopper" dart that was attached to the tag by a multistrand stainless-steel cable crimped into loops at each end and covered with heat shrink. The final change in 2018–2019 was to remove one of the two crimps in the tether by using the cable as a single loop with only one crimp.

2.3 | Ethical statement

This study and the tagging process were conducted in line with ethical guidelines as provided for under university research and the Ethics Review Committee (ERC) of Pwani University and the conditions of sport fisheries licensing under the Fisheries Management and Development Act No35 of 2016. All *K. audax* were tagged from licenced recreational fishing boats, and BF operated under Kenyan research permit NACOSTI/P/19/2101.

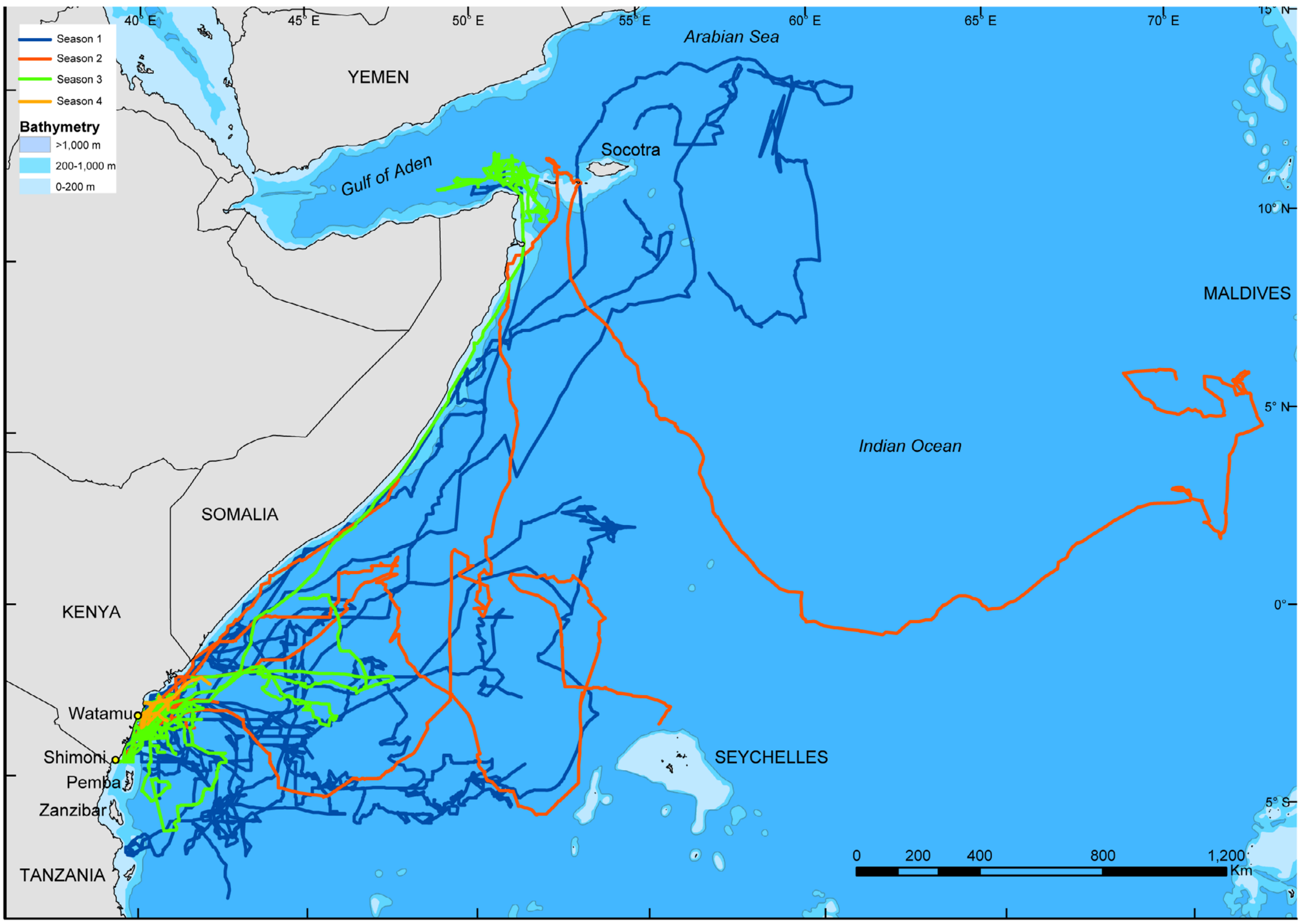

FIGURE 1 Overview of the study area and the most likely tracks for 40 striped marlin *K. audax* tagged off Kenya, colour-coded by tagging season (2015–2019)

TABLE 1 Details for all striped marlin *K. audax* tracks split by season. Tag number, estimated fish weight, tag deployment and pop-up date, retention time, minimum distance covered and mean daily distance covered

Tag number	Weight (kg)	Deployment	Pop-up	Retention (days)	Distance (km)	Daily distance covered (km/day)
142,276	45	22 Jan 2016	22 Jun 2016	153	5474.7	36.2
142,284	90	11 Feb 2016	29 May 2016	109	5239.6	48.7
142,285	50	2 Jan 2016	8 Mar 2016	67	2055.6	31.0
142,286	50	22 Dec 2015	20 Jun 2016	182	8655.3	48.0
142,288	45	26 Dec 2015	17 Jan 2016	23	3151.2	141.2
142,292	20	30 Dec 2015	18 Apr 2016	111	4920.0	44.8
142,294	45	24 Dec 2015	7 Feb 2016	46	2499.5	55.0
142,297	8	26 Dec 2015	8 Jan 2016	14	624.4	49.8
151,777	20	6 Jan 2016	4 Jun 2016	151	7179.2	48.0
151,780	40	29 Dec 2015	11 Feb 2016	45	2113.3	47.8
151,781	20	7 Jan 2016	5 Feb 2016	30	1733.4	60.0
151,782	55	24 Jan 2016	24 Apr 2016	92	3813.1	41.7
151,783	50	26 Dec 2015	28 Mar 2016	94	6637.2	71.3
151,784	30	31 Dec 2015	12 Jan 2016	13	671.1	58.0
142,273	25	7 Jan 2016	DNR			
142,291	20	8 Jan 2016	DNR			
142,293	40	10 Dec 2015	DNR			
159,231	50	2 Jan 2017	15 Mar 2017	73	4370.7	61.0
159,233	55	26 Jan 2017	27 Jul 2017	183	9187.2	50.6
159,234	50	5 Jan 2017	19 Jan 2017	15	289.3	20.2
159,235	50	2 Feb 2017	4 Feb 2017	3	189.0	86.0
159,240	60	27 Feb 2017	13 Apr 2017	46	1641.0	36.9
159,241	23	8 Jan 2017	3 Feb 2017	27	1311.7	51.5
159,229	100	14 Feb 2017	Mortality			
159,238	50	4 Jan 2017	DNR			
159,249	50	19 Jan 2018	22 Jan 2018	4	2.8	1.0
159,250	25	10 Mar 2018	18 Mar 2018	9	341.1	42.3
159,253	60	14 Feb 2018	5 Apr 2018	51	2455.9	48.6
159,255	75	13 Jan 2018	18 Jan 2018	6	144.9	29.1
159,258	70	12 Feb 2018	20 Mar 2018	37	1182.8	33.2
159,259	50	15 Feb 2018	25 Feb 2018	11	276.3	27.7
159,265	45	3 Feb 2018	6 Feb 2018	4	37.1	11.6
159,266	45	9 Feb 2018	14 Feb 2018	6	252.6	53.9
164,976	75	11 Feb 2018	21 Mar 2018	39	2367.6	62.2
164,977	60	5 Feb 2018	11 Feb 2018	7	132.3	21.0
164,982	40	16 Mar 2018	26 Mar 2018	11	281.9	27.6
164,983	65	10 Feb 2018	28 Feb 2018	19	433.6	24.1
164,996	50	14 Feb 2018	20 Feb 2018	7	342.7	63.1
164,997	70	12 Feb 2018	11 Aug 2018	181	7857.2	43.6
159,256	40	24 Dec 2017	Mortality			
159,263	50	16 Feb 2018	NLL			
164,987	80	10 Feb 2018	DNR			
159,254	70	14 Jan 2019	9 Feb 2019	27	987.5	38.6
164,978	50	29 Dec 2018	2 Jan 2019	5	136.9	31.9
164,984	60	8 Jan 2019	11 Jan 2019	4	114.6	36.8

TABLE 1 (Continued)

Tag number	Weight (kg)	Deployment	Pop-up	Retention (days)	Distance (km)	Daily distance covered (km/day)
164,989	75	14 Jan 2019	16 Jan 2019	3	139.5	67.6
164,992	50	16 Jan 2019	20 Jan 2019	5	225.3	67.2
164,993	65	3 Jan 2019	7 Jan 2019	5	271.9	64.6
164,995	45	4 Dec 2018	DNR			
Mean	50.1			48.0	2243.5	47.1
S.D.	18.97			55.74	2673.2	23.1
Min.	8			3	2.8	1.0
Max.	100			183	9187.2	141.2

Note: Tags are grouped into the four deployment periods. DNR, did not report; NLL, no light level data received.

2.4 | Movement analyses

We used Wildlife Computers' GPE3 state-space model to estimate fish positions from the received tag data reporting twilight, sea surface temperature and dive depth. Input variables were GPS locations of tag deployment and satellite-derived locations of where the tag popped up when ARGOS transmissions began. Swim speed, representing the standard deviation of a normal distribution of diffusion rate for the animal, is another required input variable for this model. *K. audax* covered a maximum of 170 km and a mean of 45 km day^{-1} in a near real-time tracking study in the Pacific Ocean (Holdsworth *et al*., 2009). We therefore set the maximum swim speed to 200 km day^{-1}, except for three tags for which a faster speed was required when the model could not find a solution for the 200 km day^{-1} limit. These three tags, #164976, #151783 and #142288, required swim speeds of 250, 300 and 500 km day^{-1}, respectively. Furthermore, the GPE3 model was restricted to locations at sea. The model ideally estimated two locations per day (dusk and dawn) based on light levels, two additional locations per day at noon and midnight, and several locations based on SST data. Duplicate locations based on SST data were removed from spatial analyses. As not all locations were estimated on all days, we had a mean of 7.9 locations per day of tracking. Model outputs included 50%, 95% and 99% confidence area ellipses on 0.25° grid cells for up to 50 estimated locations per track, as well as generating the most likely location multiple times per day. Track length was the sum of the shortest straight-line distances between estimated locations, which is equivalent to the most likely track in the figures. The daily distance covered considered these horizontal movements only and was calculated as track length divided by track duration, expressed as km day^{-1}. The estimated nature of light-level based locations, with errors of ~60–180 km (Hammerschlag *et al*., 2011), means that track length and daily distance are also themselves approximate values. We mapped the most likely tracks in ArcMap 10.4 and display the 200 m and 1000 m bathymetry, as *K. audax* are unlikely to dive deeper than 1000 m (Brill *et al*., 1993; Domeier *et al*., 2019). For maps of individual fish, we also show the 50% and 95% confidence areas of locations along the tracks.

To investigate seasonal changes in the habitat use of *K. audax* in the Western Indian Ocean, we mapped the activity hotspots for all tracks combined and binned by month of the year. First, we temporally standardised *K. audax* locations by calculating centres of activity (COA) for each individual track at 12 h intervals. These COA are position estimates based on weighted means of location estimates over a time period (Simpfendorfer *et al*., 2002). We chose the COA approach over an interpolated location along the track at a regular interval because the most likely tracks have a relatively large location error, and the weighted means of location estimates are likely to better reflect where *K. audax* were active within a given time period. We then calculated monthly kernel utilisation distribution (KUD) areas based on the COA locations with the *ad hoc* smoothing method (href) as the smoothing parameter and a grid of 7000 using the *adehabitatHR* package (Calenge, 2006). The 25% KUD represented the core habitat and the 50% KUD area was the extent habitat during each month. We tested the influence of short tag retention on KUD areas by excluding 13 tags with a tag retention of <10 days in a separate analysis. There were only negligible differences between the two results and we therefore used the KUD areas based on the full dataset.

We investigated environmental conditions at *K. audax* locations to examine potential drivers for their observed movements. Thirty-six tags successfully recorded and transmitted SST data. We compared these tag-recorded temperatures to satellite-derived SST from the GPE3 process for all 40 tracks, which are synoptic SST data provided in the NOAA High Resolution Optimally Interpolated daily SST data (Banzon *et al*., 2019). To examine the vertical habitat, we used bathymetric values at fish locations from the ETOPO1 dataset (Amante & Eakins, 2009). Chlorophyll-*a* (chl-*a*) values for each location of all tags were extracted using the *rerddapXtracto* package in R (Mendelssohn, 2019), with chl-*a* as a monthly composite level-3 data with a 4 km resolution from NASA's MODIS Aqua satellites. We chose monthly over 8-day means to reduce the number of missing values due to cloud cover. To investigate seasonal variation in the wider region, we calculated monthly climatologies, *i.e*., monthly means of SST and chl-*a*, using the same data product for chl-*a* as described above, and monthly composite daytime SST level-3 data with a 4 km resolution from NASA's MODIS Aqua satellites for SST. Chl-*a* data were log-transformed for plotting and we used oceanographic colour scales from the package *cmocean* (Thyng *et al*., 2016). We only used data from months that had at least one tag active. For example, for

January, data from 2016–2019 were averaged; for December, data from 2015–2018 were averaged.

3 | RESULTS

Tagged *K. audax* ranged from 8 to 100 kg in estimated weight (mean ± S.D. = 50.1 ± 18.97 kg, *n* = 49; Table 1). Most individuals (84%) were larger than the minimum weight at first maturity of 29 kg (Hanamoto, 1977). Their fight times ranged from 2 to 45 min (16.8 ± 7.92 min), handling times ranged from 1 to 10 min (2.9 ± 1.56) and revive times ranged from 0 to 10 min (2.0 ± 1.91). Fight time was positively correlated with the weight of the fish ($F = 22.29$, $P < 0.05$), with heavier individuals taking longer to be brought to the boat.

3.1 | Tag performance

Six of the 49 tags (12.3%) did not report any data (Table 1). Another tag did not report any light level data, with ancillary data indicating possible ingestion by a mesopelagic animal. Two individuals appeared to have died immediately after being tagged, with one tag surfacing after 2 days at a constant depth of ~460 m and the second tag surfacing after 5 h at ~300 m (Table 1). These nine tags were excluded from further analyses.

Of the remaining 40 tags, only three tags made the full programmed release after 180 days. Thirteen tags (32.5%) detached after <10 days (Table 1). The overall tag retention ranged from 3 to 183 days, with a mean of 48.0 ± 8.81 S.E. days. Tag retention (mean ± S.E.) decreased over the course of the study, from season 1 (80.7 ± 14.83 days, *n* = 14), to season 2 (57.8 ± 26.97, *n* = 6), to season 3 (28.0 ± 12.43, *n* = 14) and to season 4 (8.17 ± 3.78, *n* = 6). None of the fight, handling or revive times, nor fish weight were correlated with tag retention. Tags transmitted between 37% and 95% (mean 85.4%) of their data before their battery reached exhaustion, with a higher percentage of data received from shorter deployments.

3.2 | Species-level horizontal movements

K. audax tagged off the Kenyan coast were highly mobile, with a mean track length of 2244 ± 2673 km (range 3–9187 km). Tagged individuals generally swam northward and eastward (Figure 1). The waters off Somalia were frequented by many of the tagged fish, with some

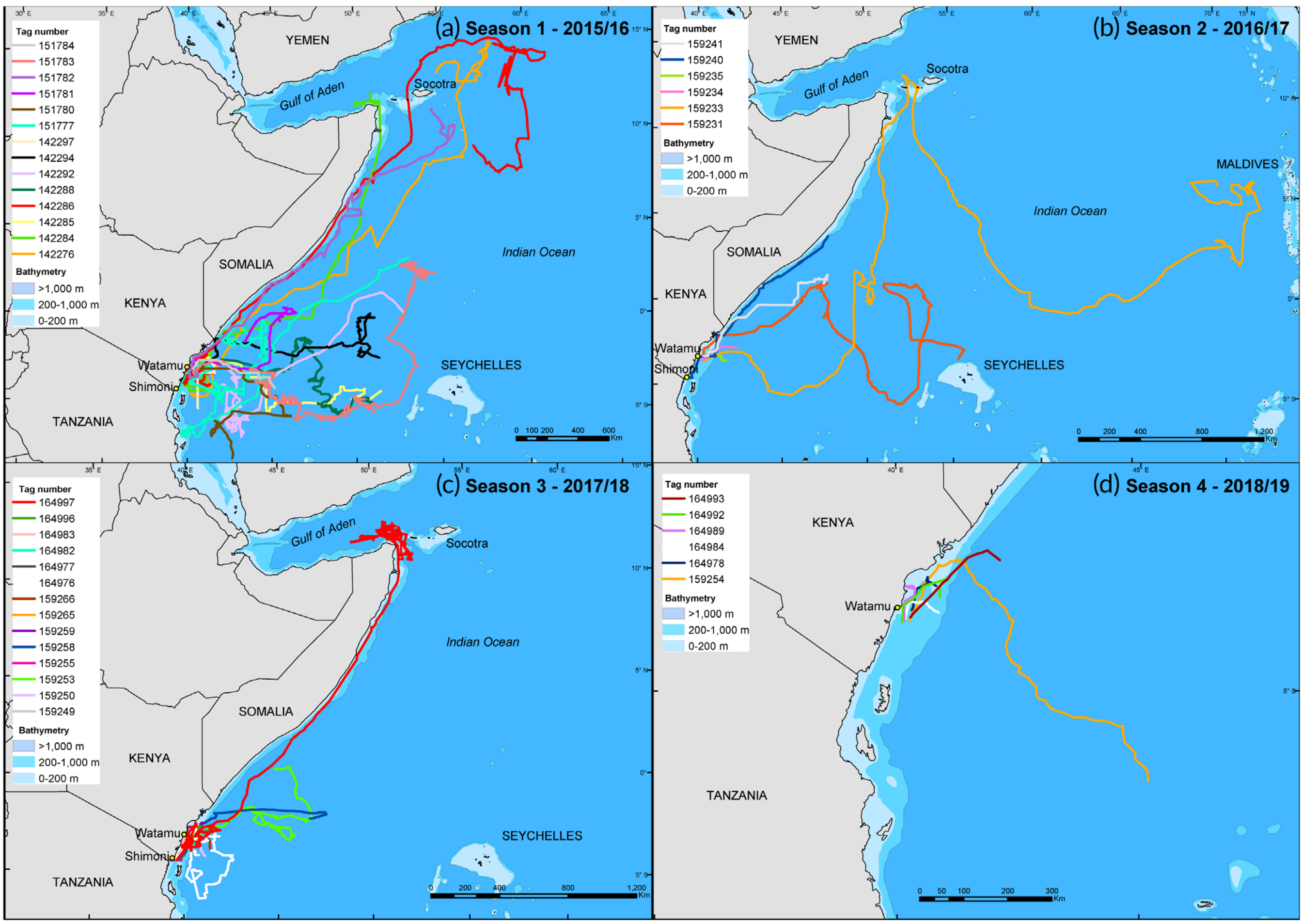

FIGURE 2 The most-likely tracks for 40 striped marlin *K. audax* tagged off Kenya

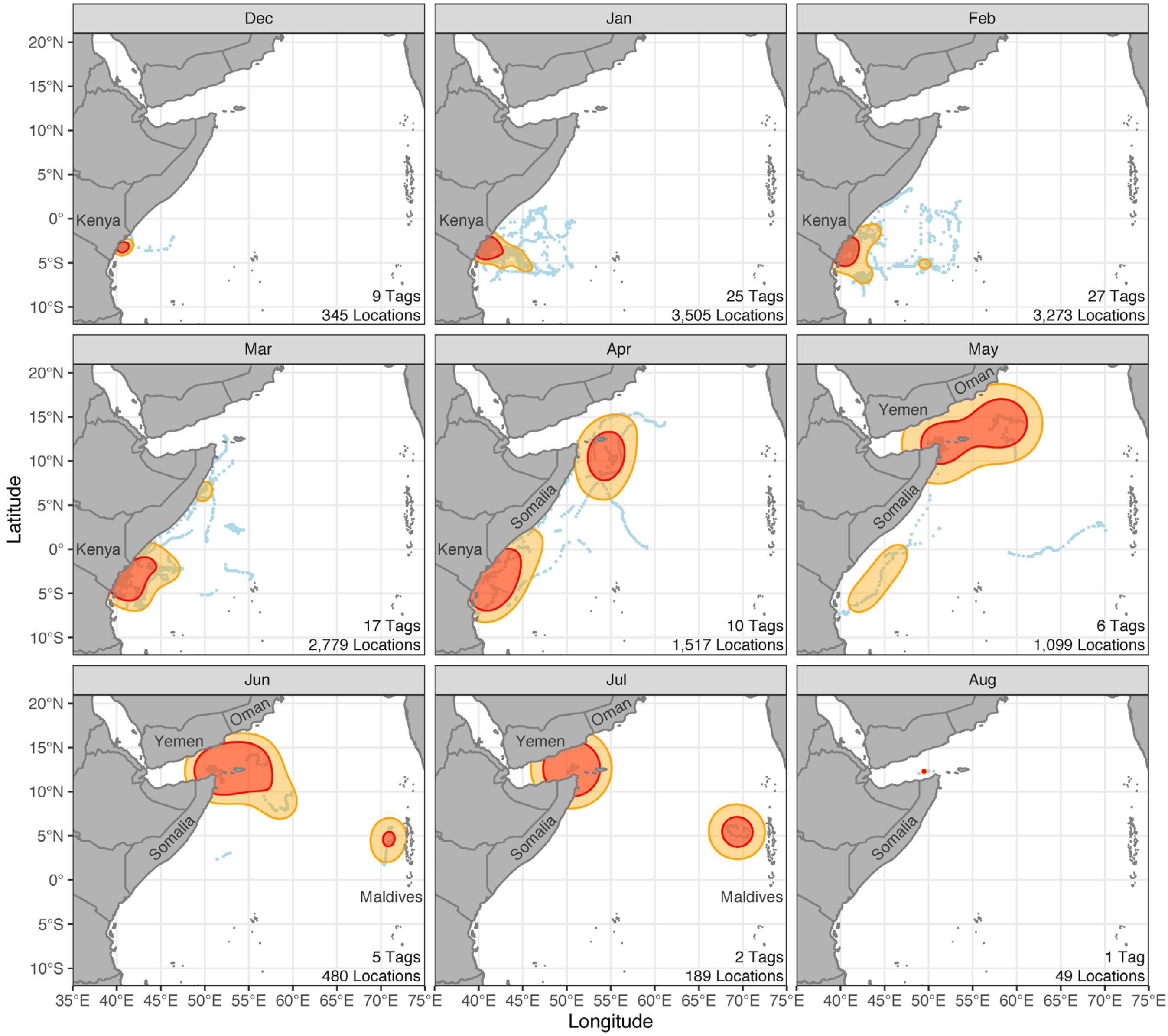

FIGURE 3 Kernel utilisation distribution for all 40 striped marlin *K. audax* tracks combined and binned by month, with centres of activity at 12 h intervals (light blue dots) and 50% (orange) and 25% (red) home ranges. The number of tagged individuals and the number of locations available in each month are shown in the bottom-right corner of each panel

swimming along the shelf edge, ~25 km offshore, and others swimming in deeper waters ~500 km offshore. Some of the northward movements extended as far as the Gulf of Aden and the Arabian Sea, over 2000 km north of the tagging location. The area around the island of Socotra, off the Horn of Africa, was visited by six of the tagged individuals. Eastward movements were often orientated towards and sometimes past the Seychelles archipelago, ~1700 km from the tagging location. None of the tagged individuals swam south of the East African coast (*i.e.*, Kenya and Tanzania) for a notable distance (Figure 1).

With all tracks combined, the tagged *K. audax* covered a horizontal distance of 89,740 km during the 1875 tracking days, resulting in an overall daily distance of 47.9 km day^{-1}. They covered a reduced distance during the night (mean ± S.D. = 1.9 ± 1.22 km h^{-1}) than during the day (2.6 ± 1.24 km h^{-1}; one-way ANOVA, F = 19.6, P < 0.001). Individually, too, half of the tagged *K. audax* (52.5%) covered less distance during the night (P < 0.05). Fish weight was not related to track length (F < 0.0001, d.f. = 38, P = 0.994) or to the daily distance covered (F = 0.279, d.f. = 38, P = 0.60). There were also no differences in track length (t = –0.759, d.f. = 38, P = 0.45) or swim speed (t = –0.4593, d.f. = 22.8, P = 0.63) between small (≤29 kg) and large *K. audax*.

3.3 | Temporal patterns

K. audax tagged in season 1, during the austral summer 2015–2016, largely dispersed north-east. Four of the six tracks to the area around the Horn of Africa were recorded in this season (Figure 2a). The two most easterly tracks were made during season 2 in 2016–2017,

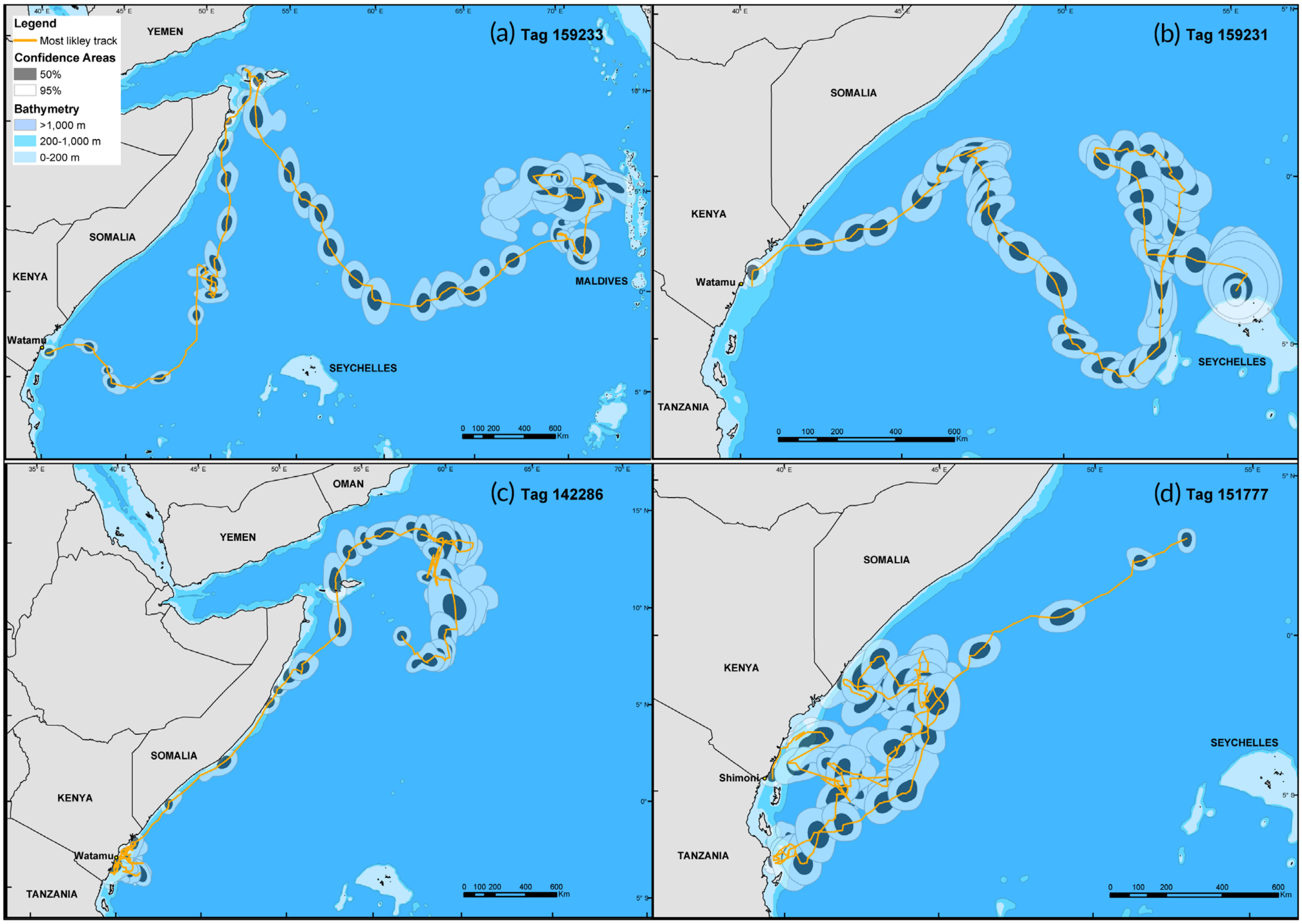

FIGURE 4 Individual tracks of four striped marlin *K. audax*, displaying the most likely tracks based on state-space model estimates, including 50% and 95% confidence intervals. Striped marlin (a) tag #159233, (b) tag #159231, (c) tag #142286 and (d) tag #151777

including the longest track of over 9000 km that ended close to the Maldives after 182 days at liberty (Figure 2b). For season 3, from 2017 to 2018, results were hampered by short retention times for many of the tags. Most tracks in that season were restricted to the waters between southern Somalia and northern Tanzania, but this season also included another long track north to the area around Socotra (Figure 2c). Season 4 in 2018–2019 had the shortest tag retention times, and all individuals stayed within Kenyan and Tanzanian waters during the tag attachment periods (Figure 2d).

Kernel utilisation distribution varied among the tracking months (Figure 3). Tagged *K. audax* remained off Kenya and southern Somalia during the December to March peak fishing season for sport fishers in Kenya, then their home ranges continually moved north along the Somali coast to the Gulf of Aden and the Arabian Sea from April to August. An additional, smaller, hotspot was recorded in June and July by one track, from tag #159233, that moved from Socotra to the Maldives during that period. There were more tag locations in the austral summer (December 345, January 3505, February 3273, March 2779) than later in the year (April 1517, May 1099, June 480, July 189, August 49) due to tags being shed over time.

3.4 | Individual movements

There was clear individual variation in *K. audax* movements. The longest track, 9187 km long over 6 months, was recorded by fish #159233. It started with an eastward movement away from the coast, followed by a northward leg to the Horn of Africa, then an eastward swim to waters near the Maldives (Figure 4a). Other long eastward tracks also featured a northward component, but limited movement to the south (Figure 4b). Fish #142286 exhibited a typical northward dispersal along the Somali coast into the Gulf of Aden and the Arabian Sea, covering 8655 km over the full 6 month programmed deployment (Figure 4c). Some individuals did not disperse widely, but still covered a large horizontal distance. For example, fish #151777 covered 7179 km in 149 days, but largely stayed off the coast of northern Tanzania, Kenya and southern Somalia (Figure 4d). The 50% and 95% confidence areas, calculated for up to 50 locations per track, showed that the most likely tracks in Figure 1 have to be interpreted with some caution. The general patterns remained the same, despite many locations having a relatively large confidence area. All tracks, with the 50% and 95% confidence intervals included, are shown in Supporting Information Figure S1.

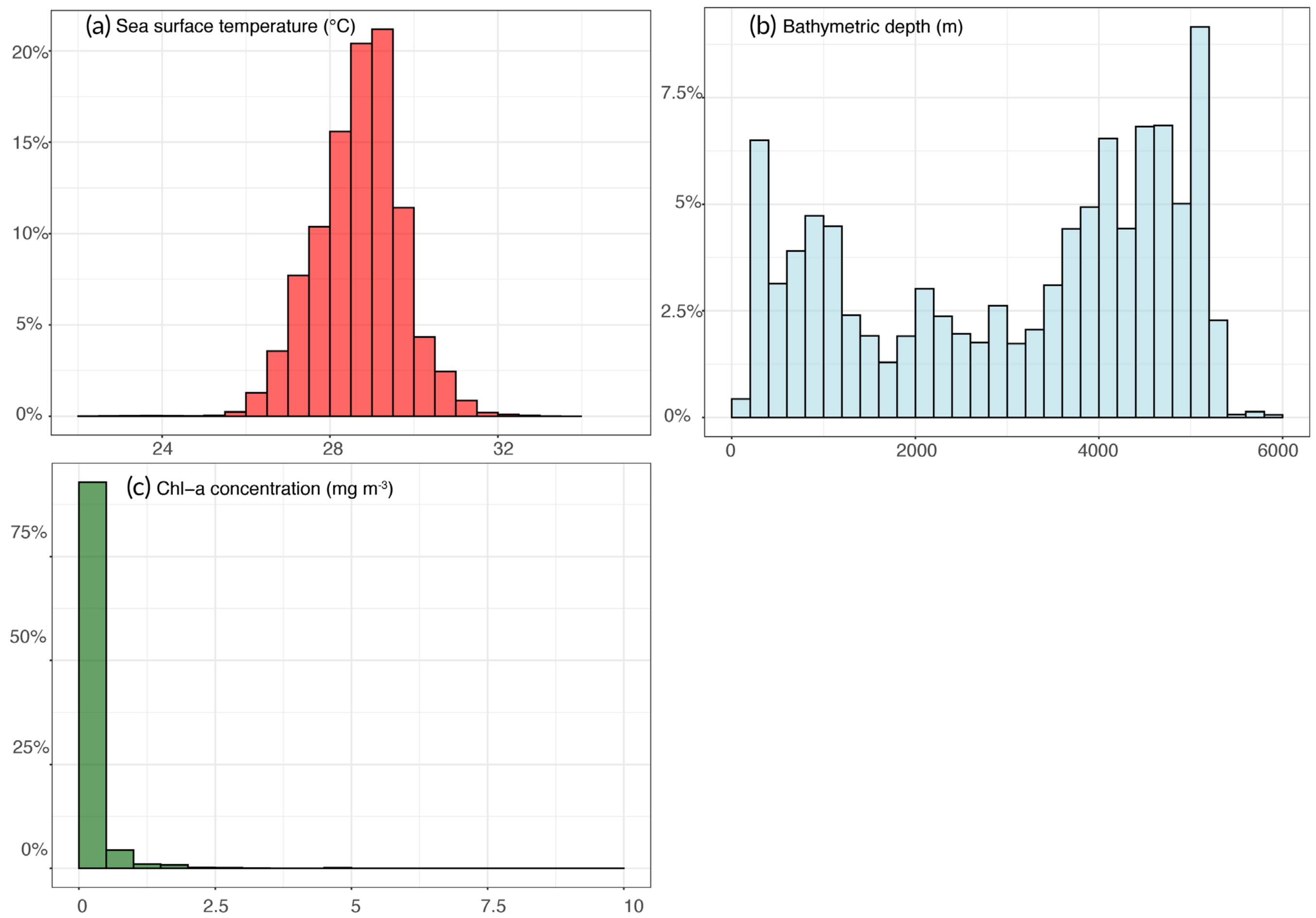

FIGURE 5 Histograms of (a) tag-derived sea surface temperatures, (b) bathymetric depths, and (c) satellite-derived chlorophyll-*a* concentrations at striped marlin *K. audax* positional locations

3.5 | Environmental variables

During the time *K. audax* were in the top 5 m of the water column, and their tags recorded surface water temperatures, they spent most of their time (75.4%) in surface temperatures of 28–30°C. Over 99% of their surface time was spent in warm surface waters between 26 and 31°C (n = 23,858; Figure 5). Monthly mean tag-recorded surface temperatures varied only slightly on an absolute level, from a minimum of 28.4°C in February to a maximum of 29.7°C in April, although most month–month combinations were statistically different in a Tukey test ($P < 0.05$). Tag-recorded and satellite-derived SSTs were similar, with a mean difference of 0.2°C. Most positional locations for *K. audax* were recorded over deep water, with only 0.4% of locations from areas shallower than 200 m and 18.3% of locations from areas shallower than 1000 m (total n = 23,686). Mean bathymetry depth at locations was 3079 m (±1677 m S.D.) for all tagged fish combined, with 29 individual tracks (72.5%) featuring a mean depth of >1000 m. Satellite-derived chl-*a* values ranged from 0.06 to 9.87 mg m^{-3} (mean ± S.D. = 0.23 ± 0.32 mg m^{-3}), with 6191 data points and 976 missing values (15.8%). *K. audax* mostly frequented water with low chl-*a* concentrations, with 68.5% of locations having <0.2 mg m^{-3} of chl-*a* and 96.1% having <0.6 mg m^{-3} (Figure 5).

SSTs and chl-*a* concentrations showed pronounced seasonal variation within the broader study region. During our tagging months, and in the north-east monsoon season from December to February, the relatively cooler waters of the Somali Current met the warmer waters of the East African Coastal Current (EACC) off Kenya (Figure 6a and Supporting Information Figure S2). Chl-*a* was high in that frontal zone, extending east to the South Equatorial Counter-current off northern Kenya (Figure 6b, Figure S3). During the south-west monsoon from June to August, the warm, low chl-*a* EACC extended further north and cold, high chl-*a* upwelling waters driven by the Great Whirl and Socotra Eddy persisted off central and northern Somalia (Figure 6c,d and Supporting Information Figures S2 and S3). The highest temperatures in the region varied only slightly, but the monthly minimum was lowest in July at 14.4°C and highest in April and May at 22.4°C.

4 | DISCUSSION

K. audax dispersed widely from their tagging location in Kenya. Tracks extended north into Somali waters, the Gulf of Aden and the Arabian

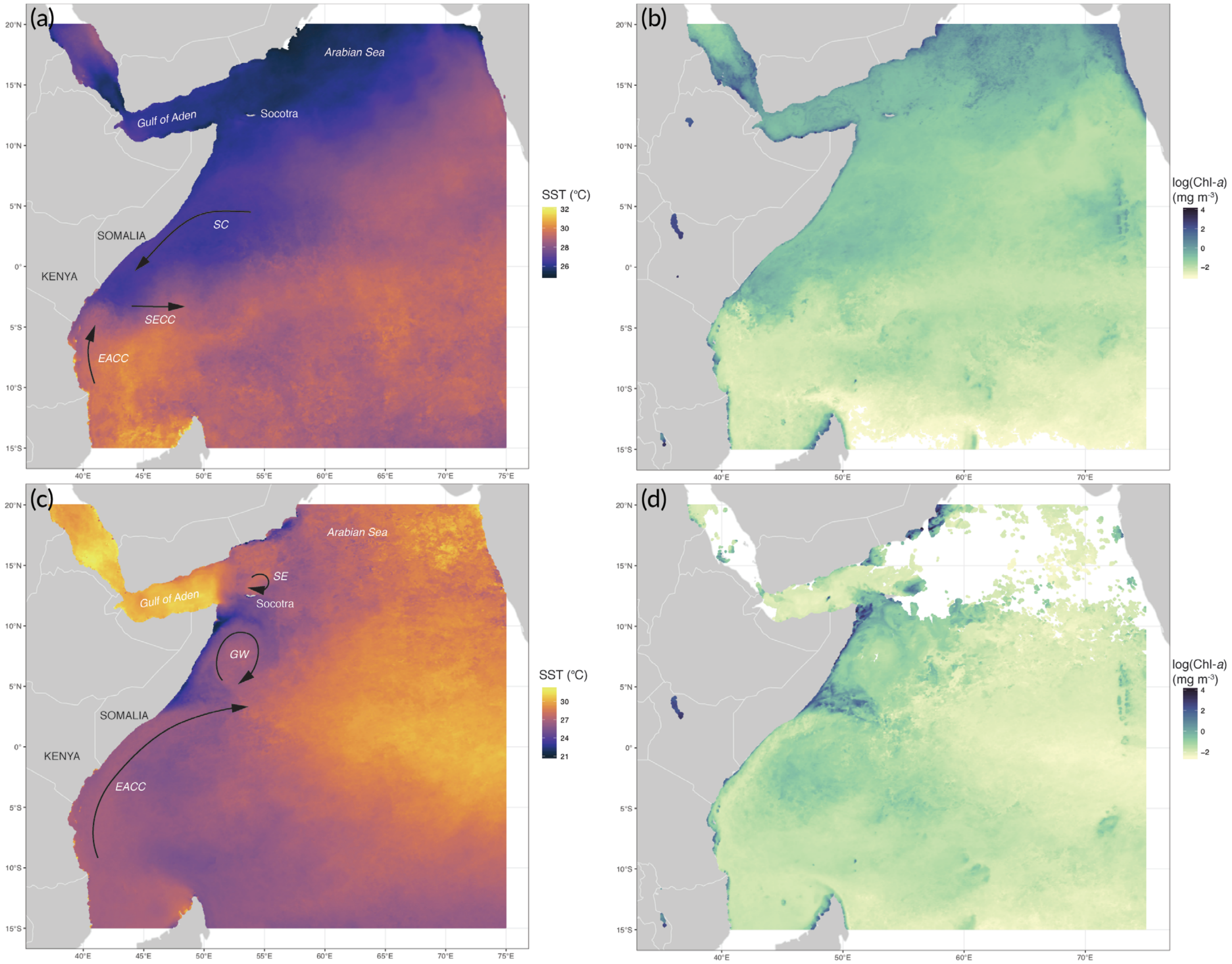

FIGURE 6 Climatologies of sea surface temperatures (panels a and c) and log-transformed chlorophyll-a concentrations (b and d) during January (a and b), representing the north-east monsoon, and during July (c and d), representing the south-west monsoon. Only months and years in which tags were active were included in the climatology calculations. Predominant currents off eastern Africa are shown as black arrows and were taken from Schott & McCreary (2001), with EACC, East African Coast Current; SECC, South Equatorial Countercurrent; SC, Somali Current; GW, Great Whirl; SE, Socotra Eddy

Sea, east to the Seychelles and the Maldives, and south to Tanzania. These first *K. audax* tracks from the Indian Ocean underline the fast swimming and high mobility of this species. Tracks measured up to 9187 km in length, with a mean distance of over 2200 km, with *K. audax* covering similar distances to those previously documented from the Pacific Ocean (Domeier, 2006). The mean daily distance covered, 48 km day^{-1}, was also similar to results from the Pacific Ocean (Holdsworth *et al.*, 2009). Transoceanic movements were not recorded over the tracking duration of this study, which was limited to 6 months maximum, although one individual swam close to halfway across the Indian Ocean in that time, with the tag popping up in the Maldives. Trans-equatorial movements were common, while they were rarely recorded from the Pacific (Domeier, 2006), likely because our tagging location was close to the equator.

4.1 | Tag retention

Tag retention was the major challenge of this study. The mean track duration was 48 days, with only three tags reaching the full 6 months programmed mission prior to detachment. The main reason for the short retention appeared to be that the anchor pulled out of the fish. Only one tag (#142292) reported a mechanical fault, with its pin breaking prematurely. Our results corroborate the difficulty of keeping pop-up archival satellite tags on billfish for extended periods (Domeier *et al.*, 2019). Our experience with changing the tag attachment mechanisms showed no clear ways to improve tag retention. Interestingly, there was no correlation between tag attachment duration and fight, handling or revive times, nor with fish weight. Alternatively, individual fish behaviour, such as frequency of breaching or "free jumping", may play a role in tag retention times. It is also possible that shorter tag retentions were caused by the tag anchor not "locking in" on the pterygiophores. Inserting the dart deep into the shoulder is thus an important consideration for future tag deployments on billfishes.

4.2 | Activity hotspots

K. audax were caught and tagged off the Kenyan coast for this study in waters that have traditionally been a hub for sports fisheries (Kadagi *et al*., 2011). Tagged individuals heavily utilised the area around and offshore from the tagging locations, indicating that northern Kenya is not simply a transit point but rather an important hotspot within their range in the Western Indian Ocean. A second hotspot is located off the Horn of Africa and around the island of Socotra, through which five of seven tracks longer than 100 days passed. This is also an area with high catch rates in commercial fisheries (Pillai & Ueyandagi, 1978; Wang, 2018a), demonstrating that it is an important long-term habitat for *K. audax*. Our tracking data have now shown that these two hotspots in the Western Indian Ocean are utilised by the same individuals swimming between them on a seasonal basis. Other areas frequently visited by tagged individuals, including the waters off the Somali coast and the offshore waters between Kenya and the Seychelles, did not result in activity hotspots based on the KUD analysis, indicating that these are transit areas.

4.3 | Monsoonal influence on activity hotspots

The distributions of *K. audax* varied seasonally, with the timing of these broad-scale movements corresponding to the monsoonal cycle in this region. During the north-east monsoon, from December to February, activity hotspots were off Kenya, northern Tanzania and southern Somalia. At this time of year, the Somali Current flows southwards along much of the Somali coast to just south of the equator, where it meets the northward flow of the EACC. The two currents merge and veer offshore to the east as the South Equatorial Countercurrent (Schott & McCreary, 2001; Shankar *et al*., 2002). During our tracking years, the merging of the relatively cooler water of the Somali Current and the warmer water of the EACC resulted in higher primary production extending eastward from the northern Kenyan coast. This is a common pattern, although the exact location and intensity of the primary production varies temporally (Jacobs *et al*., 2020). While *K. audax* do not feed on phytoplankton, high chl-*a* frontal zones can attract and concentrate their prey, such as pelagic fishes and squid (Evans & Wares, 1972; Ichii *et al*., 2009; White, 1995). This is a likely driver of their seasonal abundance off Kenya.

During the south-west monsoon, from June to August, the main hotspot was off the Horn of Africa and Socotra Island, with an additional hotspot (based on one track) located west of the Maldives. In these months, the surface flow reverses to northward along the Somali coast, and eddies in northern Somalia and off Socotra create upwelling which increases primary production (Schott & McCreary, 2001; Shankar *et al*., 2002). During our tracking years, upwelling along the Somali coast cooled surface waters to ~20–22°C, including in the eddy area extending east from northern Somalia. Although primary production was high in these same areas, *K. audax* stayed slightly north of the upwelling zone. It is possible that the cool temperatures off Somalia lead to individuals staying in the warmer northern waters of the Gulf of Aden and Arabian Sea, either directly due to physiological preferences or indirectly as a result of prey distribution.

4.4 | Site fidelity

K. audax generally stayed within the Western Indian Ocean region over the tracking duration. Such regional site fidelity is common for the species, with most tracked individuals from the Pacific Ocean staying within a 2500 km radius of the tagging location (Domeier, 2006). This regional site fidelity suggests that the Western Indian Ocean stock is separate from the Eastern Indian Ocean stock. A recent genetic study, which included samples from some of our tagged individuals, also showed a separation between the Western and Eastern Indian Ocean populations (Mamoozadeh *et al*., 2018). Low genetic diversity and a high degree of separation from other populations suggest that the Western Indian Ocean population is the most isolated (Mamoozadeh *et al*., 2018). How the two stocks within this population are connected is unclear at present. *K. audax* catches off south-eastern Africa are largely reported from January to March (Pillai & Ueyandagi, 1978), but their year-round movements are not understood. We encourage future research on *K. audax* in the south-west Indian Ocean to allow a better assessment and management of the Western Indian Ocean stock as a whole. Our results support the need for a separate stock assessment of *K. audax* in the Western Indian Ocean, coupled with specific management measures to ensure the sustainability of this distinct stock.

4.5 | Environmental drivers of movement

K. audax in the Western Indian Ocean had a preference for relatively warm SSTs between 26 and 31°C. In other areas, temperature preferences were within a cooler band from 20 to 27°C (Lien *et al*., 2014; Sippel *et al*., 2007). Tracked individuals in the Western Indian Ocean also had access to cooler waters but appeared to avoid these. This variation in apparent surface temperature preference suggests that the species' physiological tolerance may be broad, resulting in indirect influences on habitat use, such as the temperature preferences of their prey, being more important as a driver of their movements. Alternatively, there may be variation among separate stocks in optimal physiological temperatures. Chl-*a* concentrations at fish locations were low, similar to levels found in fishing-dependent data from the north Pacific (Lien *et al*., 2014). Spatio-temporal distributions of chl-*a* showed that areas of higher primary production were available within the region, but tagged individuals did not frequent those waters. The lag from phytoplankton to zooplankton to prey species may explain the low observed chl-*a* values in the areas of distribution of *K. audax*. It is also possible that clearer water with low chl-*a* concentrations represent better conditions for the visual hunting strategy of *K. audax* (Brill *et al*., 1993; Fritsches *et al*., 2003).

4.6 | Future research and management suggestions

Identifying spawning areas for *K. audax* in the Western Indian Ocean is an important next step to aid the management and recovery of their local stock. Evidence from other regions suggests that they spawn near oceanic islands, seamounts and even in coastal waters with local increases in primary productivity (González Armas *et al*., 1999; Hyde *et al*., 2006). Considering our tracking and spatio-temporal environmental data, *K. audax* might thus potentially spawn off the Island of Socotra or the northern Somali coast. The only *K. audax* larvae in the north-western Indian Ocean were found in an area roughly halfway between the Horn of Africa and the Maldives (Pillai & Ueyandagi, 1978), and spawning in the Western Indian Ocean is likely to occur in the south-west monsoon (Merrett, 1971). Although we had fewer tags active during the south-west compared to the north-east monsoon, our tracking data show that *K. audax* are mainly off the northern Somali coast during that time, and the regional circulation during the south-west monsoon would transport these larvae east towards the Maldives (Schott & McCreary, 2001). Further investigation into spawning locations for the species should thus focus on the area around Socotra Island during the south-west monsoon.

Our movement data for *K. audax*, coupled with recent genetic results, indicate that a distinct Western Indian Ocean stock exists for this species. Separate assessment and management should be implemented to ensure the future sustainability of commercial catches and to support the important artisanal and recreational fisheries for billfish along the East African coastline. Management options, such as species-specific billfish harvest limits paired with the use of nonoffset circle hooks that reduce post-release mortality, are being promoted by other regional fisheries management organizations, and the Indian Ocean Tuna Commission (IOTC) could follow these initiatives. A precautionary management approach could also include spatio-temporal management of fisheries. Our movement data, combined with the limited information available on the spawning ecology of *K. audax*, suggest that a seasonal area closure for surface longline fishing covering a suitably large radius around the hotspot off the Horn of Africa and Socotra Island, as well as in the hotspot off Kenya, would facilitate recovery of this stock.

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CONTRIBUTIONS

SP and CR designed the study, RB and BF organised and conducted field work, CR analysed the data and wrote the draft manuscript with SP, and all authors edited the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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