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Vertical habitat use by black and striped marlin in the Western Indian Ocean

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ABSTRACT: Black marlin *Istiompax indica* and striped marlin *Kajikia audax* are large, fast-swimming, oceanic apex predators. Both species are increasingly exploited by fisheries with varied gear encounter rates at different depths, causing concern for their status. Here, we examined vertical habitat use by 34 black and 39 striped marlin caught off Kenya, using pop-up satellite tags to compare their diving behaviours. Tags recorded depth and temperature time-series for a mean (±SD) of 43 ± 53 days per track. Marlin dived extensively moving up to ~14 vertical km in cumulative dives per day in addition to a daily mean of ~50 km in horizontal movements. Both species had similar maximum depths (460–470 m). Striped marlin dived deeper more frequently than black marlin, and also spent more of their time at the water surface (top 5 m: 50.7 vs. 32.3% in black marlin). Most striped marlin had a normal diel vertical migration dive pattern over their track (61.5% of individuals), while ~35% of black marlin showed a crepuscular pattern, diving particularly deep at dusk and dawn. Striped marlin spent almost twice as much time (7.4%) inside the oxygen minimum zone (<150 µmol kg^{-1} dissolved oxygen) than black marlin (4%). The extensive use of surface waters by striped marlin may be a behavioural response to re-oxygenate and/or warm up after dives into cold or oxygen-poor waters. Two free-jumping events immediately before tag detachment demonstrated why it is challenging to keep tags attached to these highly active fishes. Their vertical habitat use shows that both species are highly susceptible to capture in regional drift gillnet and longline fisheries.

KEY WORDS: Billfish · Satellite telemetry · Animal movements · Diving behaviour · Oxygen minimum zone · OMZ · Generalised additive mixed model · Diel vertical migration · DVM

1. INTRODUCTION

Billfishes are some of the largest extant teleost fishes (up to 700 kg) and are apex predators in oceanic habitats (Collette & Graves 2019). Several species are important in commercial fisheries (Sharma et al. 2018, Braun et al. 2019), while others are caught as bycatch (IOTC 2018a,b, Sharma et al. 2018), as well as in artisanal and high-value recreational fisheries (Kerstetter & Schratwieser 2018, Kadagi et al. 2020). Monitoring of billfish stocks lags substantially behind other sympatric fishes, such as tuna (Collette et al. 2011c). Abundance trend data are lacking for some istiophorid billfish species, including black marlin *Istiompax indica*, while other species are decreasing, including striped marlin *Kajikia audax* (Collette et al. 2011a,b). Many billfish stocks have experienced long histories of overfish-

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ing, with all Atlantic istiophorid billfish stocks having shown an overfished stock state for at least a decade (Bealey et al. 2019). Commercial harvests of billfish in the Indian Ocean are increasing, and already likely exceed sustainable limits in multiple species (IOTC 2018a,b, Sharma et al. 2018). Improved management is necessary and requires a better understanding of the ecology of these species (Braun et al. 2015, Collette & Graves 2019). This includes identifying distinct stocks to inform the horizontal distribution and size of management units and describing their vertical habitat use and diving behaviour to assess their vulnerability to different fishing gears.

The use of 3-dimensional habitat by billfish is influenced by physical variables such as temperature, hydrostatic pressure, light, and dissolved oxygen, as well as by prey availability (Braun et al. 2015, Rohner et al. 2020). These factors vary in space and time. Resolving where and at what depth billfish swim is important to understand their interactions with fishing gear and develop specific management strategies (Brill & Lutcavage 2001), particularly when the aim is to reduce bycatch. Since physical properties of the water column vary in space and time, regional studies are important to characterise the diving behaviour of regional stocks and to tailor regional management options. Vertical movements of black and striped marlin have been examined in the Pacific Ocean (Chiang et al. 2015, Lam et al. 2015, Williams et al. 2017), but no vertical movement information exists from the Indian Ocean. In the Indian Ocean, black and striped marlin have recently been shown to disperse widely and move seasonally among areas of high fishing intensity (Rohner et al. 2020, 2021). Although Kenyan and Somali waters were the main habitat of tracked individuals of both species, some habitat partitioning was evident, with black marlin occupying cooler surface waters off central Somalia compared to striped marlin preferring the waters off northern Somalia at the same time (Rohner et al. 2020, 2021). It is possible that the use of vertical habitat by these 2 species tagged simultaneously in the same location also varies, but such vertical habitat niche partitioning has not yet been investigated.

Physiological limits and preferences influence the diving behaviour of billfish in general. Body size has been linked to the frequency and depth of dives in black marlin, with larger individuals diving deeper and more often, potentially because their larger bodies cool more slowly than smaller individuals (Williams et al. 2017). Small shortbill spearfish *Tetrapturus angustirostris* (<20 kg) displayed stenothermy, staying largely in the mixed layer and in a narrow temperature band (Arostegui et al. 2019). If this trend is consistent across billfish species, it is expected that the larger species here (black marlin) would dive deeper than the smaller species (striped marlin). Temperature may also influence their vertical movements. Although billfishes can dive deep into cold waters, they spend most of their time in surface waters and warm up in the sunlit surface layer after short, deep dives. Billfishes are fast-moving, highly migratory, and thus energetically demanding obligate ram-ventilators that must swim constantly to move oxygenated water over their gills (Braun et al. 2015). Therefore, dissolved oxygen levels may also have a large influence on their distribution and movements. Areas with low dissolved oxygen concentration, termed oxygen minimum zones (OMZs), are mostly found in deep water and are thought to exclude billfishes (Kerstetter et al. 2009). Since these OMZs are expanding towards the surface with climate change (Stramma et al. 2008), the habitat of billfishes may decrease vertically, constraining some billfish species to shallower sections of the water column (Stramma et al. 2012). It is unclear at present whether the tolerance to low oxygen concentrations varies among billfish species.

The diving behaviour of billfish is also influenced by the behaviour, availability, and location of their prey. Black marlin are apex predators that feed on fishes, such as hairtail *Trichiurus lepturus* and needlefish (Belonidae), and squid, particularly purple-back flying squid *Sthenoteuthis oualaniensis*, in the Arabian Sea (Varghese et al. 2014, Chiang et al. 2020). Striped marlin in the northeastern Pacific consume mostly squid, particularly Humboldt squid *Dosidicus gigas*, and epipelagic schooling fishes such as chub mackerel *Scomber japonius*, pilchard *Sardinops caeruleus*, and herring *Etrumeus sadina* (Evans & Wares 1972, Abitia-Cardenas et al. 1997). There is variation in diet with size in some billfish species, with larger black marlin targeting mesopelagic prey while smaller individuals mostly feed on epipelagic fishes (Chiang et al. 2020). The ontogenetic differences in prey preferences are likely to influence vertical movements (Williams et al. 2017). For example, if squid are the main target, marlin would have to hunt in deep water during the day, as their identified squid prey species mainly undergo diel vertical migration, feeding at night near the surface and staying in deeper water during the day (Snÿder 1998, Gilly et al. 2006).

This study examined the vertical movements and habitat use by black and striped marlin concurrently tagged with archival pop-up satellite tags off the

Kenyan coast. We aimed to (1) identify their vertical habitat, specifically the depths and temperatures they occupy, (2) examine the influence of the OMZ on their dive depth in different regions, (3) identify environmental variables that drive their dive depth preferences, and (4) assess differences in the vertical movements and the environmental drivers of the diving behaviour to investigate vertical niche partitioning between the 2 sympatric species.

2. MATERIALS AND METHODS

2.1. Tag deployment and datasets

Black and striped marlin were tagged off the Kenyan coast between 2015 and 2019. Wildlife Computers miniPAT tags set to detach after 6 mo were deployed off recreational fishing boats by experienced skippers, researchers, or trained crew, who also estimated fish weight based on prior measured catches. Marlin were kept in the water alongside the boat at all times. See Rohner et al. (2020, 2021) for more details on tag set-up and deployment in each species. Tags recorded depth and temperature time-series and reported daily mixed layer data (its depth and temperature, and the proportion of time spent in the mixed layer) and light-level data. Tags that did not report any data or had a <1 d attachment period were excluded from analysis. In addition to the 9 tag exclusions reported by Rohner et al. (2020), we also excluded tag #159254, which did not have usable depth and temperature time-series data. Wildlife Computers state-space model GPE3 was used to estimate the location of tagged marlin based on light-level, sea surface temperature (SST), dive depth, bathymetric data, and a maximum speed filter of 200 km d^{-1}. We used the most likely track locations from the model output in all analyses. The estimated nature of light-level based locations, with errors of ~60–180 km (Hammerschlag et al. 2011), means that track length and daily swim speed are also themselves approximate values. Prior to analyses, the datasets were trimmed to the time the tag was attached to the fish. All analyses were run in R v.4.1.2 (R Core Team 2021).

2.2. Time-series

Tags recorded depth and temperature every few seconds and, upon detachment, transmitted time-series data summarised in either 5 or 10 min intervals while floating at the surface post deployment. Tags also reported the potential error associated with transmitting a subsample, which was relatively small, with a median error of 1.75 m and a mean ± SD of 3.98 ± 4.17 m for depth readings, and a median error of 0.25°C and a mean of 0.28 ± 0.15°C for temperature. To characterise the extent of vertical movements, we calculated the integrated vertical movement (IVM) index on a daily scale as the sum of the absolute differences between consecutive depth readings within a day (Hays et al. 2012). Tags with a 5 min sampling interval (n = 31) did not have a different daily IVM than tags with a 10 min sampling interval (n = 42; $t = -0.46$, df = 70.9, p = 0.65) allowing us to compare the daily IVM among all individuals. We also calculated the IVM and the vertical speed for 13 physically retrieved tags that had depth readings every 3 or 5 s. Additionally, for retrieved tags, we calculated the diving ratio, which is the proportion of consecutive observations with a different depth (i.e. time spent vertically moving) from all observations. For diurnal analyses, we defined the day from 06:00 to 18:00 h and the night from 18:00 to 06:00 h.

2.3. Mixed layer

Tags recorded daily aggregate data on the mixed layer, including the percentage of time spent in the mixed layer, its average, minimum, and maximum temperatures, and its maximum depth. The mixed layer was calculated using sea surface temperature and any depth–temperature pairs in the top 200 m of the water column. Locations were considered in the mixed layer if they were within 0.5°C of the inferred mixed layer temperature. Additionally, the daily maximum depth of the mixed layer for each fish was used to calculate whether each individual depth record was in or below the mixed layer. A positive value of this relative depth, termed ΔD, means that the fish was in the mixed layer. Similarly, we calculated ΔT as the difference between the recorded temperature in the time-series and the average temperature of the mixed layer, so that a negative value indicated how much colder the water around the fish was compared to the average water in the mixed layer. All positive values were set to 0, as they indicate that the fish was within the mixed layer. ΔT removes possible bias from seasonal temperature fluctuations, while the absolute temperature allows examination of potential physiological temperature limits.

2.4. Environmental influences on depth use

We assessed the influence of several predictors on the mean and maximum daily swimming depth of tagged black and striped marlin with generalised additive mixed models (GAMMs). The maximum swimming depth of black marlin off eastern Australia (Williams et al. 2017) and striped marlin in the Pacific (Lam et al. 2015) was influenced by the oxygen concentration at depth, the depth of the mixed layer, SST, and location, so we also included these predictors in our models. We used the threshold of <3.5 ml l^{-1} or <150 µmol kg^{-1} to define the OMZ for marlin, following Stramma et al. (2012). Dissolved oxygen data were downloaded from the World Ocean Atlas 2018 as the annual mean in a 1 × 1 degree resolution. The climatological nature and coarse resolution means that inferences made from these oxygen data need to be treated with caution. The oxygen level predictor was modified to be the minimum depth of the OMZ rather than the oxygen concentration at an arbitrary depth. We also used fish weight as a predictor considering the ontogenetic variation in vertical swimming behaviour seen in black marlin (Williams et al. 2017). Surface chlorophyll *a* (chl *a*) concentration was added as a predictor because water clarity is likely to influence the visual hunting strategy of marlin. Mean 8 d chl *a* data at 4 km resolution from NASA MODIS Aqua satellites was downloaded with the 'rerddapXtracto' package (Mendelssohn 2021). Bathymetric depth at marlin locations was extracted from the ETOPO dataset using the 'marmap' package (Pante & Simon-Bouhet 2013) and added as a predictor to examine whether seafloor depth had an influence on marlin swimming depth. SST was recorded by the tags. To account for a seasonal effect, the day of the year was added using a cyclic cubic spline smoother. We also used the illuminated fraction of the moon as a predictor, extracted with the 'suncalc' package (Thieurmel & Elmarhraoui 2019), because the moon can influence biorhythms of fish due to differences in available light (Agenbag et al. 2003, Pohlot & Ehrhardt 2018). Tag number was the random variable in the GAMMs to account for multiple observations from the same tagged individual. GAMMs were constructed with the 'mgcv' package (Wood 2015). We used a Gaussian family with an identity link function after visually assessing the error distribution (Wood 2017). We tested the data for collinearity between predictors using a Pearson rank coefficient with a cut-off correlation value of 0.5. To account for the correlation between SST and month or day of year (0.57) we fitted an autoregressive moving average process to the residuals that was nested within each month. The naive model was compared to models with 3 orders of autoregression (1–3) using a generalised likelihood ratio test for linear mixed-effect objects. ANOVAs on single-predictor deletion were then used to evaluate the inclusion of each predictor with the *t*-test assessing their significance. All predictors except for month were continuous and smoothed.

2.5. Overlap with fisheries

We estimated the gross vertical habitat overlap with fisheries for these 2 species. Gillnets account for >50% of black marlin catches in the Indian Ocean, followed by troll and handlines (32%), and longlines (12%) (IOTC 2020). Gillnets also account for an estimated 50% of total catch of striped marlin in the Indian Ocean, followed by longlines (40%) (IOTC 2020). We focussed on vertical habitat overlap with gillnet and longline fisheries for these analyses. There are significant issues with catch reporting, particularly in pelagic gillnet fisheries, and high variability within some gear types occurs because, for example, gillnets vary in length from ~100 m to over 30 km, and from <5 to >20 m depth (Anderson et al. 2020). Although nets exceeding 2.5 km in length are banned in the high seas within the IOTC management area, their use does still occur (Aranda 2017). We followed Roberson et al. (in press) and assumed that gillnets are deployed with a depth of 0–20 m (Aranda 2017). Limited data are available on longline depth profiles, and they can be adjusted during individual fishing trips to best target available species, but this fishing method has a large depth range, from 0 to 400 m and sometimes deeper (Song et al. 2009, 2012). Again, we followed Roberson et al. (in press) by applying 0–400 m as a precautionary value.

3. RESULTS

3.1. Tag performance

Of the 49 tags deployed on black marlin, 34 tags reported data from individuals with estimated weights of 40–227 kg (mean ± SD = 93.2 ± 44.2 kg; Rohner et al. 2021). These tags transmitted data over 1098 tag-days with 126 314 depth readings and 126 062 temperature readings. Of the 49 tags deployed on striped marlin, 39 tags reported data from individuals with estimated weights of 8–90 kg (49.6 ±17.6 kg;

Rohner et al. 2020). These tags transmitted data over 1642 tag-days with 192 107 depth readings and 190 854 temperature readings. There were gaps in the depth and temperature time-series of both species, because black marlin tags transmitted 83.0 ± 9.8 % (mean ± SD) and striped marlin tags transmitted 85.1 ± 11.6 % of their data before running out of battery (Tables 1 & 2). We physically recovered 7 black marlin tags and 6 striped marlin tags (Tables 1 & 2). Recovered tags stayed attached to the fish for between 3 and 52 d (mean ± SD = 13.1 ± 12.9 d) to provide a total of 170 d of high-resolution depth and temperature data.

3.2. Depth and temperature habitat use

Black marlin dived to a maximum depth of 472.5 m (Table 1), and striped marlin dived to 463.5 m (Table 2). The mean maximum depth of each black marlin track was 173 ± 88.0 m, with 10 tagged individuals (29.4 %) diving deeper than 200 m. The mean maximum depth of each striped marlin track was 222 ± 97.9 m, with almost half of the tagged individuals (48.7 %) diving deeper than 200 m. On a daily scale, the mean daily maximum depth was 106 m for black marlin and 135 m for striped marlin. Smaller black marlin had a deeper daily maximum depth than

Table 1. Details of black marlin tracks, with the integrated vertical movement (IVM) and time in the mixed layer (ML) and in the oxygen minimum zone (OMZ). Tag numbers in **bold** represent tags that were physically retrieved

Tag number	Weight (kg)	Retention (d)	Transmitted (%)	Horizontal distance (km)	Mean (SD) daily IVM – transmitted (m)	Max depth (m)	Mean (SD) depth (m)	Temp range (°C)	Mean (SD) time in ML (%)	Time in OMZ (%)
142274	80	51	76	2539	1212.3 (942.9)	175.5	16.2 (26.6)	16–28.9	85.8 (9.9)	0.2
142275	55	23	92	497	2333.5 (1281.1)	336.5	84 (38.3)	14.2–28.2	66.4 (20.5)	5.1
142277	70	28	91	830	1977.6 (1009.5)	224	55.6 (34.1)	21.2–29.2	62.3 (23.5)	2.7
142279	73	11	80	447	1281.4 (829.9)	157	17.7 (26)	18–29.7	79.8 (12.8)	0.2
142280	65	180	68	9505	1646 (1222.7)	239.5	31 (38.3)	13.6–30.7	68.9 (16.4)	3.4
142281	60	184	73	8187	1714.8 (1373.8)	253.5	38.7 (34.8)	14.4–33.8	54.1 (24.5)	19.4
142282	109	167	75	11944	632.5 (464.4)	168	17.8 (18.6)	15.2–30.4	85.7 (14.6)	0.1
142287	60	4	92	920	2569.5 (1056.5)	101.5	23.2 (27.3)	21–29.1	72.7 (15.7)	0.2
151779	50	50	73	1942	808.8 (740)	202	15.4 (26.3)	16.4–29.7	89.9 (9.9)	0.7
159225	70	51	89	40715	1591.7 (1014.6)	266	19.9 (33.7)	14.1–26.6	88.7 (13.5)	3.2
159226	50	11	94	494	572.5 (277.3)	84.5	25 (12.3)	24.4–28.3	85.6 (14.5)	0.0
159228	150	5	72	98	2323.9 (907)	352.5	153.6 (80)	13.4–28.5	15.3 (12.8)	53.9
159230	80	6	90	102	885 (457)	82	41.5 (14.5)	26.4–29.1	78.7 (16.4)	0.0
159236	90	3	81	112	596 (221.6)	66	7.5 (13.4)	24.4–28.6	74 (29.9)	0.0
159237	55	11	82	416	1661.3 (1008.3)	176.5	17.2 (28)	22.7–25.9	88.7 (27.9)	0.0
159239	60	10	82	159	1045.4 (142)	168	58.1 (24.5)	23.3–26.3	96.6 (5.3)	0.0
159242	70	7	93	419	1674.9 (695.7)	103.5	17.2 (26.7)	21.6–29.2	85 (8.6)	0.0
159243	160	46	87	771	1374.5 (878)	161	13.3 (25.6)	13.9–28	88.5 (6.9)	0.2
159244	120	24	92	796	1823.9 (676.9)	229	12.9 (30.6)	13–28.5	88.8 (5.7)	1.7
159246	227	29	92	1299	1503.3 (819.1)	82.5	11.1 (15.5)	24.1–28.9	83.1 (12.6)	0.0
159248	110	47	63	1864	910.8 (979.7)	183.5	21.1 (30.6)	14.8–25.8	96.7 (3.5)	0.3
159251	90	4	90	30	1483.5 (1019.6)	162	53 (34)	25–26.1	100 (0)	3.8
159252	80	14	92	754	1609.5 (537.4)	120	28.1 (29.6)	18.1–29.9	84.5 (9.2)	0.3
159257	150	8	74	90	983.6 (387.6)	140.5	52.6 (24.1)	25.3–25.9	99.9 (0.4)	0.4
159260	150	4	95	341	2048 (1456.8)	94	23.6 (28)	19.5–30	75.5 (14.7)	0.0
159261	70	16	92	1394	1415.6 (811)	105	11.5 (20.4)	21.7–26	95.5 (4.4)	0.0
159262	40	8	83	123	511.3 (606.2)	79	31.2 (18)	24.7–26.1	96.5 (4.9)	0.0
159264	80	94	91	1259	2273.2 (1846.4)	187	16.9 (32)	16.2–25.5	89.6 (9.8)	0.9
159267	60	12	71	4577	1025.9 (646.3)	150	31.3 (29.6)	16.3–30.9	65.9 (23.3)	0.7
164973	130	53	58	1459	559.2 (506.4)	128.5	21.5 (21.7)	15–29.5	78.8 (20.3)	0.0
164975	75	26	77	971	6356.4 (4485.5)	472.5	76.8 (64.5)	14.3–28.8	87.4 (11.6)	4.5
164979	80	49	81	1193	1626.4 (944)	206	25.6 (28.1)	16.4–27.8	92.5 (6.7)	0.7
164981	100	6	91	2473	2409.3 (332.3)	107	15.1 (26.6)	21.3–26.5	93.7 (4.8)	0.0
164991	200	5	89	101	1752.6 (1585.9)	121	21.8 (24.6)	20.8–29.3	76.3 (18.5)	
Mean	93.2	36.7	83.0	1828.6	1468.3	173.1	32.6		77.4	4.0
(SD)	(44.2)	(49.1)	(9.8)	(2795.8)	(1478.1)	(88.0)	(28.4)		(21.6)	
Minimum	40	3	58	30	511.3	66	7.5	13	15.25	0.0
Maximum	227	184	95	11944	6356.4	472.5	153.6	33.8	100	53.9

Table 2. Details of striped marlin tracks, with the integrated vertical movement (IVM) and time in the mixed layer (ML) and in the oxygen minimum zone (OMZ). Tag numbers in **bold** represent tags that were physically retrieved. DNR: did not report; NA: not available

Tag number	Weight (kg)	Retention (d)	Transmitted (%)	Horizontal distance (km)	Mean (SD) daily IVM – transmitted (m)	Max depth (m)	Mean (SD) depth (m)	Temp range (°C)	Mean (SD) time in ML (%)	Time in OMZ (%)
142276	45	153	37	5475	1234 (942.8)	335.5	55.6 (50.4)	14.2–31	48.4 (16.1)	16.9
142284	90	109	84	5240	3180.1 (1362.4)	365.5	45.1 (53.5)	10.4–32.9	54.4 (16.6)	10.0
142285	50	67	90	2056	738.7 (781.2)	345	9.9 (25.6)	11.6–30.6	89.8 (16.5)	1.5
142286	50	182	66	8655	2089.7 (1523)	343.5	52.2 (60.9)	12.7–32.3	57.6 (13.3)	22.7
142288	45	23	93	3151	1031.7 (795.1)	222	12 (25.3)	12.3–30.4	88 (17.2)	0.3
142292	20	111	83	4920	2391.6 (996.1)	288	46.1 (42.9)	11–32.2	48.1 (12.1)	2.7
142294	45	46	89	2500	3061.5 (1234.7)	220.5	40.2 (49.9)	12.5–29.3	63.1 (10.9)	10.1
142297	8	14	93	624	2133.9 (543.4)	144	39.7 (36.1)	16.2–29.9	55.6 (19.6)	0.0
151777	20	151	78	7179	2222.4 (1390.7)	371	35.2 (46.5)	10.2–31.5	66.1 (15.9)	3.6
151780	40	45	78	2113	1934.9 (691.9)	176	35.5 (38.7)	14.1–30.3	58.4 (11.3)	2.8
151781	20	30	88	1733	2147.4 (918)	202	30.4 (32.7)	14.3–29	75.4 (21.5)	1.5
151782	55	92	83	3813	3035.7 (1613.9)	294	43.8 (54.1)	14.3–31.8	61.5 (14.6)	13.7
151783	50	94	83	6637	1293.9 (896.3)	401	35.9 (53.5)	12.9–32	70.9 (28.9)	15.6
151784	30	13	93	671	2990.5 (749.8)	157	27 (33.7)	15.8–29.2	66.5 (18)	0.3
159231	50	73	80	4371	1265.1 (646.4)	168	23.5 (32.3)	14.1–29.5	75 (17.4)	1.9
159233	55	183	84	9187	1330.5 (704)	307	32.6 (34.4)	11.9–31.6	59.7 (16.1)	9.4
159234	50	15	87	289	3212.4 (1308.4)	217.5	27.7 (41.4)	14.9–28.6	93.5 (3.5)	1.0
159235	50	3	94	189	1092.2 (469.8)	110.5	10.1 (21.9)	20–28.1	92.3 (8.8)	0.0
159240	60	46	90	1641	3487.5 (1442.2)	284.5	41.2 (44.6)	12.9–31	62.1 (21.2)	5.1
159241	23	27	88	1312	2245.5 (732.5)	164.5	20.5 (29.9)	13.8–28.7	82.4 (9.8)	0.5
159249	50	4	94	3	1981.7 (758.3)	116.5	20.6 (30)	18.9–27	83.3 (7.1)	0.0
159250	25	9	95	341	2917.2 (1143.1)	131	24.9 (31.5)	17.6–29.8	72.7 (18.6)	0.1
159253	60	51	75	2456	1424.9 (1059.3)	292	22.8 (35.3)	12.8–30.3	79.7 (14.6)	1.6
159255	75	6	93	145	2079.8 (700.4)	116	18.2 (27.1)	18.4–26.9	84.2 (15.7)	0.0
159258	70	37	79	1183	1528.9 (1033.6)	463.5	33.9 (57)	14.4–30.9	73.0 (0.0)	4.6
159259	50	11	89	276	2876.7 (900.3)	138.5	19.6 (30.7)	17.9–30.7	74.4 (7.2)	0.0
159265	45	4	93	37	1839.7 (1056.6)	144	22.6 (38.5)	16.1–28.2	86 (11.3)	0.0
159266	45	6	95	253	2465.8 (952.7)	153	25.2 (33.3)	18.3–28.5	72.2 (14.1)	0.5
164976	75	39	92	2368	2537.3 (553.7)	292	25.5 (40.2)	12–30	74.9 (8.5)	1.0
164977	60	7	64	132	2035.4 (1478.1)	119.5	28.3 (34.5)	17.5–28	DNR	NA
164978	50	5	94	137	2184.3 (793.8)	153	30.7 (36.2)	18.9–29.1	80.7 (13.3)	0.3
164982	40	11	88	282	2085 (840.1)	176.5	16.1 (23.9)	15.2–30	67.6 (24.5)	0.2
164983	65	19	95	434	2028.4 (825.8)	329.5	26 (41.3)	12.3–30	74.2 (15.9)	0.8
164984	60	4	94	115	2740 (816.4)	157	34 (41.9)	16.6–29.2	76.5 (17.3)	1.5
164989	75	3	92	140	1728.8 (1205.6)	144	26.7 (36.4)	17.5–28.4	92.5 (7.8)	0.0
164992	50	5	93	225	1810.7 (915.3)	107	15.7 (27.3)	20.5–28.5	82 (18.4)	0.0
164993	65	5	94	272	2289.3 (760.7)	131.5	31.5 (38.5)	18.6–28.8	78.3 (15)	0.0
164996	50	7	73	343	1139.2 (696.4)	95.5	10.9 (22.3)	17.1–29.7	90.6 (5.5)	0.0
164997	70	181	67	7857	1786 (1378.6)	262	43.4 (42.5)	12.9–31.1	36.7 (25.1)	19.2
Mean	49.6	48.5	85.1	2275.7	2022.0	221.5	29.3		63.6	7.4
(SD)	(17.6)	(56.4)	(11.6)	(2700.3)	(1338.0)	(98.0)	(11.5)		(21.9)	
Minimum	8	3	37	3	738.7	95.5	9.9	10.2	36.7	0
Maximum	90	183	95	9187	3487.5	463.5	55.6	32.9	93.5	22.7

larger individuals (*F* = 17.8, df = 1118, p < 0.001), with a weight range of 40–227 kg (mean = 93 kg). By contrast, the relationship was reversed for striped marlin (*F* = 5.6, df = 1642, p = 0.02), although they had a relatively small weight range of 8–90 kg (mean = 50 kg).

The temperature range for black marlin spanned from 13.0 to 32.8°C. Striped marlin had a wider temperature range, extending to cooler waters (10.2–32.9°C) than black marlin. Although black marlin had a cooler mean temperature of 26.7 ± 2.15°C than striped marlin (27.2 ± 2.9°C; *W* = 9 160 197 529, p < 0.005), black marlin spent only 1.6% of their combined time below 20°C compared to 4.9% in striped marlin. Temperature broadly correlated with depth, although some of the deepest dives were in relatively warm water (Fig. 1). There was no correlation of fish weight and daily minimum temperature for either species (black marlin *F* = 1.1, df = 1117, p = 0.3; striped marlin *F* = 1.1, df = 1661, p = 0.3).

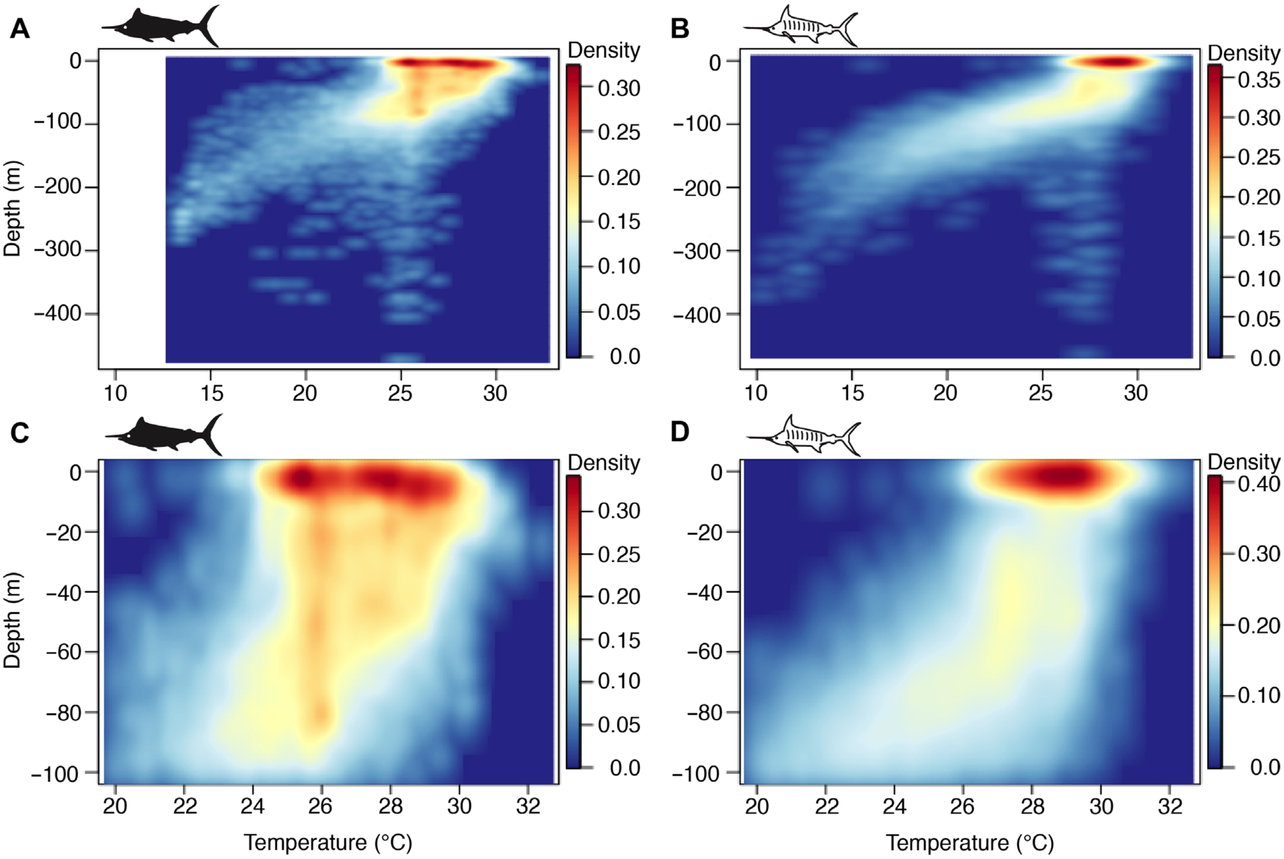

Fig. 1. Depth and temperature use by (A,C) black marlin (n = 34) and (B,D) striped marlin (n = 39), with panels C and D zooming into the highly-used habitat between the surface and 100 m depth and between 20 and 32°C

Black marlin had a broader temperature habitat in surface waters (25–29.5°C) and used the whole top 100 m of the water column more extensively than striped marlin (27–29.5°C; Fig. 1). However, striped marlin spent more than twice as much time below 100 m (10.7%) than black marlin (4.8%) and had a wider temperature range, to a minimum of 10.2°C (Fig. 1). Deep dives were relatively rare overall, with black marlin (54.8%) and striped marlin (56.7%) spending most of their time in surface waters <20 m deep. At a finer scale, there were clear differences in the use of surface waters between the species. Striped marlin spent 50.7% of their time in the top 5 m of the water column and 39.8% in the top 2 m. On the other hand, black marlin spent only 32.3% in the top 5 m and 14.4% in the top 2 m of the water column (Fig. 1).

3.3. Extensive vertical activity

Both marlin species displayed a high level of daily vertical movements. Striped marlin had a higher daily IVM (mean ± SD = 2022 ± 1338.0 m) than black marlin (1468.3 ± 1478.1 m; $W = 657230$, $p < 0.005$). Marlin had a lower horizontal swim speed when IVM was larger ($F = 13.97$, df = 2762, $p < 0.001$). High-resolution archival data from physically retrieved tags showed that vertical movement was ~3.5 times higher than the IVM estimated from transmitted data. The 13 recovered tags recorded a daily mean of 8456 vertical meters, with a maximum of 14745 m for striped marlin #159234, compared to a daily mean of 2547 vertical meters estimated from transmitted data of these same 13 tags. The diving ratio was similar for both species, with black marlin moving vertically on 57% of consecutive depth readings and striped marlin moving vertically 58% of the time.

3.4. Black and striped marlin spend most of their time in the mixed layer

The mixed layer depth varied in time and space, but for all tracks combined, it extended from the surface to a mean depth of 67.0 ± 31.6 m, with a maximum of 199.3 m. It had a mean temperature of 28.3 ± 1.5°C and had a narrow temperature range with a mean of 1.6 ± 1.2°C. Daily aggregate data showed that both marlin species spent most of their time in the mixed layer, with black marlin spending more time in the mixed layer (77.4 ± 21.6%) than striped marlin (63.6 ± 21.9%; $W = 796157$, $p < 0.005$). Individually, the mean daily time spent in the mixed layer ranged from 15.3 to 100% in black marlin (Table 1), and from 36.7 to 93.5% in striped marlin (Table 2). Overall, marlin spent less time in the mixed layer at warmer SSTs ($F = 685$, $R^2 = 0.25$, $p < 0.005$), and when the mixed layer depth was shallower ($F = 72.2$, $R^2 = 0.03$, $p < 0.005$).

More detailed time-series data confirmed that most depth records (80.2%) were shallower than the maximum depth of the mixed layer, having a positive relative depth ΔD and demonstrating extensive use of the mixed layer. Black marlin had more positive ΔD records (89.7%) than striped marlin (73.9%; Fig. 2), which means that they spent more time in the mixed layer than striped marlin. ΔD also showed a more pronounced difference in the use of deeper water between the species than absolute depth alone. Although both species had similar maximum depths, striped marlin made ~3 times greater use (7.1%) of waters more than 50 m deeper than the mixed layer, compared to black marlin (2.35%; Fig. 2).

Black marlin had a cooler surface temperature range (~22.5–30°C) than striped marlin (~25–32.5°C). The mean ΔT, or the difference between the temperature of the tag and the average mixed layer temperature, was colder for striped marlin (−1.68) than for black marlin (−0.84; $W = 1.3921 \times 10^{10}$, $p < 0.005$), opposite to the pattern in absolute temperature. Striped marlin also spent more time in cold water, with a $\Delta T < -5$ (12.2%), than black marlin (3.5%; Fig. 2).

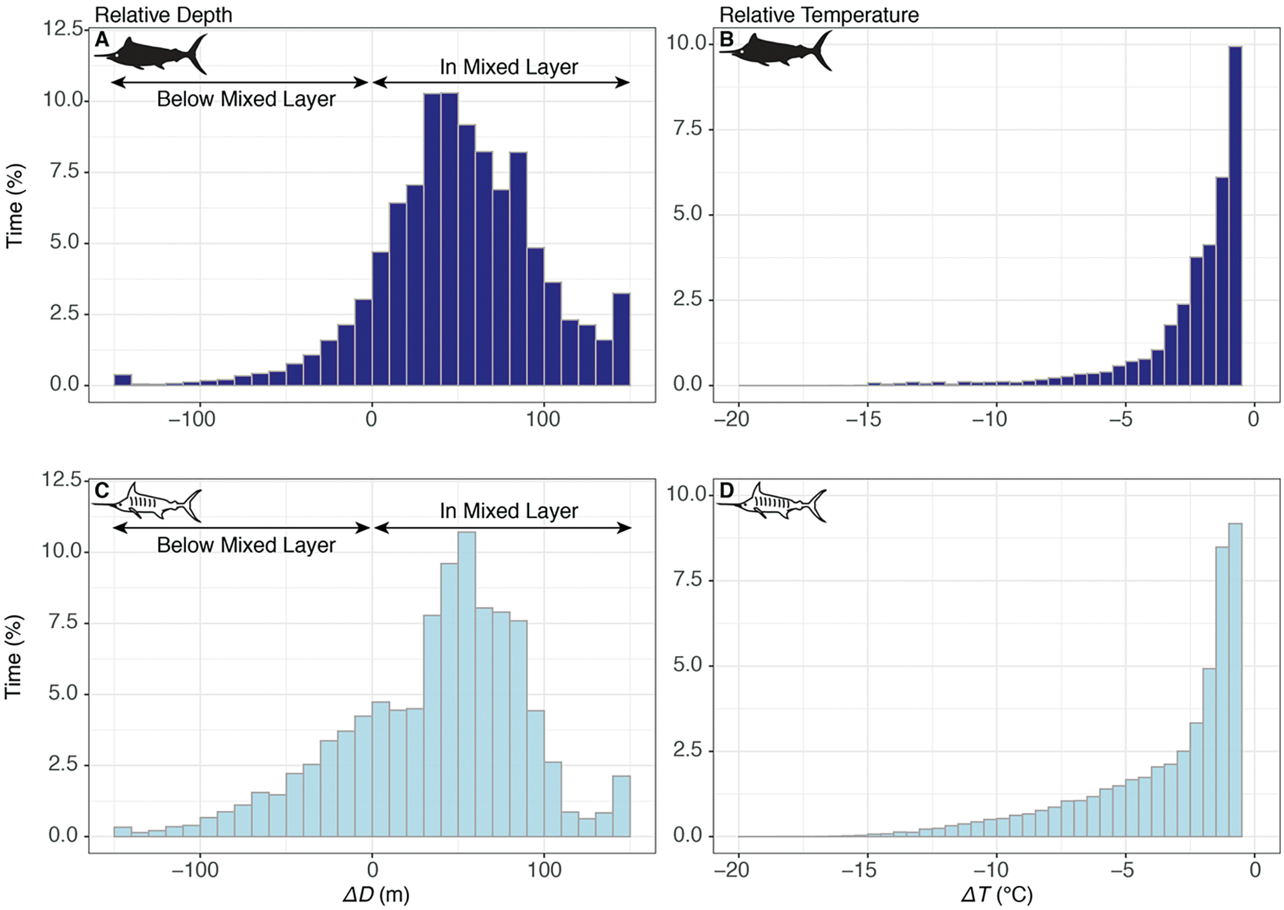

Fig. 2. Swimming depth relative to the daily maximum depth of the mixed layer (ΔD) for (A) black marlin and (C) striped marlin. Temperature relative to the mean temperature of the mixed layer (ΔT) for (B) black marlin and (D) striped marlin. The ΔT bin for 0–0.5°C was removed from plotting, as it is far larger than the others and represents the fish swimming in the mixed layer

3.5. Dissolved oxygen

The depth of the OMZ with <150 µmol kg^{-1} dissolved oxygen varied regionally, not restricting vertical movements in the south but being shallow in the north around Oman (Fig. 3A,C). Marlin movements were associated with areas of relatively shallow OMZ with a mean depth of 167 ± 129.6 m and ranging from 20 to 900 m. Despite being able to dive deeper than the OMZ depth in many cases, marlin spent only 6% of their time in the OMZ. Striped marlin spent almost twice as much time (7.4% of their combined time) in the OMZ than did black marlin (4%) and only 2 black marlin spent >10% of their time in the OMZ compared to 7 striped marlin. There was individual variation among both species (Tables 1 & 2), and the individuals spending more time in the OMZ also spent less time in the mixed layer ($F = 77.1$, $p < 0.0001$) and had a deeper mean swimming depth ($F = 93.2$, $p < 0.0001$). When marlin were in the OMZ, its depth was shallower (88.3 ± 35.6 m) than when they were above the OMZ (172.3 ± 131.7 m; $t = 239.5$, df = 65, 508, $p < 0.0001$). Spatial trends of the percentage of time marlin spent in the OMZ broadly reflected the shallower OMZ in the north of our study region where marlin spent more time in the OMZ (Fig. 3B).

3.6. Marlin swim deeper during the day than at night

The mean swimming depth varied with time of day, with both species staying shallower during the night and swimming deeper during the day (Fig. 4). Striped marlin had a more pronounced diurnal pattern, staying shallower than black marlin during the night and swimming deeper during the day. Black marlin had a crepuscular signal on top of the general pattern, with the deepest mean depths at sunrise and sunset (Fig. 4). Striped marlin had a deeper mean depth of 52.9 ± 50.76 m during the day than during the night (17.0 ± 29.59 m; $W = 2\,521\,445\,976$, $p < 0.005$). Black marlin also had a deeper mean depth of 37.9 ± 41.53 m during the day than at night (23.6 ± 32.64 m; $W = 1\,530\,915\,021$, $p < 0.005$). Absolute temperature followed the same pattern as depth, with cooler mean temperatures during the day for black marlin (day = 26.4 ± 2.4°C; night = 27.1 ± 1.9°C; $p < 0.005$) and for striped marlin (day = 26.1 ± 3.4°C; night = 28.2 ± 1.8°C; $p < 0.005$).

The swimming depth relative to the maximum depth of the mixed layer had a similar pattern to absolute depth, with a lower ΔD during the day than at night for black marlin (day = 42.2 ± 46.36 m, night = 56.5 ± 40.59 m; $p < 0.005$) and striped marlin (day = 10.0 ± 53.51 m, night = 45.84 ± 34.93 m; $p < 0.005$).

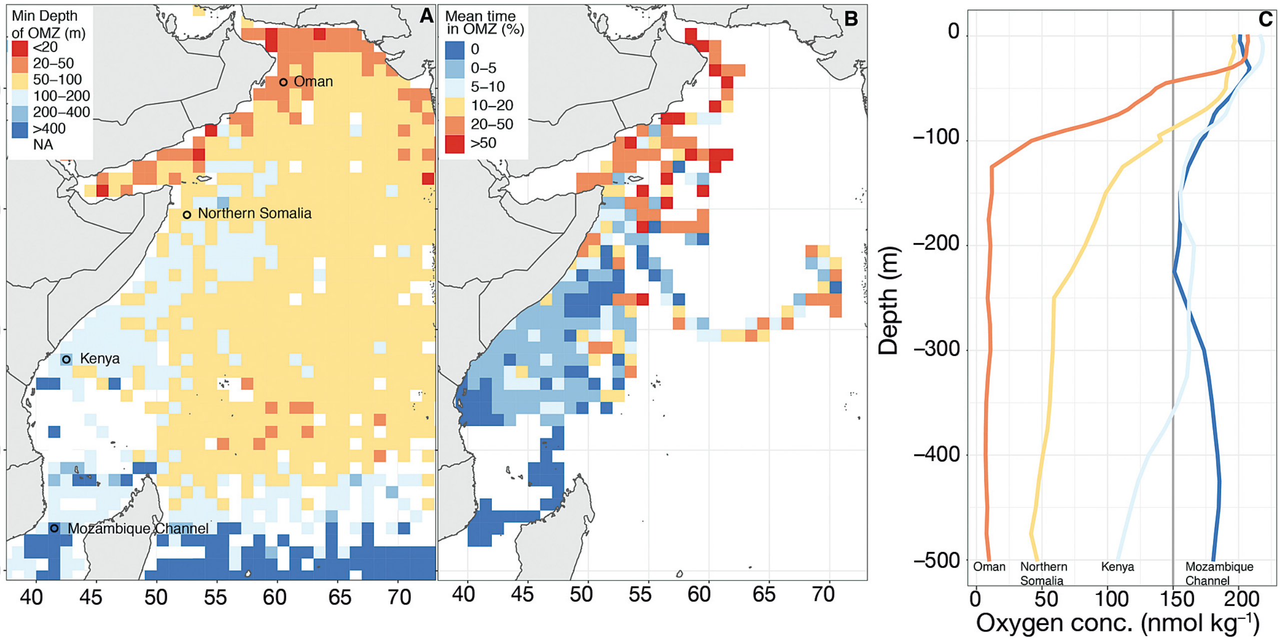

Fig. 3. (A) Minimum depth of the oxygen minimum zone (OMZ; <150 µmol kg^{-1}) in the Western Indian Ocean. (B) Mean percentage of time marlin spent in the OMZ. (C) Dissolved oxygen at 4 locations of marlin activity (see map in panel A), with the 150 µmol kg^{-1} limit indicated in grey

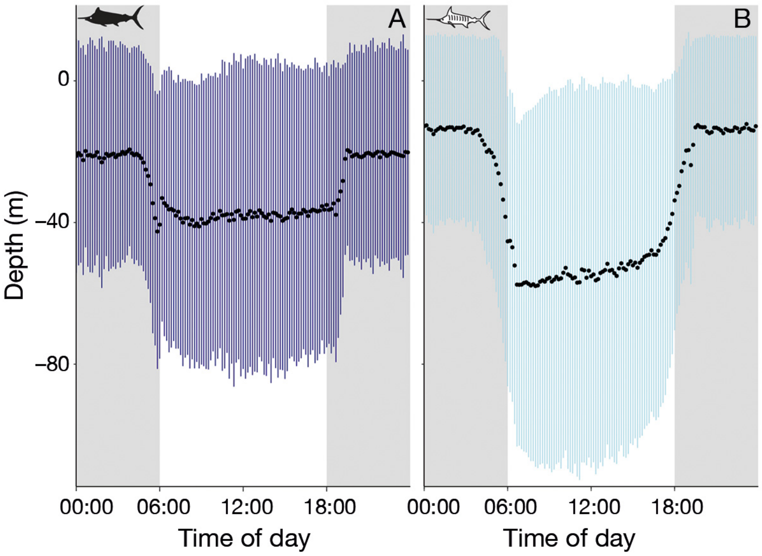

Fig. 4. Mean and SD of swimming depth of (A) black marlin and (B) striped marlin in 10 min intervals, with night-time (18:00–06:00 h) shaded in grey

The same was true for relative temperatures, with a cooler ΔT during the day than at night for black marlin (day = −1.0 ± 2.09, night = −0.4 ± 1.09; $p < 0.005$) and for striped marlin (day = −2.8 ± 3.56, night = −0.7 ± 1.59; $p < 0.005$). Time spent in the mixed layer per hour, derived from depth data relative to the daily maximum depth of the mixed layer, ranged from 83.6 to 95.0% in black marlin and from 58.8 to 92.6% in striped marlin. Time in the mixed layer had the same diurnal pattern as depth and temperature, with more time spent in the mixed layer during the night than during the day for both species.

There was some individual variation in diurnal depth-use patterns (Fig. 5). Some marlin had a normal pattern, swimming deep during the day and shallower during the night, while others had a crepuscular pattern, diving particularly deep at dusk and dawn, or no clear pat-

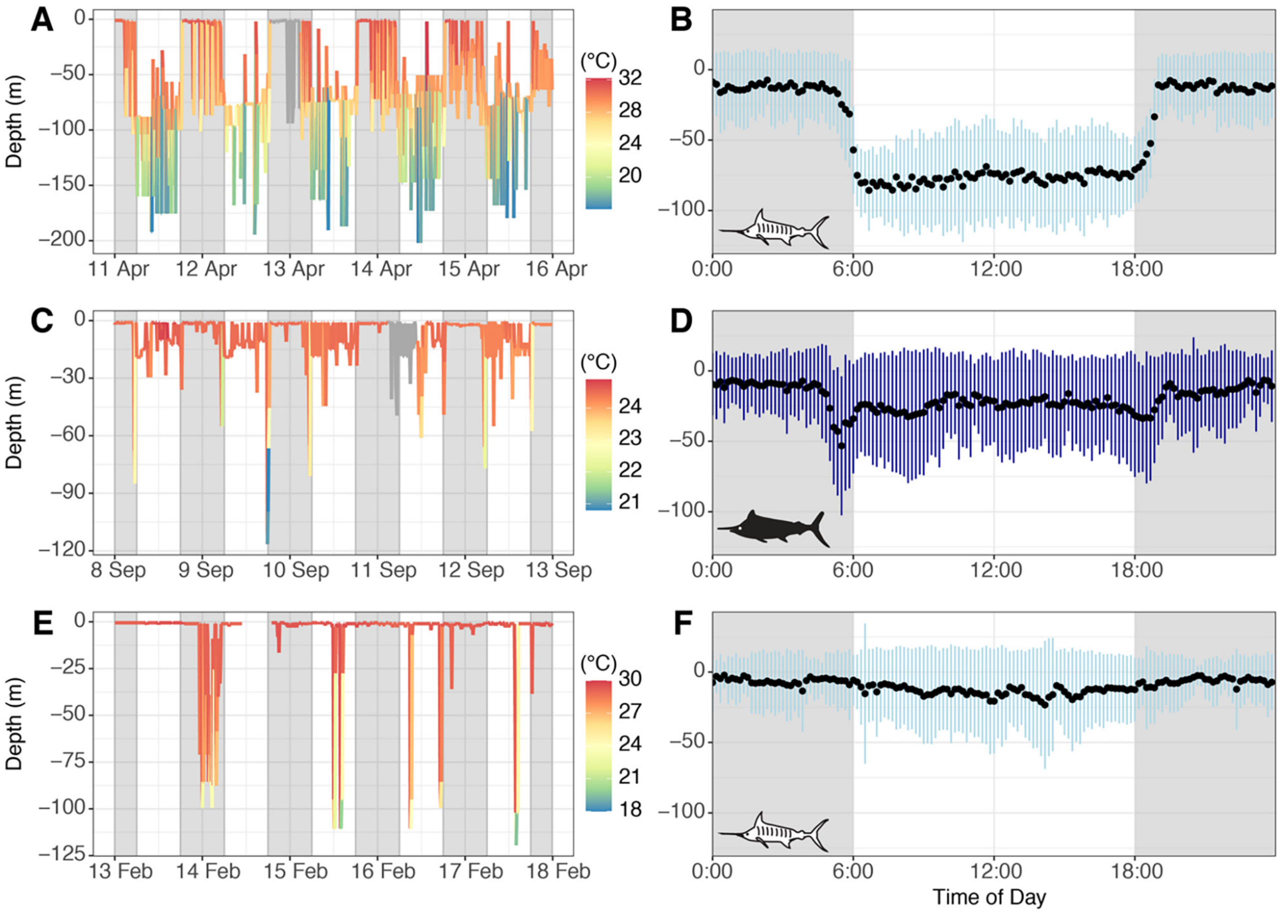

Fig. 5. Diurnal patterns in dive depth, with (A,C,E) a 5 d subset of the depth and temperature time-series and (B,D,F) the means and SD of swimming depth over the whole track. Grey shading indicates night-time. Panels A and B are from striped marlin #142292 and show a normal pattern; panels C and D are from black marlin #159225 and show a crepuscular pattern; and panels E and F are from striped marlin #142285 and show no clear pattern

tern (Fig. 5). Black marlin had more individuals with a crepuscular pattern (n = 12, 35.3%) than striped marlin (n = 3, 7.7%), while striped marlin had more individuals with a normal pattern (n = 24, 61.5%) than black marlin (n = 11, 32.4%). A detailed examination of crepuscular dives in the high-resolution data from a retrieved tag showed a rapid descent followed by prolonged time at the deepest depth (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m690p165_supp.pdf). There was no clear relationship of depth-use pattern with fish weight, with the smallest individuals also generally diving deeper during the day than at night.

3.7. Free-jumping

The 13 recovered tags with depth and temperature readings every 3 or 5 s showed that marlin had a similar mean ascent (0.207 m s^{-1}) and descent speed (0.208 m s^{-1}), with bursts of up to 11 m s^{-1} on ascents and 18.2 m s^{-1} on descents. Two of the recovered black marlin tags recorded positive depth readings immediately prior to falling off and floating at the surface, indicating a 'free-jumping' event, whereby the marlin breaches into the air and falls back to the water surface on its side, dislodging the tag (Fig. 6). Black marlin #159242 had 2 'free-jumping' events, and the second event consisted of 2 jumps which dislodged the tag. Black marlin #164991 ascended from 22 m to above the water surface in 6 s and then lost the tag (Fig. 6).

3.8. Environmental influences on daily depth use

The final GAMMs with daily mean depth as the response variable retained the maximum depth of the mixed layer and SST as predictors for both species, with black marlin also retaining the minimum depth of the OMZ and bathymetric depth, and striped marlin also retaining day of year as predictors (Table 3). The final models with daily maximum depth as the response retained the maximum depth of the mixed layer and SST in both species, with black marlin also retaining the minimum depth of the OMZ and striped marlin also retaining location and day of year as predictors (Table 3). Overall, the

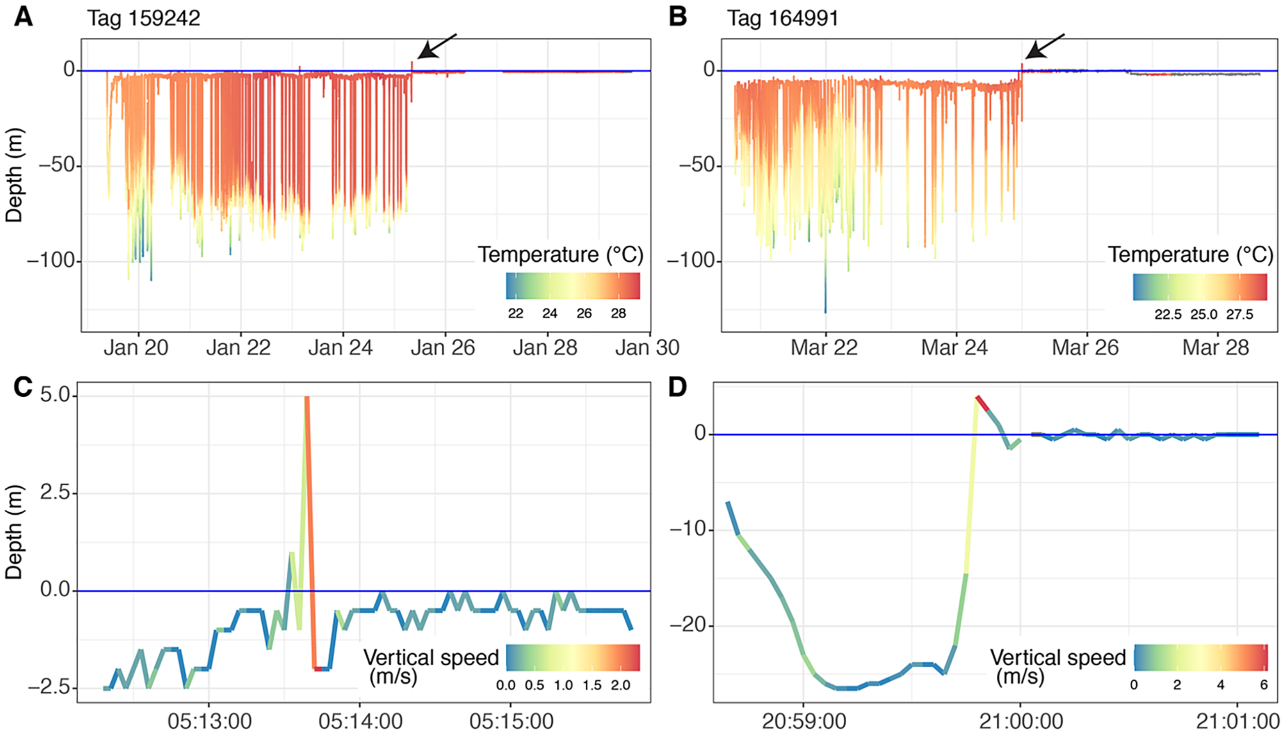

Fig. 6. High-resolution depth and temperature data at 3 s intervals from 2 recovered black marlin tags showing evidence of 'free-jumping' immediately prior to losing the tags. The water surface is indicated by a horizontal blue line. (A,B) Full depth and temperature time-series; arrows point to the 'free-jumping' event above the water surface after which the tag floats at the surface. (C,D) Zoomed in view of the jumps, showing the depth and absolute vertical speed. Note that the black marlin with tag #159242 made an earlier jump on 23 January 2018 without dislodging the tag

Table 3. Significance levels for fixed predictors in generalised additive mixed models (GAMMs) with the daily mean swimming depth and the daily maximum swimming depth as response variables. Blank cells indicate that the predictor was not retained in the final GAMM. MLD: mixed layer depth; SST: sea surface temperature; OMZ: oxygen minimum zone. Overall model r^2 and n are also listed. *marginally significant predictor

Predictor	Daily mean depth		Daily maximum depth	
	Black marlin	Striped marlin	Black marlin	Striped marlin
Maximum MLD	<0.001	<0.001	<0.001	<0.001
SST	<0.001	<0.001	<0.001	0.01
Minimum OMZ depth	0.003			
Day of year		<0.001		<0.001
Bathymetric depth	0.006			
Chl *a*			0.08*	
Location				0.02
Total r^2	0.298	0.227	0.275	0.148
Total n	1001	1618	701	1618

maximum depth of the mixed layer and SST were the most influential predictors, and black marlin GAMMs had a higher r^2 than striped marlin GAMMs.

For black marlin, the maximum depth of the mixed layer was an important predictor of their daily mean swimming depth, with a deeper mixed layer resulting in a deeper mean depth. Black marlin also had a deeper mean swimming depth when SST was warmer and when the OMZ was shallower (Fig. 7A). Bathymetric depth was also retained but had an ambiguous trend with large confidence areas (Fig. 7A). For striped marlin, the maximum depth of the mixed layer and SST had the same effect as with black marlin, with the mean swimming depth deeper with a deeper mixed layer and warmer SST (Fig. 7B). The striped marlin GAMM also retained day of year as a predictor, but the relationship was ambiguous and there was a gap in observations from August to November (Fig. 7B). The maximum depth of black marlin was influenced by the mixed layer depth and by SST, with the same trend as in their mean swimming depth GAMM (Table 3). They also had a deeper maximum depth with less chl *a*, although the relationship was weak with large confidence areas (Fig. S2). For striped marlin, the maximum diving depth was deeper with a deeper mixed layer depth and warmer SST, similar to the mean swimming depth model. The seasonal trend was more pronounced, with deepest maximum depths in March–April and the shallowest maximum depths were off Kenya, Tanzania, and southern Somalia (Fig. S2).

3.9. Overlap with fisheries

Marlin had a large gross overlap with fisheries. More than half of all depth records (56%) were within the depth range of gillnets (0–20 m), with black marlin (55.3%) and striped marlin (56.8%) having similar overlap. There was less overlap with gillnets during the day than at night for both species. Black marlin had a higher day-time overlap with gillnets than striped marlin, with hourly percentages of overlap ranging from 40 to 46% for black marlin compared to 33–41% for striped marlin. This pattern was reversed during the night, with hourly percentages of overlap ranging from 52 to 73% for black marlin compared to 61–81% for striped marlin. Vertical overlap with the potential to interact with longlines, extending from the surface to 400 m depth, was almost complete (99.9%), as both species rarely dived below 400 m.

4. DISCUSSION

Black and striped marlin showed extensive vertical movements, had a wide depth range from the surface to over 400 m, and had a broad temperature range extending into cool (<15°C) waters. Both spent most of their time in the warm mixed layer. Within these broad similarities, the 2 species exhibited some differences in their vertical habitat use that suggest niche partitioning. Striped marlin spent 51% of their time in surface waters <5 m deep, but spent more time below 100 m (11%) than black marlin (5%). Black marlin also spent most time near the surface (<5 m, 32%), but used the top 100 m of the water column more extensively than striped marlin. More individual striped marlin had a normal diel depth-use pattern, diving deeper during the day than at night, than black marlin, which often had a crepuscular dive pattern, diving particularly deep at dawn and dusk. Their brief dives past the mixed layer were not obviously constrained by an OMZ of <150 µmol kg^{-1} dissolved oxygen. The OMZ was shallow in the northern part of the Western Indian Ocean, where marlin continued to dive, and as a result spent more time within the OMZ. We also report the first recorded instances of 'free-jumping' behaviour by billfish resulting in tag shedding.

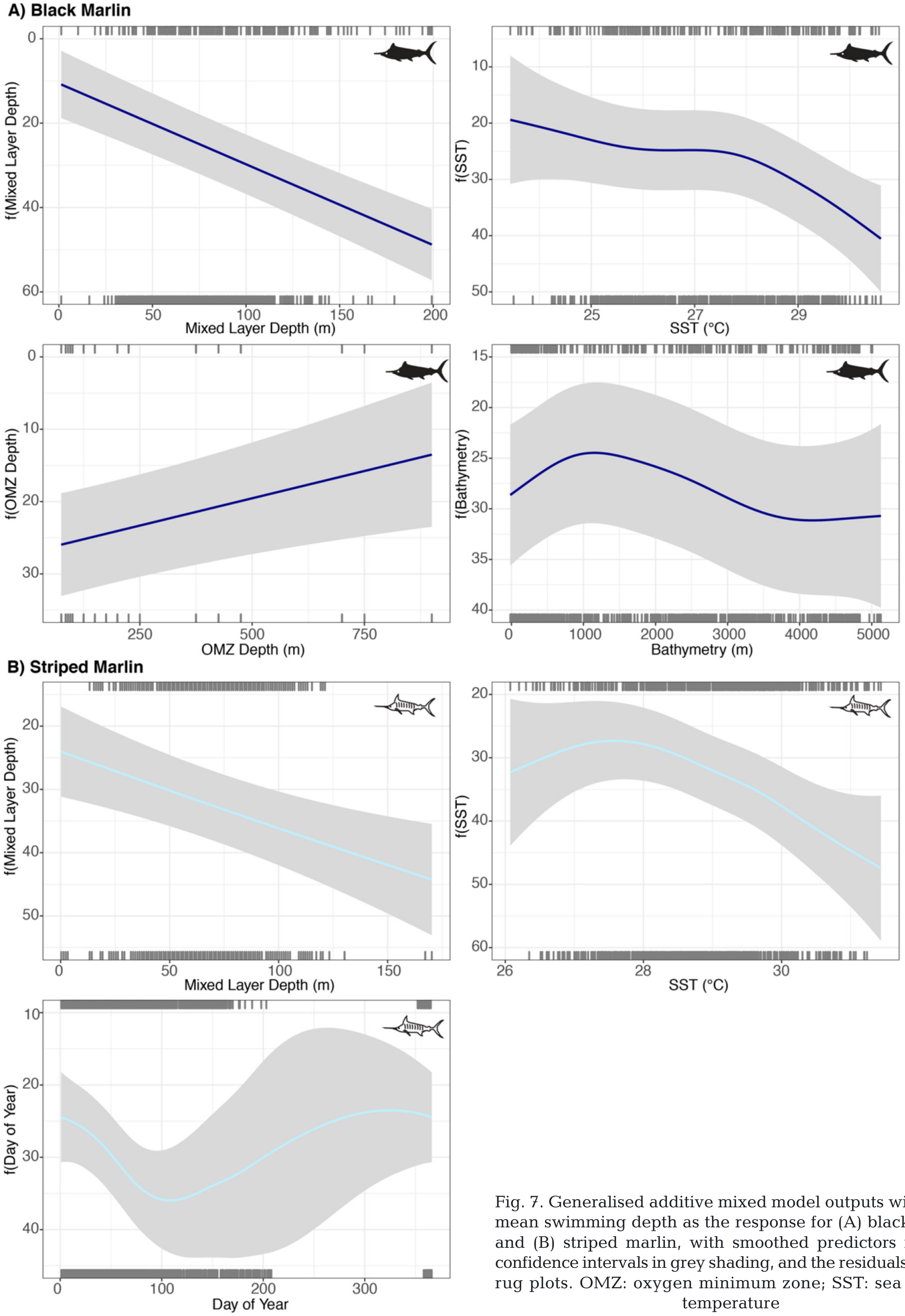

Fig. 7. Generalised additive mixed model outputs with daily mean swimming depth as the response for (A) black marlin and (B) striped marlin, with smoothed predictors in blue, confidence intervals in grey shading, and the residuals as grey rug plots. OMZ: oxygen minimum zone; SST: sea surface temperature

4.1. Vertical habitat use

Both marlin species had a wide depth and temperature habitat, extending from the surface (and above) into the mesopelagic zone to over 450 m deep, and to temperatures as low as 10.2°C. We add to the mounting evidence that marlin undertake deep dives, with even small ~50 kg individuals of both species routinely accessing the mesopelagic zone and being exposed to broad temperature ranges. While some prior tagging studies suggested that black marlin stay above 260 m (Pepperell & Davis 1999, Gunn et al. 2003, Chiang et al. 2015), larger studies have demonstrated that they can dive to 600 m and a minimum temperature of 7.4°C (Williams et al. 2017). Similarly, striped marlin have been tracked to a maximum depth of 532 m and a minimum temperature of 8.6°C (Lam et al. 2015). Other marlin species also had a wide depth use, with white marlin *Kajikia albida* diving to 456 m and waters as cold as 10°C (Vaudo et al. 2018) and blue marlin *Makaira nigricans* diving to over 700 m and waters as cold as 5.4°C (Carlisle et al. 2017). The maximum dive depths and minimum temperatures for both species in our study show that, similar to those tracked in the Pacific and to other marlin species, they have a wide vertical habitat in the Western Indian Ocean.

Both species spent most of their time in the mixed layer, similar to their vertical habitat use in the Pacific (Chiang et al. 2015, Lam et al. 2015). Black and striped marlin both had a deeper mean and maximum daily swimming depth when the mixed layer was deeper. This is likely due to the mixed layer being heavily used by both species, and presumably by their prey, and shows that the conditions of the mixed layer (warm temperatures, high oxygen concentration, high productivity) are more important than hydrostatic pressure alone. This predictor was highly significant in both black and striped marlin GAMMs.

Larger fish often have a wider vertical habitat than smaller individuals of the same species, in part due to greater physiological tolerances or ontogenetic changes in prey type or breadth (Weng et al. 2007, Afonso & Hazin 2015). We found an inverse relationship of daily maximum depth and fish weight, with smaller individuals diving deeper. There was no discernible pattern of weight and horizontal distribution (Rohner et al. 2020, 2021) and no correlation of weight and minimum daily temperature. This suggests that factors such as prey depth or temperature, rather than physiological limitations on depth, may have more influence on the vertical movements of smaller marlin. However, the correlation was weak, and weight was not supported as a predictor in the GAMMs, using daily maximum and mean depth as a response for either species. Our tagged black marlin weighed up to 227 kg, and striped marlin weighed up to 90 kg, with neither close to spanning the full range of the potential sizes of each species. Given this, it is plausible that our upper size range was too small to detect an ontogenetic trend in dive behaviour. Black marlin larger than the maximum size range tagged in our study (>250 kg) regularly dived deeper than smaller individuals in the Pacific (Williams et al. 2017).

4.2. Niche partitioning between sympatric species

Despite similar maximum depths and minimum temperatures for black and striped marlin, indicating similar physiological limits for both species, their vertical habitat use differed. The differences may be related to their diet and hunting strategies that in turn may influence their thermoregulation (Watanabe et al. 2021). Striped marlin spent 40% of their time in surface waters <2 m deep, more than double that of black marlin. Striped marlin also spent more than double the amount of time below 100 m compared to black marlin. Striped marlin have a varied diet, but squid and surface schooling fishes are often their main prey (Abitia-Cardenas et al. 1997), including off East Africa where they fed on frigate tuna and squid (Williams 1963). It is thus possible that they spend extended time hunting for epipelagic fishes in surface waters and also targeting squid during the day below the mixed layer, explaining their overall vertical habitat use. It is also possible that their longer time in surface waters may indicate a need to warm up or re-oxygenate between deep dives. Our observations from Kenyan waters further support this theory, where striped marlin, but rarely black marlin, are routinely seen basking at the surface without any interest in chasing fishing lures (R. Bealey pers. obs), perhaps reflecting behavioural thermoregulation or re-oxygenating between deep foraging dives. This behaviour may relate to the sleeker body shape and smaller surface area:volume ratio of striped marlin compared to black marlin, leading to striped marlin cooling faster and requiring more frequent thermoregulatory recovery at the surface between deep dives into colder waters.

Black marlin also feed on squid, tuna, and other epipelagic fishes. The extensive use of the top 100 m of the water column in our study suggests that they were mostly hunting prey in the mixed layer. Black marlin diet changes with increasing size, with large individuals targeting mesopelagic prey, and small individuals hunting epipelagic fishes (Shimose et al. 2008, Varghese et al. 2014, Chiang et al. 2020). The comparatively small size of tracked individuals in this study, with a mean of 93 kg and all <230 kg, supports a hypothesis that they were generally targeting epipelagic prey. Since sympatric striped marlin dived extensively below the mixed layer, it is unlikely that mesopelagic prey was not available, but rather that black marlin preferentially hunted within the mixed layer. More data on marlin diet from this area would be informative.

4.3. Dissolved oxygen and metabolic rate

Both marlin species made extensive vertical movements, with a mean daily IVM of ~1500 m for black marlin and ~2000 m for striped marlin. High-resolution data from retrieved tags demonstrated that the 10 min binned depth readings transmitted via ARGOS underestimated IVM by a factor of ~3.5. Retrieved tags also showed that both species move vertically more than half of their time. This underlines that marlin dive frequently, and are even more active than their wide horizontal movements suggest (e.g. Domeier & Speare 2012, Rohner et al. 2020). Billfish metabolism is relatively poorly understood, but their fast horizontal and vertical movements indicate they have a high energy demand and require a high concentration of dissolved oxygen (Prince & Goodyear 2006, Stramma et al. 2012).

The Arabian Sea and the area off the Horn of Africa are particularly low in dissolved oxygen (Stramma et al. 2008), and we thus expected the OMZ to have a strong influence on marlin vertical movements. The depth of the OMZ did influence the mean daily dive depths of black marlin, with a shallower OMZ correlating with deeper swimming depths. However, an OMZ of <3.5 ml l^{-1} or <150 µmol kg^{-1} was not a hard limit for either species here, with striped marlin spending 7.4% and black marlin 4% of their time in the OMZ. Billfishes were hypothesised to get stressed when oxygen concentrations fall below this limit, based on inferences from oxygen consumption rates of small tunas and juvenile sailfish (Prince & Goodyear 2006). Our results suggest that striped marlin can tolerate this stress, with a potential trade-off being a longer re-oxygenation interval at the surface between dives into the OMZ. One important caveat here is the climatological nature and the low spatial resolution of oxygen concentration data that were available here, and the relatively large error in geolocation of tagged marlin. More detailed studies, with tags that record ambient oxygen concentration, would progress this field of study considerably. In the meantime, inferences from these coarse oxygen data need to be made with caution (Carlisle et al. 2017). Despite this limitation, spatial patterns in the depth of the OMZ are consistent, and marlin off the coast of Oman and Yemen will be exposed to a shallow OMZ.

4.4. Marlin swim deeper during the day than at night

Normal diel vertical migration is ubiquitous in pelagic animals of all sizes and involves moving towards the surface during the night and staying deeper during the day (Brierley 2014). The main driver of diel vertical migration is assumed to be prey species avoiding visual predators in surface waters during the day (Brierley 2014). Most tagged marlin appeared to target vertical migrators and frequently dived into deeper waters during the day while swimming near the surface during the night. Black and striped marlin tagging studies in the Pacific largely found the same result, underlining the importance of diel vertical migration of their prey to these species (Chiang et al. 2015, Lam et al. 2015). The depth-use pattern was more pronounced in striped marlin than black marlin, suggesting that striped marlin targeted prey that dived deeper during the day, such as squid. Many black marlin dived particularly deep during dusk and dawn, but overall stayed mostly in the mixed layer, indicating that they target vertical migrators while they are in well-lit, warm water, rather than when they are below the mixed layer. The crepuscular pattern seen in some of the tagged marlin of both species could also be related to navigation (Willis et al. 2009). While maximising feeding opportunity is a key driver of crepuscular diving (Thygesen & Patterson 2019), some large pelagic predators, including marlin, have a light-mediated pineal organ that could act as a compass (Braun et al. 2022). Rapid deep dives around dusk and dawn have been hypothesised to be related to navigation in other species (Willis et al. 2009), particularly if they coincide with changes in swimming direction (Braun et al. 2022). The example crepuscular dives in our high-resolution data from a retrieved tag are also characterised by a rapid descent, indicating potential navigational diving. However, the prolonged time spent at the deepest depth ~150 m suggests that this was, at least in part, likely to be a foraging related dive.

Fish weight did not play a role in deep diving, with small individuals of both species also diving deeper during the day than at night. This contrasts to tagged black marlin in Australia, where the smallest (<50 kg) individuals had no diel depth-use pattern, likely because they target different prey than larger individuals (Williams et al. 2017). Moon illumination was not retained in the GAMMs of either species, in contrast to other observations from elsewhere. In diurnal trolling sport fisheries, striped marlin were caught less frequently during full moon (Ortega-Garcia et al. 2008), potentially because they tend to swim deeper in response to changes in the diel vertical migration of their prey, feed at night under moonlit conditions, or both. Black marlin were more frequently caught during the full moon in Australia (Lowry et al. 2007), showing that the lunar phase influences vertical movement and catches of marlin species differently. However, overall, moon phase is generally a weak predictor of marlin catches (Ortega-Garcia et al. 2008) and of vertical movement patterns, including in our study where it was not retained in the final GAMMs.

4.5. Other environmental influences on daily depth use

Black marlin had a deeper maximum depth when chl *a* was lower, and hence the water was clearer, while chl *a* was not retained in the corresponding GAMM for striped marlin. Considering that black marlin spent more time in the top 100 m and in the mixed layer than striped marlin, this trend may indicate that clearer water conditions allow black marlin to forage at greater depth within the mixed layer. Less productive surface waters may also drive black marlin to forage at greater depths when prey density at the surface is low. An important caveat is the error associated with fish location estimates, and that chl *a* was an 8 d mean product. More precise locations and *in situ* measured chl *a* would improve the interpretation of this influence on vertical movements. Chl *a* was not retained in models with maximum depth as the response for either black nor striped marlin in the Pacific (Lam et al. 2015, Williams et al. 2017), indicating that it may be a regional factor that was important in our study area, which is characterised by strong upwelling events (Schott & McCreary 2001). Black and striped marlin had deeper mean and maximum depths with higher SST. This may reflect the need to warm up between deeper dives in both species.

4.6. Free-jumping and tag performance

External satellite tags on billfish have a tendency to detach earlier than their programmed release date, often limiting their mean track duration (Domeier et al. 2019). Early tag loss was also a limitation in our study, with a mean track duration of 37 d for black marlin and 48 d for striped marlin (Rohner et al. 2020, 2021). Tag shedding, rather than mechanical failure or dives beyond the crush depth of the tag, is commonly the main cause for short tracks in billfish, with their high activity and speeds often considered as the driver of tag shedding. Using the high-resolution dataset from physically retrieved tags, we show here that marlin free-jumping directly caused tag loss on 2 occasions. This observation substantiates the hypothesis that this behaviour, and likely also other fast movements in surface waters, causes early tag loss in billfish.

4.7. Overlap with fisheries

There was a high overlap of tagged marlin with potential fishing activities in both their horizontal movements (Rohner et al. 2020, 2021) and, as demonstrated here, vertical movements as well. On a gross scale, gillnet fishing from 0–20 m depth overlaps with marlin vertical habitat use ~56% of the time (55% for black marlin, 57% in striped marlin), and longline fishing from 0–400 m almost completely (99.9%) overlaps with marlin vertical habitat use. Longlines are often set deeper than 50 m, and marlin were most active in the top 20 m of the water column, which partly explains why gillnets catch more marlin than longlines do (IOTC 2020). Their vertical habitat use showed that both marlin species are less susceptible to gillnets in daylight hours than at night, as they frequently swim below 20 m depth during the day. However, this may be counteracted if they travel further horizontally during the day and thus have a higher likelihood of encountering and interacting with such static gears on a horizontal plane. Detailed depth data of fishing gear are largely lacking but would allow for a more detailed investigation into the vertical overlap of black and striped marlin with fishing gear. In a rare study that noted the depth at which bycatch species were caught, striped marlin (n = 11) were mostly caught by longlines in the shallowest range from 80–120 m and down until the 160–200 m bin, but not deeper in the 200–320 m range (Li et al. 2013). Similarly, the tracked striped marlin here dived progressively less often into increasing depths, so this trend from the small-scale longline study may persist in the wider Western Indian Ocean. Their highly mobile and fast-swimming nature puts them at high risk of encountering fishing gear. While marlin are not necessarily a valued target species, they are generally retained (IOTC 2020), or if discarded, are likely to have a high mortality rate due to their need to ram ventilate, long gear soak times, and overall restricted movements when caught. Further work to investigate overlap of billfish movement data with commercial logbook or vessel monitoring data would provide further insights into the susceptibility of billfish to fishing gear, to potentially inform novel bycatch mitigation opportunities.

4.8. Conclusions

Black and striped marlin are sympatric off Kenya but show some habitat partitioning both horizontally (Rohner et al. 2021) and vertically. Their habitat choice likely reflects their different foraging behaviours. Striped marlin dived deeper and into colder water than black marlin and likely targeted squid below the mixed layer more frequently. Further ecological studies, such as diet analysis, would be useful for interpreting these vertical movement results. The trade-off was that striped marlin also spent more time at the water surface potentially to either warm up, re-oxygenate, or both, between dives. Their horizontal distribution also reflected this, with striped marlin staying in warmer surface waters off northern Somalia while black marlin were in colder surface temperatures, but did not dive as deep. Both species are highly vulnerable to encountering fishing gear throughout this region, with high overlap in both their spatial habitat use and diving behaviours. Until further research can inform the effective application of innovative billfish bycatch mitigation options, also noting the poor and uncertain stock conditions of striped and black marlin in the Indian Ocean, input controls should be precautionarily applied to limit the capacity of fleets to overfish these stocks of broad importance to commercial, artisanal, and sport fisheries in this region.

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