

Variability in billfish vertical distribution and fishing interactions driven by environmental conditions in the Eastern Tropical Pacific Ocean

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Blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) are ecologically important predators and valuable species throughout the world's recreational, commercial, and subsistence fisheries. Comparing multi-species vertical habitat use can inform ecological uncertainties such as inter-species competition, as well as relative vulnerabilities to fishing activities. In this study, we identified key differences in both depth use and which environmental variables drive these selections, which highlights the variability in the catchability both as target species in recreational fisheries and bycatch in commercial fisheries. To understand these two species' vertical habitat use, we examined depth profiles from 26 sailfish and 48 blue marlin tagged with pop-up satellite archival tags deployed in the Eastern Tropical Pacific Ocean. While both species are surface-oriented, we found evidence of vertical niche partitioning where sailfish spend more time at deeper depths than blue marlin. Blue marlin recorded an average mean depth of 18.5 m (± 10.8 m) during daytime and 5.2 m (± 5.5 m) at nighttime (Figure 31a), while sailfish recorded an average mean depth of 23.6 m (± 11.1 m) during daytime and 6.45 m (± 4.64 m) at nighttime. Generalized additive mixed models fitted to predict mean and max depth revealed sea level anomaly (SLA), oxygen, sea surface temperature, and mixed layer depth as significant predictors of vertical habitat use for both species. We also examined catch logs from three recreational fishing lodges in Central America to understand the influence of environmental conditions on billfish sightings per unit effort. For blue marlin and sailfish, SLA was a significant predictor in each of the four depth models (mean day, mean night, max day, max night). SLA was the variable with highest percent deviance explained for all four sailfish depth models and three of the four blue marlin depth models and had a positive relationship with all response variables for all four blue marlin depth models and three sailfish depth models (mean daytime, max daytime, max nighttime), where higher positive SLA values were associated with deeper depth responses.

Keywords: billfish, blue marlin, conservation, fisheries, sailfish, satellite telemetry.

Introduction

Blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) are highly migratory billfishes that occupy the epipelagic zone of the world's temperate, subtropical, and tropical oceans (Finnerty and Block, 1992; Graves and McDowell, 1995; Prince and Goodyear, 2006; Goodyear *et al.*, 2008; Hoolihan *et al.*, 2011). Evidence from genetic markers indicates that blue marlin exist as a single genetic population throughout the Pacific Ocean (Williams *et al.*, 2020), but tracking studies have indicated that this species tends to spend a majority of its time in stock subregions (Kraus *et al.*, 2011; Carlisle *et al.*, 2017). Sailfish in the eastern Pacific Ocean are genetically distinct from those in the western Pacific Ocean and are understood to be more coastal-oriented when compared to counterparts within the Istiophoridae clade (IATTC, 2022). Therefore, it is important to understand characteristics of sub-stocks of these species and how unique local environmental conditions may drive habitat use (Horodysky *et al.*, 2016).

Biologging and electronic tags have been used for decades to inform how marine species use and interact with their local environments (Block *et al.*, 2011; Hazen *et al.*, 2013; Hussey *et al.*, 2015; Hays *et al.*, 2016). In particular, satellite tags can measure variables such as temperature, light, oxygen, and water mixing relative to the spatial and behavioural ecology of pelagic fish throughout their ranges (Brill and Lutcavage, 2001; Braun *et al.*, 2015). Analysing predator vertical habitat can indicate which environmental features may limit vertical distributions based on species-level physiology (Brill *et al.*, 1999; Block *et al.*, 2001; Saito *et al.*, 2004; Andrzejczek *et al.*, 2019; Madigan *et al.*, 2021), reveal intraspecific ontogenetic differences in habitat preference (Williams *et al.*, 2017), and provide insight on community-level interactions and dynamics, such as increases in foraging activity (Furukawa *et al.*, 2011; Pohlott and Erhardt, 2018). Tagging studies also facilitate comparisons of relatively fine-scale vertical movement and fish behaviour to fishing activity by various sectors within marine fisheries areas. Comparing species-specific depth pref-

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Table 1. Tagging study, deployment location, and tag durations.

Study	Deployment location	Blue marlin tracks (<i>n</i>)	Sailfish tracks (<i>n</i>)	Tag type	Duration of deployments	Years of deployments
Walker, Dean, and Hoffmayer	Costa Rica	0	6	MiniPAT	32–95	2014, 2015
Logan and Shivji	Panama	20	13	MiniPAT	26–365	2018, 2019, 2020, 2021
Gray FishTag Research	Costa Rica	2	0	MiniPAT	4–37	2021
Blondin, Haulsee, and Crowder	Costa Rica	26	7	MiniPAT	23–180	2019, 2020, 2021

erences and drivers of vertical movement to fishing activity enables estimations of catchability by specific gear types and fishing practices (Ward and Myers, 2005; Luo *et al.*, 2006; Orbesen *et al.*, 2017).

The unique environmental conditions in the Eastern Tropical Pacific (ETP) provide important habitat for billfish (Prince and Goodyear, 2006; Hoolihan *et al.*, 2011; Stramma *et al.*, 2012; Pohlott and Erhardt, 2018; Farchadi *et al.*, 2019; Haulsee *et al.*, 2022). Within the ETP, the oxygen minimum zone (OMZ) is an area of suboxic ($<1\text{--}2\text{ ml l}^{-1}$) water at depths as shallow as 100 m, covering most of the region (Diaz, 2001; Fielder and Talley, 2006; Espinoza-Morriberón *et al.*, 2019). Low oxygen and low temperature waters are seasonally brought close to the surface in this region by intense upwelling and can lead to vertical compression of suitable habitat with thermoclines as shallow as 25 to 50 m (Prince and Goodyear, 2006; Stramma *et al.*, 2012). This is particularly concerning as the OMZ is expanding in response to climate change in this region (Stramma *et al.*, 2008; Espinoza-Morriberón *et al.*, 2019). More ephemeral oceanographic features also aggregate marine predators in the ETP. Eddies of ~250 km are generated via winds that blow from the Atlantic through Central American mountain passes including the Gulf of Tehuantepec, the Gulf of Papagayo, and the Gulf of Panama (Muller-Karger and Fuentes-Yaco, 2000; Fiedler, 2002). These cold core eddies are characterized by lower temperatures than surrounding waters and higher concentrations of phytoplankton. Eddy generation is highest during the boreal winter and spring, when wind jets are strongest in the region (Muller-Karger and Fuentes-Yaco, 2000).

The ETP also comprises of robust recreational, commercial, and subsistence fisheries (Ehrhardt and Fitchett, 2006; Gentner, 2007; IATTC, 2022). Fishing activities range from the recreational sector, which includes overnight charter boats, fishing lodges, and annual tournaments, to commercial fishing which spans artisanal, longline, and purse seine fleets. While the vast majority of recreational fishing effort occurs during the day and is catch-and-release in this region (Graves and Horodysky, 2015; Horodysky *et al.*, 2016), commercial fishing often consists of shallow-set longlines that are set through day and night (Bigelow *et al.*, 2006; Griffiths *et al.*, 2017; IATTC, 2022). Pelagic longline fishing began to expand in the Pacific Ocean in the mid-1950s (IATTC, 2022). Commercial fishing fleets in the ETP primarily target species like yellowfin tuna, swordfish, and dolphinfish; however, billfish are occasionally targeted or are landed incidentally (Punt *et al.*, 2015; Horodysky *et al.*, 2016; IATTC, 2022). Greater quantities of these Istiophoridae species are caught in recreational fisheries or as incidental catch compared to targeted commercial fishing (Gentner, 2007; Punt *et al.*, 2015; Horodysky *et al.*, 2016). The latest IATTC report found that reported catches of sailfish were significantly lower over the last 5 years as compared to previous years, but it is likely that a

proportion of sailfish catch goes unreported (IATTC, 2022). While annual catch rates of ETP blue marlin have increased in the last decade, many populations in the Pacific Ocean are not well managed and may be declining (IATTC, 2022). However, many regions where blue marlin frequent are data-limited, preventing a thorough understanding of population sustainability in the Pacific Ocean (Billfish status review, <http://www.iucnredlist.org>).

Quantifying water column use by blue marlin and sailfish can help to inform ecological uncertainties such as inter-specific competition, as well as relative vulnerabilities to fishing gear (Ward and Myers, 2005; Horodysky *et al.*, 2016; Orbesen *et al.*, 2017; Madigan *et al.*, 2021). Here, we use the most comprehensive tagging dataset to date for these two species in the region to better understand vertical behaviour using pop-off satellite archival tags (PSATs). We also include records of recreational raises [i.e. sightings per unit effort (SPUE)] to inform catchability. Within this study, we aim to provide insights into three primary questions: (1) How do sailfish and blue marlin differ in vertical space use during day and night in the ETP? (2) How do environmental and physical variables drive these depth uses? and (3) How do these same environmental and physical variables influence the interaction of these species with fishing activity? Understanding vertical preferences from PSATs can be used to better assess interaction rates recreational and commercial fisheries, as well as even bycatch avoidance approaches in.

Methods

All analyses were performed in R (R-4.0.3).

Ethics statement

All ethical animal capture, tagging, and release methods used for this study were approved by the Stanford University's Administrative Panel on Laboratory Animal Care under protocol number 33092, and with permission from the Costa Rican Institute of Fisheries and Aquaculture (INCOPECA) under permit number 485678565. Where available, animal handling permitting information for historical tag data used in this study can be found in the primary literature describing the deployments of those tags (Table 1).

Fish capture, handling, and tagging

Blue marlin and sailfish were captured between January 2019 and August 2021 within Costa Rican's EEZ. We worked with local recreational sport fishers to target blue marlin and sailfish with hook-and-line trolling gear. Fish brought to the boat were quickly evaluated for condition and any fish exhibiting signs of distress or damage was immediately released. Fish in good health were secured alongside the boat and quickly tagged with a pop-up satellite archival tag (PSAT). We

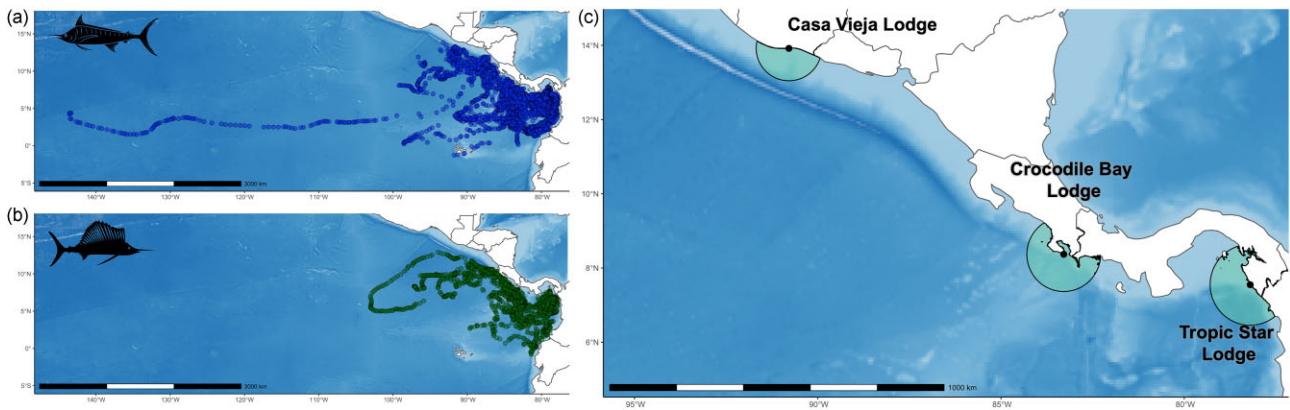


Figure 1. (a) Blue marlin tracks, (b) sailfish tracks, and (c) buffered fishing footprints (i.e. maximum extent of day trips taken) of each of the three fishing lodges.

deployed miniPATs ($n = 70$, Wildlife Computers, Redmond, WA, USA). MiniPATs were programmed to release after 90, 180, 270, or 365 d, recording geolocation data and depth time series at 150 or 450-s sampling intervals. These MiniPATs were also programmed to release from the fish if the tag was floating at the ocean's surface or other constant depth for longer than 2 d, or if the tag approached the maximum depth limit of 1400 m. Tags were attached to a large titanium anchor dart with Kevlar and heat shrink coated 300 lb monofilament tether (MoiMoi, X-Hard). Blue marlin and sailfish were tagged between the pterygiophores at the base of the tallest portion of the dorsal fin, at an angle that allowed the tag to trail parallel to the fish and with the tether sunk deep enough within the musculature tissue that kept the tag close to the body to reduce stress on the tether. Fish were then revived next to the boat, which slowly idled forward, to increase oxygenation of the gills until colour returned to the fish and sufficient tail action was observed before the fish were released. All fishing hooks and lures were removed before the fish were released. As fish were released, the time of tagging, tag deployment location, and sea surface temperature (SST), when available, were recorded.

Other data collection and processing

In addition to the tags deployed for this project, we also assimilated datasets from similar geo-location tags deployed on blue marlin and sailfish within the ETP from 2014 to 2021 (Table 1). For Wildlife Computers tag models (e.g. MK10, PAT), we ensured that estimated fish tracks and associated location errors were calculated with the most recent available geo-location estimating models by uploading the raw data collected by tags into Wildlife Computers data portal (<http://mywildlifecomputers.com>) and re-processing through Wildlife Computers proprietary Geolocation Processing Estimator 3 (GPE3) using the methods described below. Leveraging these datasets expanded both the spatial and temporal coverage of observations of blue marlin and sailfish movement in this region, allowing a more comprehensive description of these populations.

Geo-location estimation and track processing

All geo-location datasets collected for this project from Wildlife Computer PSATs deployed on blue marlin and sailfish in the ETP were processed using the proprietary software Ge-

olocation Processing Estimator 3 (GPE3; Wildlife Computers Inc., Redmond, WA, USA). This data processing uses a hidden Markov model (Patterson *et al.*, 2009) to produce two maximum likelihood position estimates per day and likelihood surfaces for each position estimate on a 0.25 by 0.25-degree grid. Prior to GPE3 processing, known locations (tagging location and first reliable pop-up location) were specified for each individual to help ground location estimates. The location processing algorithm also requires a user-defined animal speed parameter (standard deviation of the normal distribution of the maintenance speed of species). Block *et al.*, (2002) observed sustained swimming speeds for blue marlin around $0.80\text{--}1.20\text{ m s}^{-1}$, with bursts of up to 2.25 m s^{-1} , and the speed parameter is commonly set around 2 m s^{-1} for pelagic predators like tuna and billfish (Rohner *et al.*, 2021; Filous *et al.*, 2022). Therefore, we set the speed parameter to 2 m s^{-1} for both species as well, after ensuring that the resulting tracks visually appeared appropriate.

For the resulting estimated locations, there were still occasional locations that appeared unlikely, characterized by rapid speeds and high turn angles. Therefore, we performed additional filtering using the `speedfilter()` function in R trip (2006, CRAN, active) (Sumner, 2016). The most likely speed between each estimated location was calculated using the `speed()` function within the “move” package (Kranstauber *et al.*, 2021). The max speed parameter for the speed filter was set to a conservative 3 km h^{-1} since 95% of sailfish and blue marlin speeds were found to be <2.60 and 2.50 km h^{-1} , respectively. Tag time series were trimmed to remove depth recordings that (1) indicated the tag was no longer attached to the individual fish (e.g. floating at the surface) or (2) recordings that indicated the individual had died and the tag was sinking towards its programmed crush depth. Data cleaning and processing resulted in 26 sailfish and 48 blue marlin tracks with sufficient data to be used in subsequent analyses (Table 1, Figure 1a and b).

Trip logs

We collated daily logbook records from three sport fishing lodges in the ETP. Lodges fish with comparable equipment and limited maximum spatial extents of day trips (i.e. fishing footprints). Lodges included Casa Vieja Lodge in Guatemala, Crocodile Bay Resort in Costa Rica, and Tropic Star Lodge in Panama (Figure 1c). The Casa Vieja Lodge fishing footprint

extends 60 nautical miles from Puerto San José and records were available from January 2015 to December 2019. The Crocodile Bay Resort in Costa Rica fishing footprint extends 25 nautical miles from Matapalo Rock in Puerto Jimenez Costa Rica, and records were available from February 2011 to December 2019. The Tropic Star Lodge in Panama fishing footprint extends 40 nautical miles from the location of the lodge, and records were available from January 2010 to December 2019. These logs record raises, when a fish is observed following and/or attacking the baits or lures, and releases, when a fish is caught, brought to the side of the boat, and released. To reduce bias of angler skill, we calculated SPUE (see Haulsee *et al.*, 2022) where sightings were aggregated and divided by the number of boats fishing for each lodge each day. See Haulsee *et al.* (2022) for more information on logbook records and collection.

Vertical migration

Each tag time series was first classified into time classes (dawn, day, dusk, and night). To do so, tag-derived sunrise and sunset were buffered by 30 min (Wright *et al.*, 2021; Figure 2). Observations within ± 30 min of sunrise were classified as dawn. Observations within ± 30 min of sunset were classified as dusk. Observations between $+30$ min of sunrise and -30 min of sunset were classified as day. Observations prior to -30 min of sunrise or after $+30$ min of sunset were classified as night. We then calculated the mean depth and maximum (max) depth of each time class. To assess species-level differences, we compared mean daytime depth and mean nighttime depth using a two-sample Wilcoxon test with significance set at $p \geq 0.05$, as depth data were not normally distributed. We also calculated the mean estimated latitude and longitude for day and night each day. Daytime and nighttime mean latitude and longitude were used to extract spatially explicit environmental variables (see below). To assess vertical migration behaviour, we compared mean daytime depth to mean nighttime depth each day for each individual. The crepuscular phase was excluded from this analysis. Daily mean daytime and nighttime depth were compared using a two-sample Wilcoxon test with significance set at $p = 0.05$ (Griffiths *et al.*, 2020; Wright *et al.*, 2021). Comparisons were classified as “diel vertical migration (DVM)” if mean daytime depth was significantly deeper than mean nighttime depth, “reverse diel vertical migration (rDVM)” if mean nighttime depth was significantly deeper than mean daytime depth, or “none” if no significant difference between mean daytime depth and mean nighttime depth (Griffiths *et al.*, 2020; Wright *et al.*, 2021). Vertical migration was also collated by month.

Environmental variables

Billfish tracks were matched to environmental data to describe vertical habitat use of both species. Variables were selected based on those shown to be important in previous billfish studies as well as based on hypothesized drivers of depth utilization (Prince and Goodyear, 2006; Hoolihan *et al.*, 2011; Braun *et al.*, 2015; Madigan *et al.*, 2021). Daily SST data were sourced at 0.25° -grid resolution from the NOAA AVHRR Optimum Interpolation Sea Surface Temperature (OISST) dataset (Huang *et al.*, 2020). Monthly climatologies of dissolved oxygen (DO) at 100, 200, and 300 m depth and mixed layer depth (MLD) were sourced from World Ocean Atlas 2018 at 1° -grid resolution (Garcia *et al.*, 2019). Daily sea level anomaly

(SLA) data were sourced from Copernicus Marine Environment Monitoring Service at 0.25° -grid resolution. Total cloud cover (TCC) data were sourced from Copernicus Marine Environment Monitoring Service at 0.25° -grid resolution (Hersbach *et al.*, 2018). Average daytime and nighttime TCC was calculated by taking the mean of cloud cover layers during daytime and nighttime hours, excluding the crepuscular phase, each day. Daily lunar phase was sourced from the lunar package in R (Lazaridis, 2022). Distance to the coast (dist) was calculated using the *geosphere()* package in R (Hijmans, 2021).

Generalized additive mixed models

Generalized additive mixed models (GAMMs) were built with an identity link function using maximum likelihood estimates within the *mgcv* package in R (Wood, 2017), where Tag ID was set as a random variable. Separate GAMMs were fitted to examine the relationship between environmental predictor variables and depth-related response variables: (1) daytime mean depth, (2) nighttime mean depth, (3) daytime maximum depth, and (4) nighttime maximum depth. Fixed explanatory variables included lunar illumination, SST, MLD, SLA, TCC, and DO at 100, 200, and 300 m depth. For daytime specific models, the previous day's lunar illumination was used instead to capture potential effects of the previous night's lunar variables on daytime depth behaviour, as previous studies have indicated that increases in light from the moon may increase feeding activity at night (Lowry *et al.*, 2007; Pohlot and Erhardt, 2018). All explanatory variables were modelled as continuous and smoothed using the “*ts*” smoother option. Collinearity between variables was assessed by calculating Pearson's correlation coefficients (r), with a cut off of ± 0.7 (Dormann *et al.*, 2013). Most variables, aside from DO at various depths ($r < 0.7$), were weakly correlated ($r < 0.35$; Supplementary Table S2). Smoothing (k) was auto-chosen and evaluated using the *gam.check()* function. We limited smoothing to five knots to ensure that models were not overfit (Zuur *et al.*, 2012). If variables were collinear, separate models were fit using only one of the collinear variables. The final model with the highest deviance explained and lowest AIC was chosen. The full model was:

$$\text{Depth Response} \sim s(\text{SST}) + s(\text{lunar illumination}) + s(\text{MLD}) + s(\text{DO@100 m}) + s(\text{DO@200 m}) + s(\text{DO@300 m}) + s(\text{dist}) + s(\text{SLA}) + s(\text{TCC}) + s(\text{fish}_i = \text{“random”}) + \square,$$

where \square is the Gaussian error term. Fish (tag ID) was included as a random effect using the “*re*” smoother option within the *gam()* function (Wood, 2011; Andersen *et al.*, 2014; Simpson, 2021). Models for each response variable were selected by sequentially dropping non-significant explanatory variables until final models contained only significant predictors (Lewis, 2009; Williams *et al.*, 2017). During the selection process, significance was set at $p = 0.0125$ (i.e. $p = 0.05$ divided by four models per species), as these depth models were subject to multiple hypothesis testing (Jafari *et al.*, 2019). The *gam.check()* function was used to visually inspect model fit and residuals.

Similar methods for GAMMs were used to examine the relationship between environmental predictors and SPUE. The same fixed explanatory variables were included, with the exception of distance to coast. Fishing lodge was included as a random variable. Environmental variables were extracted and averaged over the fishing footprint buffers of each lodge

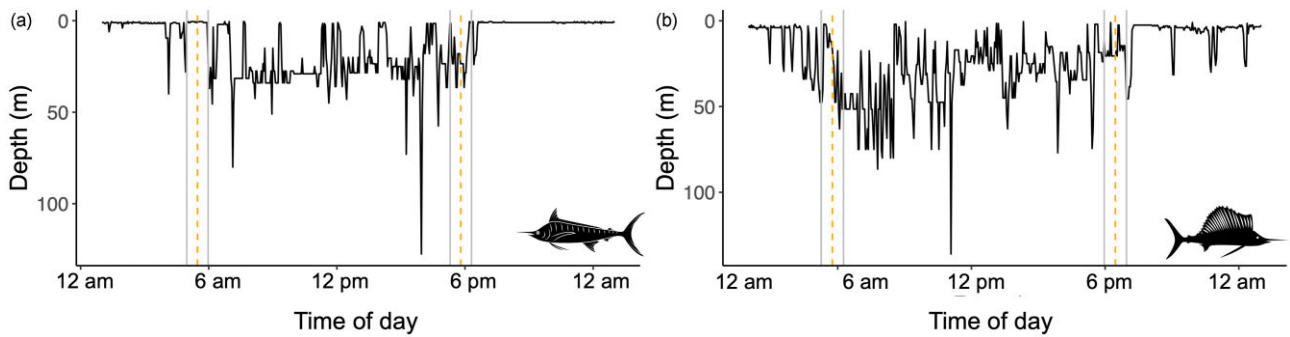


Figure 2. Representative 24-h period (00:00–24:00) depth profiles for (a) blue marlin and (b) sailfish. Sunrise and sunset are represented by the orange dashed lines and 30-min buffers representing the crepuscular phase are shown vertically in grey.

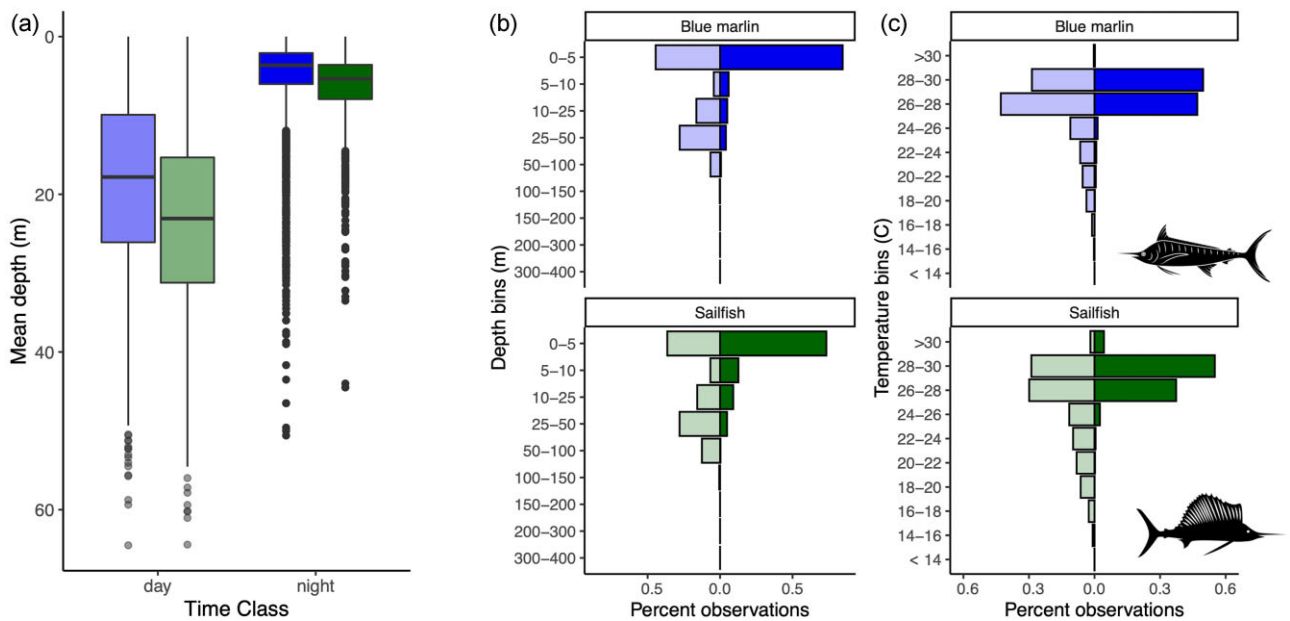


Figure 3. (a) Median mean depth (dark black line) and interquartile range of mean depth (box) for each species within each time class. Blue marlin are represented in blue and sailfish are represented in green. Lighter shades indicate daytime and darker shades indicate nighttime. Percentage of total observations at (b) depth and (c) temperature for each species.

(Figure 1). During the selection process, significance was set at $p = 0.05$, as these models were not subject to multiple hypothesis testing. The full model was:
 $\text{SPUE} \sim \text{s}(\text{year day}) + \text{s}(\text{SST}) + \text{s}(\text{lunar illumination}) + \text{s}(\text{MLD}) + \text{s}(\text{DO@100 m}) + \text{s}(\text{DO@200 m}) + \text{s}(\text{DO@300 m}) + \text{s}(\text{SLA}) + \text{s}(\text{TCC}) + \text{s}(\text{fishing lodge}_i = \text{"random"}) + \square$.

Results

Vertical habitat use

Tagged blue marlin recorded an average mean depth of 18.5 m (± 10.8 m) during daytime and 5.2 m (± 5.5 m) at nighttime (Figure 3a). Tagged sailfish recorded an average mean depth of 23.6 m (± 11.1 m) during daytime and 6.45 m (± 4.64 m) at nighttime (Figure 3a). Results of Mann–Whitney U test indicate a significant difference in both mean daytime depth ($p < 2.2\text{e-}16$) and mean nighttime depth ($p < 2.2\text{e-}16$) between the two species. Maximum depth by individual ranged from 11.5 to 396.5 m for blue marlin and 77.0 to 321.0 m for sailfish (Figure 3a). Results of Mann–Whitney U test indicate a significant difference in maximum daytime depth ($p <$

$2.2\text{e-}16$) but not maximum nighttime depth ($p = 0.6706$) between the two species. Sailfish spent 86.9% of daytime hours above 50 m, 65.6% of daytime hours above 30 m, and 43.1% of daytime hours above 10 m (Figure 3b). Blue marlin spent 93.1% of daytime hours above 50 m, 73.2% of daytime hours above 30 m, and 48.8% of daytime hours above 10 m (Figure 3b). Sailfish spent 85.9% of nighttime hours above 10 m, whereas blue marlin spent 90.4% of nighttime hours above 10 m (Figure 3b). Temperature at depth ranged from 11.6 to 31.5°C for blue marlin and 12.0 to 31.7°C for sailfish, but the highest proportion of time was spent in waters 26 to 28°C during daytime and 28 to 30°C during nighttime for both species (Figure 3c). Both species exhibited a similar diel trend in depth use, recording DVM behaviour over 70% of the time, followed by “none” or no significant difference in mean depth between daytime and nighttime over 20% of the time (Figure 4a). Both species rarely displayed rDVM behaviour (3–5% of the time). Both species were more likely to exhibit no significant difference in daytime vs. nighttime mean depth during the dry season (November through April) as compared to the wet season (May through October) (Figure 4b).

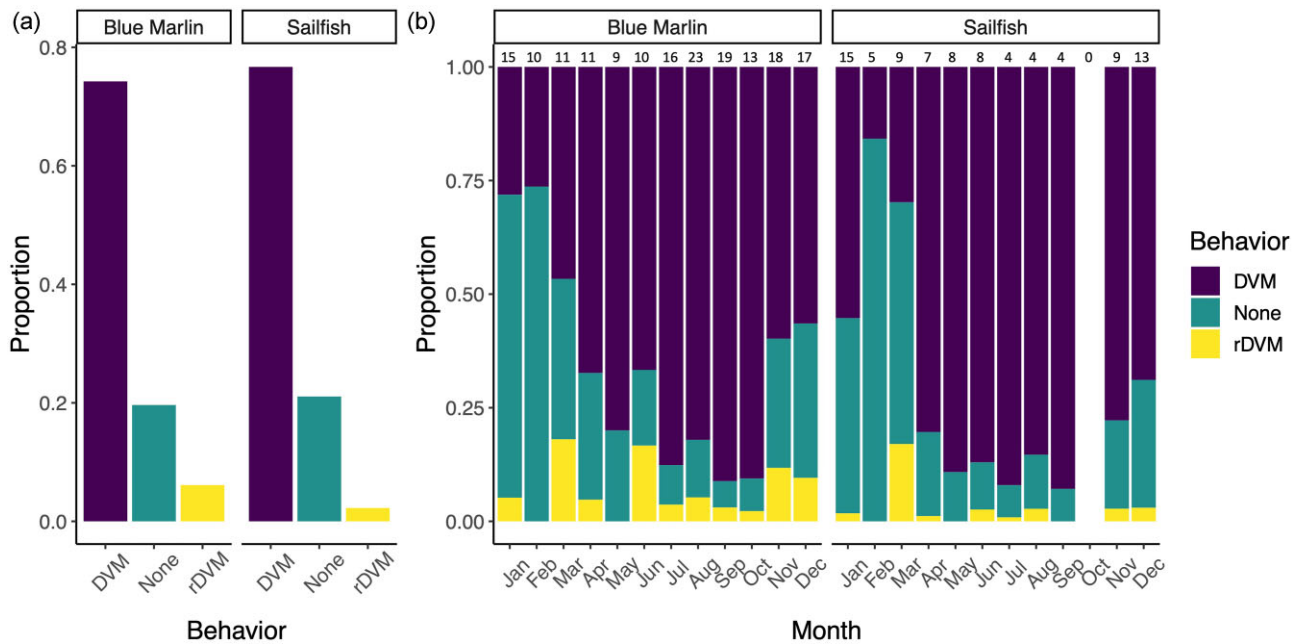


Figure 4. (a) Vertical migration behaviour of sailfish and blue marlin tagged in the ETP. (b) Vertical migration by month for blue marlin and sailfish. Numbers above bars representing each month indicate the number of tags at liberty (n) included in each bar.

Table 2. Results of best fit GAMM for each of four depth response variables and SPUE for blue marlin and sailfish.

Species	Time class	Response variable	Adj. R-sq.	Dev. exp. (%)	SST	Lunar illum.	DO @ 100 m	DO @ 200 m	DO @ 300 m	MLD	SLA	CFC
Blue marlin	Day	Mean depth	0.311	33.0	2.1		5.5	3.0		0.9	10.0*	
	Night	Mean depth	0.174	19.0				2.6			24.2*	
	Day	Max depth	0.161	18.1	2.2		5.0	8.3*	6.1		3.9	
	Night	Max depth	0.202	21.7	7.4						14.3*	1.4
		SPUE	0.112	11.4	5.3		4.4		12.3*	7.9	7.9	
Sailfish	Day	Mean depth	0.533	55.4	7.9*			4.5		4.5	7.9*	
	Night	Mean depth	0.234	25.2		7.0					11.1*	
	Day	Max depth	0.273	29.7				5.7	3.0		19.9*	
	Night	Max depth	0.294	31.0	2.9					4.5	10.3*	
		SPUE	0.604	60.5	0.3	0	0.3	0.2	0.3	0.8*	0.2	0.2

*highest percent deviance explained. Response variables include: SST, sea surface temperature; Lunar illum., Lunar illumination; DO @ 100 m, dissolved oxygen at 100 m depth; DO @ 200 m, dissolved oxygen at 200 m depth; DO @ 300 m, dissolved oxygen at 300 m depth; MLD, mixed layer depth; SLA, sea level anomaly; TCC, total cloud cover. Blank cells indicate that the environmental variable was not a significant model predictor and was therefore removed from the model.

Environmental and physical drivers of vertical habitat use

MLD and distance to coast were collinear ($r = 0.7$), so vertical models were built including either MLD or distance. Models that included MLD consistently performed better (i.e. higher model deviance explained), therefore only MLD was included in final models. The environmental variables that significantly predicted depth responses for blue marlin and sailfish varied. Only the partial responses of significant predictors are presented (Table 2, Figures 5 and 6).

SLA, DO, and SST were the most significant predictors of depth across species, diel phases, and metrics (i.e. mean and max depth). SLA was a significant predictor of depth for both species and was the variable with highest percent deviance explained for all four sailfish depth models (mean day = 7.9%, mean night = 11.1%, max day = 19.9%, max night = 10.3%) and three of the four blue marlin depth models (mean day =

10.0%, mean night = 24.2%, max night = 14.3%; Table 2). In general, positive SLA values were associated with deeper depth responses (Figure 5a and Supplementary Figures S1–S5 and S7–S8).

In general, DO showed a positive linear relationship with depth, where the use of deeper depths were associated with higher concentrations of DO (Figure 5c). DO at 100 m was significant in only the blue marlin daytime mean and max depth models, while DO at 300 m was significant in only the daytime max depth models for both species (Table 2). DO at 200 m was the most significant oxygen-related variable, showing significant correlation with depth in the mean and max daytime models for both species (Table 2). DO at 200 m exhibited the highest percent deviance explained for blue marlin daytime max depth model (Table 2). However, for all depth models in which DO at 200 m was a significant predictor ($n = 4$), there was a negative relationship between DO at 200 m

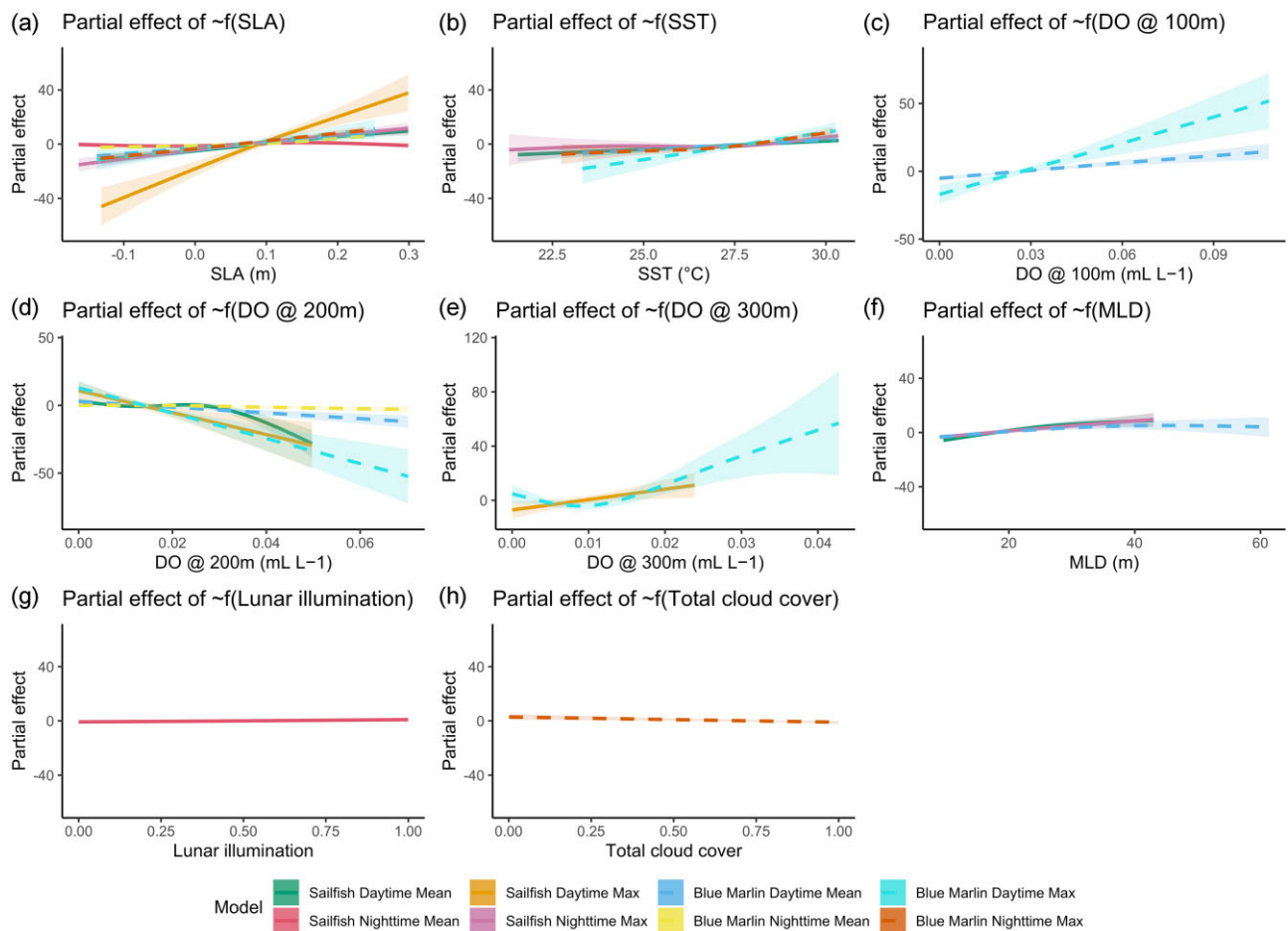


Figure 5. GAMM response curves for blue marlin and sailfish depth models. Blue marlin are represented by dashed lines and sailfish are represented by solid lines. Response curves are only shown if they were significant ($p < 0.0125$) in the species depth models. Shaded regions represent the 95% CIs. SLA, sea level anomaly; SST, sea surface temperature; DO @ 100 m, dissolved oxygen at 100 m depth; DO @ 200 m, dissolved oxygen at 200 m depth; DO @ 300 m, dissolved oxygen at 300 m depth; MLD, mixed layer depth; Lunar illumination, fraction of moon illuminated; TCC, total cloud cover. Individual species response curves can be found in the Supplementary Material.

and depth, where use of deeper depths were associated with lower levels of DO and use of shallower depths were associated with higher concentrations of DO (Figure 5d).

For all models where SST was a significant predictor ($n = 5$), use of deeper depths was associated with higher SST values (Figure 5b). Lunar illumination was only significant in the sailfish nighttime mean depth model, where use of deeper depths were associated with a fully illuminated moon (Figure 5g). For all models where MLD was significant ($n = 3$), use of deeper depths was associated with deeper MLD (Figure 5f). This relationship reached an asymptote in the blue marlin daytime depth model at ~ 45 m (Figure 5f). Blue marlin nighttime max depth showed a negative linear relationship with TCC, where use of deeper depths were associated with higher levels of cloud cover at night (Figure 5h).

Environmental and physical drivers of SPUE

SLA, SST, DO, and MLD were also significant predictors of SPUE for both species (Figure 6). DO at 300 m was the predictor with the highest percent deviance explained for blue marlin SPUE, whereas MLD was the predictor with the highest percent deviance explained for sailfish (Table 2). In general, Sailfish SPUE was negatively associated with SLA, DO, TCC, and MLD, where higher sightings correlated with negative sea

level anomalies, lower concentrations of DO at depths of 200 and 300 m, a shallower MLD, and less TCC (Figure 6), Sailfish SPUE peaked between 29 and 30°C, but was lower on the tails of SST values (Figure 6b and Supplementary Figure S10). Sailfish SPUE had a weak non-linear relationship with lunar illumination (Figure 6g and Supplementary Figure S10). Blue marlin SPUE showed a quadratic relationship with DO at 300 m, where sightings peaked at ~ 0.5 ml l⁻¹ (Figure 6e). Blue marlin SPUE had positive linear relationships with SST, SLA, and MLD, where higher sightings were associated with higher SSTs, positive sea levels, and a deeper mixed layer (Figure 6). Blue marlin SPUE had a negative linear relationship with DO at 100 m, where higher SPUE was associated with lower levels of DO (Figure 6c and Supplementary Figure S9). DO at 100 m, DO at 200 m, TCC, and lunar illumination were also significant predictors of SPUE for sailfish (Figure 6 and Supplementary Figure S10).

Discussion

This multi-year collaborative tagging effort allowed for a comprehensive analysis of blue marlin and sailfish vertical habitat use within the ETP. As a result, we found that blue marlin and sailfish spend the vast majority of time at the ocean

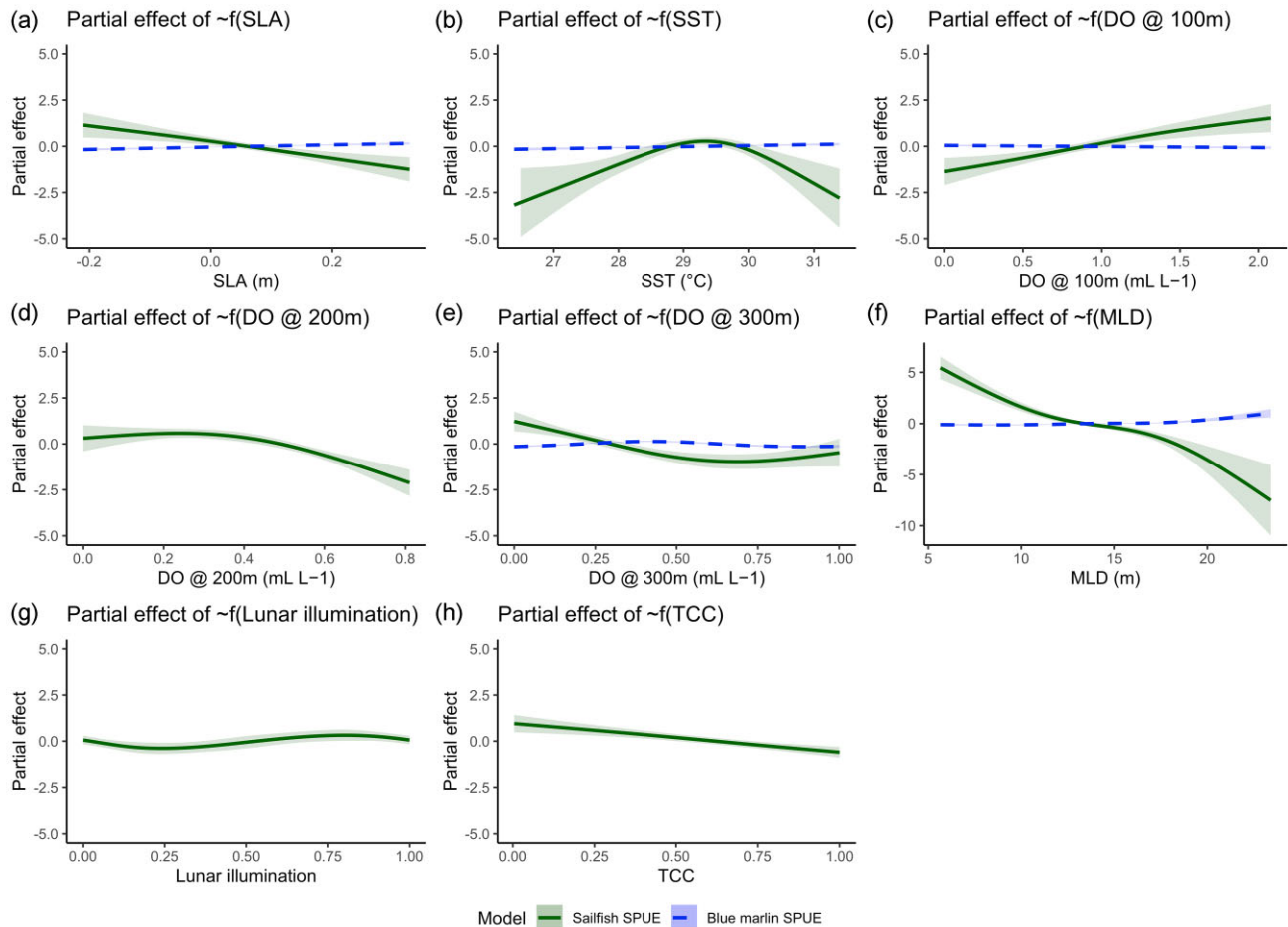


Figure 6. GAMM response curves for blue marlin and sailfish SPUE models. Blue marlin are displayed in blue and sailfish are displayed in green. Response curves are only shown if they were significant ($p < 0.0125$) in the species SPUE model. Shaded regions represent the 95% CIs. SLA, sea level anomaly; SST, sea surface temperature; DO @ 100 m, dissolved oxygen at 100 m depth; DO @ 200 m, dissolved oxygen at 200 m depth; DO @ 300 m, dissolved oxygen at 300 m depth; MLD, mixed layer depth; Lunar illumination, fraction of moon illuminated; TCC, total cloud cover. Y-axes are scaled the same for each plot. Individual species response curves can be found in the Supplementary Material.

surface; however, sailfish on average spent statistically more time at deeper depths than blue marlin. We also found significant relationships between vertical habitat use and SLA, SST, MLD, and DO. Although we found sailfish and blue marlin vertical behaviour to be similar, we identified key differences in both depth preference and which environmental variables drive these preferences, which could have significance for their catchability both as target species and as bycatch.

Vertical habitat use in the ETP

Previous studies have found that blue marlin spend more time at deeper depths in comparison to sailfish (Price and Goodyear, 2006; Goodyear *et al.*, 2008; Bubley *et al.*, 2020; Madigan *et al.*, 2021). Here, we find the opposite trend, where sailfish tend to inhabit deeper depths on average and spend more time at depth in comparison to blue marlin (Figure 3). Specifically, sailfish spent fewer daytime hours at shallow depths as compared to blue marlin in this study (Figure 3a and b). These results are similar to those in a recent study, which used high-resolution biologging tags on sailfish and blue marlin in Panama and found that sailfish performed more dives than blue marlin (Logan *et al.*, in press). Sailfish also tended to spend fewer daytime hours at the surface compared to studies on this species in other parts of their range. For example,

Hoolihan and Luo (2007) found that sailfish spent over 83% of time above 10 m in the Arabian Gulf with no significant difference between day and night, and Hoolihan *et al.* (2011) found that sailfish spent 82% of daytime hours at surface temperature when sailfish tags were pooled across the western North Atlantic, Eastern Tropical Atlantic, and ETP. In contrast, here we found that sailfish spent ~43% of daytime hours above 10 m but did spend ~87% of time above 50 m. While sailfish have been historically classified as the most surface-oriented billfish species throughout their range (Hoolihan *et al.*, 2011; Braun *et al.*, 2015; Lam *et al.*, 2016), in the ETP we find that blue marlin are more surface oriented and sailfish tend to remain consistently deeper than blue marlin; however, both species still limit depth uses to the epipelagic layer. Blue marlin in this study remained at near surface depths for a large proportion of both daytime and nighttime hours (~93% of daytime hours above 50 m and ~90% of darkness above 10 m). This finding is similar to blue marlin in the western North Atlantic, which spent 71% of time above 5 m and 89% of time above 50 m (Freitas *et al.*, 2022) and the central Pacific, on average, blue marlin spent 50% of time above 12 m and 90% of time above 84.4 m (Carlisle *et al.*, 2017). Previous studies have suggested that limited daytime penetration as a result of upwelling in the ETP may limit the vertical distri-

bution of prey in this region, which could limit depth use of pelagic predators (Hoolihan *et al.*, 2011).

Hoolihan *et al.* (2011) hypothesized that due to smaller body sizes and lateral compression, sailfish may not have the ability to retain body heat as efficiently as blue marlin when experiencing lower temperatures at depth. However, in the ETP specifically, temperature may be less of a limiting factor for sailfish. SSTs are relatively high in this region compared to other parts of these species' ranges. Smaller body size and lateral compression may be advantageous in allowing heat to dissipate more quickly than blue marlin within very warm SSTs (Hoolihan *et al.*, 2011). We also find blue marlin vertical space use to be more similar to smaller size classes of black marlin (*Istiompax indica*) observed in the southwestern Pacific Ocean (Williams *et al.*, 2017). Williams *et al.* (2017) found small and intermediate size classes of black marlin to spend greater than 90% of time at shallower depths, significantly more time than their larger counterparts. The difference in blue marlin vertical behaviour found in this study could be related to body size in addition to the influence of other biological (e.g. prey distribution), environmental or physical-related factors.

This study confirms the results of previous studies where billfish have been shown to display diel vertical migration behaviour (e.g. Goodyear *et al.*, 2008; Braun *et al.*, 2015; Carlisle *et al.*, 2017; Bubley *et al.*, 2020; Madigan *et al.*, 2021), however with additional nuance. Some previous studies have found that blue marlin do not show significant diel differences in vertical behaviour (Saito *et al.*, 2004; Saito and Yokawa, 2006), while others have found that blue marlin occupy significantly deeper depths at day as compared to night (Goodyear *et al.*, 2008; Madigan *et al.*, 2021). We found that while blue marlin often show no significant diel differences in vertical behaviour, this species consistently displays DVM behaviour during the rainy months of May to October (Figure 4b), indicating there may be seasonal differences in this behaviour that may align with the rainy and dry seasons of Central America. We hypothesize this may be due to impacts of rainwater on the top layer of the ocean. Rain may alter salinity or visibility in this top layer (Fiedler and Lavín, 2017), which could influence vertical distribution of prey species. Additionally, during the northern winter (i.e. dry season), surface chlorophyll levels are high in coastal regions due to coastal upwelling (Fiedler and Lavín, 2017), which may provide essential habitat for prey species at shallow depths.

Environmental drivers of vertical habitat use and SPUE

By modelling various depth response variables at day and night, we were able to discern what environmental features correlate with depth use within the diel cycle. While some environmental variables such as SST and sea surface height (SSH) were significant in both daytime and nighttime depth models, other variables such as DO at various depths, were more often significant in daytime depth models as opposed to nighttime depth models (Table 2, Figure 5). This could be due to "bounce-diving" behaviour, which is often exhibited by billfish and tunas, where individuals make short duration, repetitive dives through the thermocline while searching for prey and foraging (Williams *et al.*, 2017; Madigan *et al.*, 2021; Logan *et al.*, in press). While light availability may largely restrict this behaviour to occurring primarily during the day (Lam *et al.*, 2016; Williams *et al.*, 2017), oxygen concentrations may

be a limitation for the frequency or depth at which these dives occur (Prince *et al.*, 2010; Madigan *et al.*, 2021; Logan *et al.*, in press).

We found deeper mean and max depth to be associated with positive SLA values and deeper MLD, while shallower mean and max depth were associated with negative SLA values and shallower MLD in both blue marlin and sailfish (Figure 5a and Supplementary Figures S1–S8). SSH and MLD can be used as an indicator of oceanographic features, like eddies where positive values are associated with anticyclonic eddies and negative values are associated with cyclonic eddies. MLD is deeper during anticyclonic eddies and shallower within cyclonic eddies (Gaube *et al.*, 2019). Arostegui *et al.* (2022) suggest that top predator depth distribution in the North Pacific Subtropical Gyre may expand deeper during anticyclones due to downward displacement of isotherms. Our findings support this suggestion in the ETP as mean and max depth for both species was deeper in relation to positive SLA values as well as a deeper mixed layer, suggesting that distributions may expand deeper for blue marlin and sailfish in this region during anticyclonic eddies. Other predators such as northern elephant seals, dolphinfish, and tunas have been shown to aggregate within zones of warm, anticyclonic eddies where prey abundance may be more favourable (Marín-Enríquez *et al.*, 2022; Arostegui *et al.*, 2022; Keates *et al.*, 2022).

Arostegui *et al.* (2022) also found significantly higher catch odds ratios and catch rate ratios of blue marlin and other predators within anticyclones. We find similar results with blue marlin, where higher SPUE values were associated with positive SLA values and lower SPUE values were associated with negative SLA values (Figure 6a and Supplementary Figure S9). However, we found the direct opposite result in sailfish, where instead, lower SPUE values are associated with positive SLA values. Importantly, we also found that sailfish daytime max depth showed the strongest partial response to SLA out of any depth model (Table 2, Figure 5a, and Supplementary Figure S7) and that sailfish are consistently deeper than blue marlin (Figure 3a). Similarly, we found lower sailfish SPUE to be associated with shallower MLD (Figure 6f). As a result, we hypothesize that sailfish may expand their range vertically past the depth range of the recreational fishery during positive anticyclonic features. This may also help explain why sailfish take advantage of deeper depths, if they do so within anticyclonic eddies where they are able to forage at deeper depths due to an expansion of warm water at depth and therefore a lack of thermal constraints. Similar vertical behaviour has been shown in blue sharks, where this species was found to use the core of anticyclonic eddies to forage at depth (Braun *et al.*, 2019).

The relationship between fish depths and oxygen was complex across models. DO at 100 m was only significant in blue marlin daytime depth models, while DO at 300 m was only significant within daytime max depth models for both species (Table 2). Individuals from both species spent relatively little time at depths below 100 m; however, they did record depths greater than 200 and 300 m (Figure 3b). Logan *et al.* (in press) suggested that billfish in the ETP can make short duration dives to dissolved oxygen levels below the 3.5 ml l⁻¹ boundary previously suggested to cause physiological stress in tropical pelagic fishes (Bushnell and Brill, 1991), likely as a foraging strategy to search for prey from underneath via shadows. Based on our results, it is also probable that individuals from both species were able to make excursion dives (i.e. maximum

depth, here) below 200 and 300 m even when DO levels are below 3.5 ml l^{-1} . However, when DO at 200 m was a significant predictor within the model, fish depth showed the opposite (i.e. a negative) relationship. Vertical habitat compression due to shallow hypoxic zones has been suggested to increase foraging success for top predators such as billfish as prey are also aggregated in the surface layer (Prince and Goodyear, 2006; Pohlot *et al.*, 2018; Dale *et al.*, 2022). This theory could also apply to the slight differences in vertical preference between the two billfish species in this study. Blue marlin in the ETP may be more successful foraging in the near surface layer and have less need to access prey at deeper depths or employ other foraging strategies (*sensu* Logan *et al.*, in press). Sailfish, instead, may be forced to occupy deeper depths due to competition with other predators in the very near-surface layer (i.e. <10–20 m) or due to predator avoidance (e.g. sharks). A similar theory has also been suggested for billfish in the western North Atlantic where blue marlin and sailfish occupy different depths and may be a strategy to partition habitat and limit competition for prey, which could also help explain the unexpected relationship between depth and DO at 200 m (Bubley *et al.*, 2020).

In the ETP, we found that occupied temperatures varied slightly by time of day, where both sailfish and blue marlin spent the highest percentage of daytime hours in temperatures $26\text{--}28^\circ\text{C}$ and the highest percentage of nighttime hours in temperatures $28\text{--}30^\circ\text{C}$ (Figure 3c). SST has been consistently documented as a significant predictor of both horizontal and vertical billfish habitat preference (Hoolihan *et al.*, 2011; Carlisle *et al.*, 2017; Madigan *et al.*, 2021; Dale *et al.*, 2022), which is consistent with our results where SST was a significant predictor in each of the four blue marlin depth models as well as the SPUE model. Some studies have shown that billfish and other epipelagic fish species may be influenced by changes in the lunar cycle or lunar illumination (e.g. Lowry *et al.*, 2007; Pohlot *et al.*, 2018). Sailfish mean nighttime depth increased slightly with a fully illuminated moon (Figure 5g), likely as these are visual predators who require light for foraging (Brill *et al.*, 1999; Brill and Lutcavage, 2001; Goodyear *et al.*, 2008) and a fully illuminated moon may allow for increased foraging at night. However, herein, we confirm that vertical habitat use was minimally influenced by the lunar cycle, as compared to other environmental and physical variables, which is similar to findings of these two species in other parts of the world such as the South Atlantic Ocean (Madigan *et al.*, 2021).

For sailfish, we found TCC to be a significant predictor of SPUE, where higher levels of TCC were associated with lower catch rates, yet TCC was not a significant predictor for any of the depth models (Table 2). This indicates that while many of the same environmental and physical factors were significant in both depth and SPUE models, other variables, such as TCC may influence the catchability of these fishes. In this region, increased light availability was found to be associated with increases in sailfish activity and with sailfish bait encounters with recreational fisheries (Pohlot *et al.*, 2018). Similar results have been found for billfish catch per unit effort in relation to cloud cover in the central Pacific Ocean, where lower catches were associated with cloudier days (Ward and Meyers, 2005). Therefore, to accurately inform estimates of catchability and vulnerability to bycatch for these predators, we must consider environmental and physical factors that not only impact depth preference and therefore overlap of these fishes with fisheries, but also factors that influence fish activity level and foraging.

Billfish management considerations in the ETP

The results discussed here provide valuable insights into how to manage these two species based on their vertical behaviour and their interactions with fishing gear within local recreational fisheries. While both species are susceptible to bycatch in surface longline gear as a result of depth preferences above 100 m, blue marlin may be particularly vulnerable to this interaction within the ETP due to their little time spent at depth. Pelagic longline fisheries, which actively target tunas, dolphinfish, and swordfish in the ETP (IATTC, 2022), are the most significant source of istiophorid bycatch (Graves *et al.*, 2010; Punt *et al.*, 2015; Horodysky *et al.*, 2016; IATTC, 2022), often catching epipelagic species in surface waters during deployment and retrieval of gear (Boggs, 1992). Here, we also find that depth preference does not change drastically at day vs. night (Figure 3), indicating that catchability and risk of bycatch is likely similar throughout the diel cycle (Ward and Meyers, 2005), particularly for blue marlin.

Illegal fishing operations in the ETP often consist of longline and purse seine fishing in protected areas such as MPAs or coastal regions reserved for sport fishing, targeting illegal species, and/or fishing without a licence (Arias and Pressey, 2016). For example, Guatemala, Nicaragua, and Panama all prohibit the commercialization of sailfish (Staley, 2021). When considering how these results can be used to inform bycatch risk or vulnerability to illegal longline fishing, we must also account for nuances in vessel behaviour within these fisheries. Fisher behaviour is often heterogeneous, even among vessels using similar gear types within the same geographic region (Frawley *et al.*, 2021). A case study conducted on illegal longline fishing in Cocos Island, Costa Rica, found that illegal fishing was spatially concentrated along seamounts and temporally concentrated in July through September. The authors found patterns between illegal fishing incursions and the lunar cycle and suggest that reduced light during the new moon may benefit vessels fishing illegally by lowering the probability of detection (Arias *et al.*, 2016). Therefore, while lunar illumination was minimally influential on fish vertical behaviour and daytime SPUE, it may need to be considered in the context of illegal fishing.

For sailfish, SPUE in the recreational fishery was driven primarily by the MLD (Figure 6f and Supplementary Figure S10). MLD often covaries with distance from the coast (as discussed in the Results section). We can use this information to surmise that sailfish are likely more “catchable” closer to shore and therefore more vulnerable to bycatch in proximity to the coastline. In 2014, Costa Rica began prohibiting purse seine operations within 45 miles of the coastline. Management efforts like this one may be more effective for sailfish. As a result of conflict between longline operations and recreational fisheries, some countries have restricted commercial pelagic fishing from coastal regions, which would likely benefit sailfish but may be less effective for blue marlin in this region. However, further complicating this relationship is the impact of changing environmental conditions related to climate oscillations and climate change, which appear to increase catches of sailfish in offshore commercial purse-seine and long-line fisheries (Haulsee *et al.*, 2022). Future work should explore the horizontal patterns of billfish movement and bring both horizontal and vertical dimensions of behaviour together to adequately assess the spatial ecology of these species for manage-

ment solutions. Marine predators within the ETP ecosystem may be particularly vulnerable to rising temperatures during El Niño events and as a result of climate change, as these species are shown to have a limited range between oxygen demand and oxygen supply, which affects physiological performance (Clarke *et al.*, 2022). Therefore, existing hypoxic conditions along with overfishing and climate-change-related impacts may lead to synergistic effects on pelagic predators in the ETP (Clarke *et al.*, 2022). Proper management of these species is crucial to ecosystem structure and function (Pimiento *et al.*, 2020).

Conclusion

This study investigates vertical habitat use of Pacific blue marlin and Indo-Pacific sailfish populations in the ETP. Our findings indicate that both species exhibit diel vertical migration, and while vertical distributions do overlap, sailfish utilize deeper waters than blue marlin during both daytime and nighttime—the opposite of what has been recorded in other parts of these species' ranges. Assessing human–wildlife interactions and conflicts is complex due to various biotic and abiotic factors that drive both human and animal uses of the marine environment. Here, we show that dynamic environmental variables influence these species' vertical behaviour and subsequent interactions with fishing gear. The inclusion of SLA in depth and SPUE models, in particular, provides interesting context for how this dynamic feature may influence fish behaviour and lead to increases or decreases in their catchability by the recreational fishery. However, the relatively low spatial resolution and large spatial error rate of PSATs prevents researchers from exploring finer scale relationships between these fish and specific mesoscale oceanographic features like eddies. Future studies in this region would benefit from analysing catch rates from recreational and commercial vessels with finer-scale spatial data in correlation with mesoscale eddies to further explore the relationship between catchability and highly dynamic oceanographic features. Understanding the scales at which these interactions occur is crucial for successful management.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Author contributions

Each author has made significant contributions to the study. Specifically, the authors contributed in the following ways. HEB: conceptualization, field work, formal analysis, methodology, data curation, writing—original draft, and writing—review and editing; DEH: conceptualization, field work, project administration, data curation, writing—original draft, and writing—review and editing; RL: field work, funding acquisition, and writing—review and editing; MS: funding acquisition and writing—review and editing; ERH: funding acquisition, field work, and writing—review and editing; JHW: funding acquisition, field work, and writing—review and editing; JMD: funding acquisition and field work; ELH: conceptualization, validation, supervision, and writing—review and editing; and LBD: conceptualization, funding acquisition, data curation, and writing—review and editing.

Conflicts of interest

The authors have no conflicts of interest to declare.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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