



# Integrating vertical and horizontal movements of shortfin mako sharks *Isurus oxyrinchus* in the eastern North Pacific Ocean

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**ABSTRACT:** Resources in the pelagic environment tend to be patchily distributed, often resulting in animals engaging in adaptive behaviors to maximize foraging success. While these behaviors have been examined in horizontal and vertical dimensions separately, there has been limited work integrating these functionally related movements in sharks. We investigated how vertical behaviors change in relation to horizontal movements in the pelagic, highly migratory, shortfin mako shark *Isurus oxyrinchus*. Data from 30 sharks (114 to 245 cm total length), double-tagged with Pop-up Archival and Transmitting (PAT) and Smart Position or Temperature Transmitting (SPOT) tags within the Southern California Bight were analyzed. We examined shark daytime depth distributions after their horizontal movements were first classified by water column thermal structure (thermal habitat), and into 1 of 2 behavioral modes (area-restricted search or transient) using a switching state-space model. Despite high inter- and intra-individual variability, thermal habitat and behavioral mode influenced depth distribution. Within thermal habitats, sharks spent similar amounts of time near the surface in both behavioral modes, although transient animals spent more time in deeper waters within some thermal habitats. Comparing among thermal habitats, sharks performing transient movements in warmer waters spent more time at depth. Sharks experienced an expansion of vertical habitat use when they switched to transient behaviors, possibly to search for prey, and the degree of habitat expansion may be influenced by temperature. These results suggest that in a 3-dimensional habitat, such as the pelagic environment, prey searching behaviors in the horizontal and vertical dimensions are linked.

**KEY WORDS:** Dive behavior · Behavioral plasticity · Prey searching · Habitat use · Satellite telemetry

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## 1. INTRODUCTION

Prey acquisition is a key component in the time budget of predators, as energy stores are necessary to meet daily metabolic needs and contribute to growth and reproduction. Because of its importance to fit-

ness, energy acquisition should be under strong selection pressure to maximize intake while minimizing costs. As a result, evolution should favor optimizing search strategies to improve foraging success.

In pelagic environments, prey tend to be patchily distributed, can be ephemeral, and may not always be

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predictable in time and space (Steele 1978). Thus, it is in the best interests of a predator to maximize time in a prey patch where feeding can occur and minimize time traveling between patches. Predators should, therefore, display behavioral plasticity in their movements. Movements within prey patches should be slower and punctuated by many turns, thereby keeping the predator within the patch. Predators engaged in such movements are often referred to as engaging in area-restricted search behavior. In contrast, transient behavior, such as transiting between patches (i.e. searching for prey patches) should be highly directed to minimize time between patches and search costs. Tracking horizontal movements of various marine predators has shown that such behaviors are common (e.g. Newlands et al. 2004, Paiva et al. 2010, Block et al. 2011, Bailey et al. 2012, Dragon et al. 2012), with a variety of techniques corroborating that prey encounters and foraging are more frequent during area-restricted search behaviors (e.g. Bailey & Thompson 2006, Dragon et al. 2012).

The pelagic environment, however, is 3-dimensional and prey patches are not always located at the surface. Searching the water column vertically is energetically expensive, so diving behaviors are also under selection pressure and should vary, as do horizontal movements. Indeed, a wide variety of vertical behaviors have been described for marine species, including dives thought to be associated with traveling and foraging (e.g. Lesage et al. 1999, Hochscheid 2014, Queiroz et al. 2017). For example, white sharks *Carcharodon carcharias* traveling to the shared offshore habitat in the central Pacific display a bimodal depth distribution with substantial time at the surface, whereas once they reach their destination their behavior shifts to repetitive diving (Nasby-Lucas et al. 2009). Furthermore, changes in dive behavior (i.e. the shape and frequency of dives) are often concomitant with changes in horizontal behaviors and prey encounter rates (e.g. Dragon et al. 2012, Kuhn et al. 2015, O'Toole et al. 2017). For example, restricted horizontal movements in southern elephant seals *Mirounga leonina* are associated with foraging dives and improved body condition (Dragon et al. 2012).

Elucidating relationships between diving and horizontal movements have primarily focused on air-breathing marine species. Regular surface intervals to breathe allow for fine-scale estimates of horizontal movements using satellite telemetry, and dives in such species are easy to identify and quantify because they have a fixed starting and ending location (i.e. the surface). Many of these species also return to predictable haul out or breeding grounds, so data

loggers can be retrieved to collect the archive of fine-scale vertical data and match it with corresponding horizontal movements. For fish, it is much harder to collect fine-scale horizontal and vertical movement data in the pelagic environment because fish are not dependent on the surface and recapturing individuals to recover data loggers is infrequent. Despite these limitations, behavioral plasticity in horizontal (e.g. Bestley et al. 2010, Block et al. 2011) and vertical movements (e.g. Walli et al. 2009, Queiroz et al. 2012, Vaudo et al. 2016) has been observed in a variety of fish moving over large distances; however, the relationships between transient and area-restricted search behavioral modes and vertical movement patterns have received limited investigation, although new technology is allowing such work to become increasingly common (e.g. Andrzejaczek et al. 2019, Logan et al. 2023).

Further complicating matters for assessing such relationships are oceanographic conditions that limit or otherwise influence the vertical habitat use of pelagic fishes regardless of horizontal movements. Water temperatures tend to decrease with increasing depth, creating limits on how deep fishes can dive while remaining within their thermal limits and heterogeneity in their daily vertical habitat use as they move through water columns with different thermal characteristics (Musyl et al. 2011, Vaudo et al. 2016, 2018, Braun et al. 2019). Similarly, oxygen concentration decreases with depth, likely creating a barrier to depth distributions (Carey & Robison 1981, Prince & Goodyear 2006, Nasby-Lucas et al. 2009). Little is known about how these physical factors influence vertical search behaviors; however, these barriers have the potential to aggregate prey, increasing search efficiency of predators (Prince & Goodyear 2006, Pelletier et al. 2012, Logan et al. 2023).

The shortfin mako shark *Isurus oxyrinchus* (hereafter mako shark) is a good candidate for investigating the relationship between horizontal and vertical movements in a large, highly mobile marine predator. Mako sharks are widely distributed, epipelagic predators, found from temperate to tropical waters worldwide (Cliff et al. 1990, Maia et al. 2006, Wood et al. 2009, Preti et al. 2012). Their large size and sturdy dorsal fin make them amenable to carrying multiple types of satellite transmitters that provide highly accurate location data and that record and transmit their vertical distribution. Importantly, mako sharks spend a great deal of time near the surface (Abascal et al. 2011, Vaudo et al. 2016, Andrzejaczek et al. 2022), allowing fin-mounted transmitters frequent opportunities to transmit to satellites, thereby providing fre-

quent and accurate estimates of their locations. As a result, relatively fine-scale tracks of mako shark movements can be attained across ocean basins (Block et al. 2011, Rogers et al. 2015, Vaudo et al. 2017, Francis et al. 2019, Nasby-Lucas et al. 2019, Gibson et al. 2021). Additionally, electronic tagging has revealed that mako sharks show a great deal of inter- and intra-individual variability in their horizontal and vertical behaviors (Vaudo et al. 2017, Nasby-Lucas et al. 2019, Gibson et al. 2021, Santos et al. 2021), suggesting they may be altering horizontal and vertical behaviors in response to environmental conditions.

Understanding the links between foraging and horizontal and vertical movements is important for many reasons. Foraging is a key driver of movements and behaviors; thus, understanding the foraging ecology of a predator provides insights into shifts in distribution and 3-dimensional habitat use in response to ocean conditions and prey availability. An improved understanding of both horizontal and vertical distributions of predators contribute to better understanding of regionally variable catchability of species captured in fisheries and applications towards dynamic ocean management (Maxwell et al. 2015). Mako sharks are taken either as secondary targets or as bycatch in all oceans, and in the Atlantic they are considered overfished (Byrne et al. 2017, ICCAT 2019); thus, information on their ecology and habitat use is of fundamental importance for understanding interactions with fisheries and effective management of populations.

Using 2 types of satellite transmitters (1 for depth and 1 for location), we examined the horizontal movements and corresponding vertical distributions of mako sharks in the eastern North Pacific Ocean. Our goals were to examine relationships between vertical distributions and horizontal behaviors presumed to be associated with foraging. We hypothesized that the depth distribution of mako sharks should become more constrained (shallower) when sharks are engaged in area-restricted search behavior because sharks will confine their use of the water column when prey are plentiful.

## 2. MATERIALS AND METHODS

### 2.1. Shark tagging

Mako sharks used for this study were captured and tagged in the Southern California Bight during fishery-independent longline surveys conducted in 2003 to 2008 (see Runcie et al. 2016). Sharks were

brought along the side of the boat and into a cradle, which was raised to the deck to facilitate processing. While each shark was in the cradle, a wet cloth was placed over its eyes and a saltwater hose was inserted into the mouth to run water over the gills. Sharks were sexed and length was measured to the nearest cm. A total of 35 sharks were double tagged with both a Smart Positioning or Temperature Transmitting (SPOT) tag that was fixed to the dorsal fin and a Pop-up Archival Transmitting (PAT) tag (both Wildlife Computers) that was attached to the shark via a tether anchored in the dorsal musculature. These sharks are a subset of data analyzed in Nasby-Lucas et al. (2019) (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m732p085\\_supp.pdf](http://www.int-res.com/articles/suppl/m732p085_supp.pdf)).

The 2 types of satellite tags differ in the information they provide. SPOT tags communicate with the Argos satellite system when the dorsal fin is out of the water and the tag is exposed to air, providing a location estimate of the shark. Each estimated location is associated with a location class based on the number of transmissions received and the number of Argos satellites receiving transmissions. Location classes with estimated errors (1 SD) are as follows: 3 (<250 m), 2 (250–500 m), 1 (500–1500 m), 0 (>1500 m), A, and B; there are no spatial estimates of accuracy for location classes A and B (CLS 2016). PAT tags record and archive data on light levels, temperature ( $\pm 0.05^\circ\text{C}$ ), and pressure that can be used to estimate depth ( $\pm 0.5$  m) at regular sampling intervals. Light data can also be used to estimate tag locations; however, these estimates are far less accurate than those from SPOT tags. After a predetermined amount of time, PAT tags detach from the tether, float to the surface, and transmit summaries of the archived data via satellite.

### 2.2. Horizontal movements

To estimate daily locations and behavioral states of sharks from Argos locations we used a behavioral switching state-space model (Jonsen et al. 2005). The state-space framework allows for modeling movements while accounting for error in the location estimates and irregular collection intervals. The model estimates locations at discrete time steps, and partitions movement into 2 behavioral modes: 'transient' and 'area-restricted search.' Transient movements are relatively linear with a mean turning angle near  $0^\circ$  and a high correlation in speed and direction. Area-restricted search behavior is characterized by low correlation in speed and direction and more frequent turns (i.e. a high variance in mean turn angle).

We modeled males and females separately because of computational constraints. Within each sex, all individual tracks were modeled simultaneously, which improves resolution of behavioral state estimations, as well as the ability to efficiently include tracks of relatively short duration (Jonsen 2016). Using the 'bsam' package (Jonsen et al. 2015) in R (R Core Team 2017), we ran 2 Markov-chain Monte Carlo (MCMC) chains in tandem and after a 60 000 sample burn-in, 10 000 additional samples were thinned by retaining every 10th sample and used to estimate model parameters, locations, and behavioral modes. Each estimated location was assigned a value representing the proportion of MCMC samples classified as area-restricted search. We classified proportions  $\leq 0.3$  as transient behavior and proportions  $\geq 0.7$  as area-restricted search behavior; locations with values between 0.3 and 0.7 were designated as 'uncertain' and not used in further analyses.

As outliers and long time-gaps between observed locations can bias state-space model results (Bailey et al. 2008), we applied a speed-distance-angle filter to the Argos data (location classes: 3, 2, 1, A, and B) before model fitting (Freitas et al. 2008). Using the filter, we removed locations  $> 5$  km from the previous location if they required travel speeds  $> 4.47$  m s<sup>-1</sup>, as well as locations requiring turn angles of  $\geq 165^\circ$  and  $\geq 155^\circ$  if distances traveled exceeded 5 and 8 km, respectively. In addition, to avoid lengthy gaps in the tracks, we split tracks into segments when gaps in Argos data exceeded 10 d. These individual track segments were included in the state-space model as independent tracks. Only tracks that exceeded 20 d were included in the state-space model analysis. Error estimates associated with Argos locations (Vincent et al. 2002) were used to inform the movement model.

### 2.3. Vertical distribution

PAT tags were programmed to detach from mako sharks after periods up to 240 d. Bandwidth constraints limit transfer of data via satellite to packets of summarized data. These data packets included frequency distributions of the proportion of time spent within user-defined depth bins, and temperature-depth profiles. Temperature-depth profiles included up to 8 depths distributed between the minimum and maximum depths recorded during the summary interval. Summaries of the frequency distributions and the temperature-depth profiles were programmed to cover time periods of 1, 2, 4, 6, or 12 h. Because settings differed between tags, depth bins were merged

to create bins compatible for all tags ( $< 5$ , 5–10, 10–50, 50–100, 100–150, 150–200, 200–300, and  $> 300$  m). Gaps in satellite coverage and tag battery life generally limited the number of successfully received data packets, resulting in an incomplete data set from each tag.

### 2.4. Data analysis

Because sharks were tagged across years and their movements covered large areas, environmental conditions varied both among and within shark tracks. Differences across water columns were accounted for by grouping, via cluster analysis, similar water columns into categories (thermal habitats) that could be used as a factor in analyses (Vaudo et al. 2016). Prior to cluster analysis, for each shark, we pooled temperature-depth profile data from each day, averaging temperature values for each available depth, so that there was only 1 temperature-depth profile per day. Because sampling depths differed across temperature-depth profiles, daily temperature-depth profiles were standardized by linearly interpolating temperatures at 4 m intervals between the minimum and maximum depth of each daily temperature-depth profile. We performed divisive hierarchical cluster analysis on the matrix of Euclidean distances between all temperature-depth profiles using the 'cluster' package in R (Maechler et al. 2015). An elbow plot was used to determine the number of thermal habitats (i.e. clusters) retained for analyses.

We matched daily thermal habitat with its corresponding daily horizontal movement behavioral estimate and used linear mixed-effects models to examine how behavioral mode and thermal habitat influenced mako shark vertical distributions. Because mako sharks tend to cover a greater range of depths during the daytime (Vaudo et al. 2016, Nasby-Lucas et al. 2019, Santos et al. 2021, Andrzejczek et al. 2022) and appear to be visual predators (Yopak et al. 2007, Yopak 2012), and to ensure that a mixture of daytime and nighttime behaviors did not confound results, only data summaries that covered periods between sunrise and sunset (i.e. daytime) were used in analyses. Data summaries were pooled per day and these daily daytime summaries were assumed to be reflective of the entire daytime period. The specific aspects of vertical distributions investigated were proportion of time spent at depths of  $< 5$ ,  $< 10$ ,  $> 50$ , and  $> 100$  m, and the maximum recorded daily depth. Maximum recorded daily depths were obtained from temperature-depth profiles.

For models of proportions of time spent at depth, generalized linear mixed-effects models using a beta distribution with logit link and an AR(1) process to account for autocorrelation were fit in R using the 'mgcv' package (Wood 2017). Daily proportion of time in each depth strata was modeled as a function of the explanatory variables: sex, behavioral mode, thermal habitat (a categorical variable based on the cluster analysis described in this section), the behavioral mode–thermal habitat interaction, projected total length, and random effects allowing for random intercepts and slopes per individual for behavioral mode, thermal habitat, and the interaction between behavioral mode and thermal habitat. Projected total lengths were estimated at daily intervals for each shark from total length at capture and von Bertalanffy parameters calculated by Wells et al. (2013) for mako sharks off southern California. Maximum daytime depth was modeled with the same fixed and random effects and AR(1) process using a generalized linear mixed-effects model with a negative binomial distribution and log link in 'mgcv.'

### 3. RESULTS

All 35 sharks reported horizontal movement data via SPOT tags; however, because of limited retrieval of PAT tag data transmissions, only 30 sharks (114 to 245 cm total length, TL) provided usable vertical distribution data to pair with SPOT tag locations and analyses were limited to these individuals. Track durations of the paired data sets ranged from 31 to 240 d (mean 141 d). From SPOT tag data, 3762 daily locations, largely confined to the California Current Ecosystem, were estimated (Fig. 1). Behavioral classification of these locations resulted in 1685 area-restricted search (44.8%), 1515 transient (40.3%), and 562 (14.9%) uncertain locations, with area-restricted search locations occurring most frequently in the Southern California Bight and in Bahía Sebastián Vizcaíno, Baja California (Fig. 1). Periods of area-restricted search behavior lasted up to 143 d (median 11 d), with 41% of residency bouts lasting at least 2 wk. Transient behavior also often lasted extended periods, up to 82 d (median 9 d), with 37% of transient bouts lasting at least 2 wk. From the PAT tags, 8 to 100% (mean 55%) and 8 to 99% (mean 52%) of temperature-depth profile and time at depth data summaries were received, respectively. After filtering for time of day, tags provided 84 to 1188 h (mean 303 h) of daytime data.

From a cluster analysis of the 1803 available daily temperature-depth profiles, we identified 4 thermal

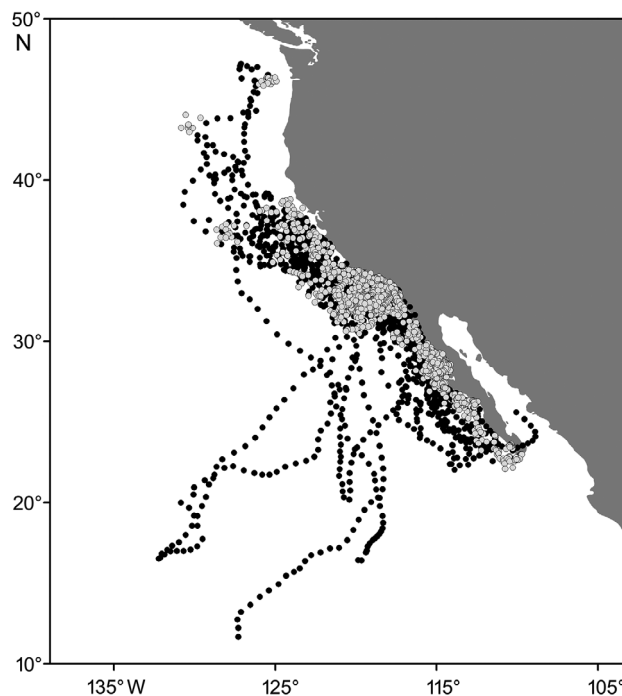


Fig. 1. Modeled daily locations and behavioral modes of 30 mako sharks tagged in the Southern California Bight. Daily locations classified as transiting (●) and area-restricted search (○)

habitats (Fig. 2, Fig. S1), although there was overlap between some clusters (see Fig. S1). Hereafter, the 4 thermal habitats are referred to alphabetically, corresponding to their mean temperature–depth profile across the upper 200 m of the water column from coldest (Habitat A) to warmest (Habitat D). Habitat A had a mean surface temperature of 15.9°C, with a thermocline occurring between 18 and 88 m; within the thermocline, temperatures dropped from 15.1 to 10.5°C. The mean temperature–depth profile for Habitat B had a surface temperature of 19.6°C and a thermocline from 10 to 48 m, where temperatures ranged from 18.8 to 13.2°C. The mean surface temperature of Habitat C was 20.6°C, with temperatures dropping from 19.8 to 13.4°C in a thermocline that extended from 16 to 92 m. Habitat D, the warmest of the water columns, had a mean surface temperature of 22.4°C and a thermocline between 26 and 128 m where temperatures decreased from 21.6 to 15.0°C.

While there was overlap among the thermal habitats, especially Habitats A to C, there was some geographic and temporal separation (Fig. 3). Habitat A was predominantly observed during the autumn (65% of Habitat A observations and 42% of autumn observations) from north of the Channel Islands in the Southern California Bight. Habitat B was observed

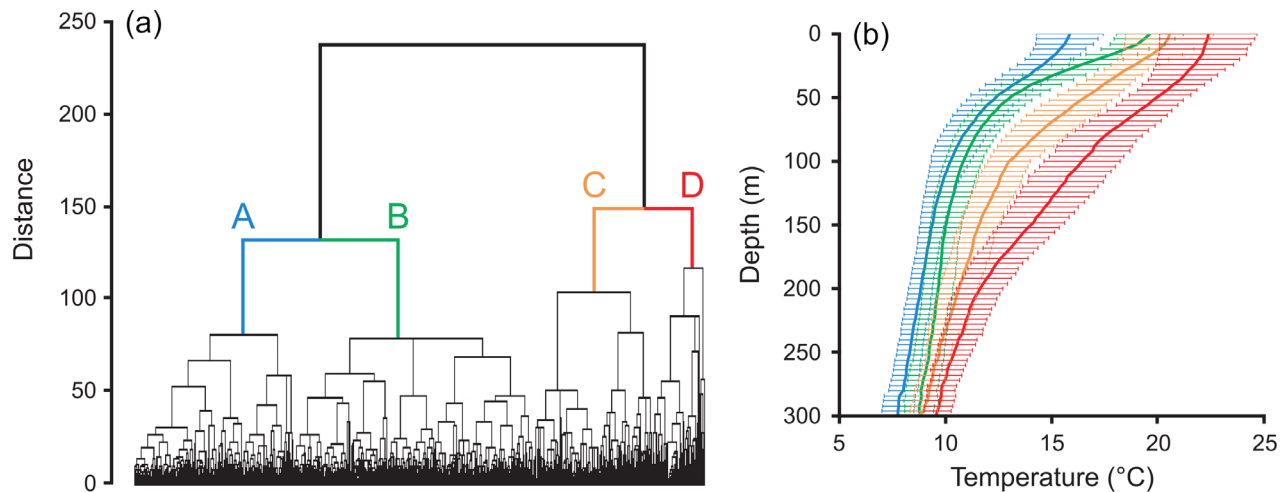


Fig. 2. Clustering of temperature-depth profiles showing (a) the 4 thermal habitats used for analysis and (b) the mean temperature-depth profiles ( $\pm$ SD) of those thermal habitats

mostly in the Southern California Bight south to Bahía Sebastián Vizcaíno, Mexico, and predominantly in the summer (59% of Habitat B observations and 61% of summer observations). Habitat C was largely confined to the waters off the Baja California Peninsula, Mexico, especially Bahía Sebastián Vizcaíno; Habitat C observations were spread roughly equally from summer to winter (~33%), although they were the most observed habitat during the winter (41% of winter observations). Habitat D was observed predominantly in the winter (50% of Habitat D observations and 29% of all winter observations) and off the southern Baja California Peninsula and pelagic waters extending to the southwest. Of the 1803 temperature-depth profiles, 1797 could be coupled with a daily location estimate. Of these locations, Habitat B was the most common (42.1% of profiles), followed by Habitats A (27.9%), C (21.0%), and D (9.0%).

Overall, from the 30 mako sharks, there were 1510 days with an estimated location, temperature-depth profile, and daytime vertical distribution data, and these days were subsequently used in analyses. Within this data set, the proportion of locations within each habitat attributed to area-restricted search and transient behaviors were approximately equal for Habitats A, C, and D. Both behavioral modes were more frequently observed and performed by more sharks in Habitat B than either behavioral mode in any other habitat, with area-restricted search behavior in Habitat B being the most frequent of all (25.8% of the data set; Table 1).

Despite high intra- and inter-individual variability (Table S2), shark size, behavioral mode, and habitat

influenced mako shark vertical distribution. Generalized linear mixed models explained 11 to 47% of model deviance, although the deviance was largely explained by random factors with fixed factors accounting for only 4 to 20% of the deviance explained (Table S3). With regard to size, larger sharks spent less time in the upper 5 and 10 m of the water column with the proportion of time near the surface dropping ~50 to 70% across the range of sizes observed (114 to 245 cm TL; Figs. 4 & 5). Despite larger sharks spending less time near the surface, there was no evidence of them spending more time at > 50 or > 100 m (Figs. 6 & 7). However, maximum daytime dive depth did increase by ~60 to 125 m with animal size (depending on habitat and behavioral mode), over the range of sizes examined (Fig. 8).

Within habitats, behavioral mode influenced time at depth and depth range. Although there were no differences in the proportion of time spent at < 5, > 50, and > 100 m in the transient mode than in the area-restricted search mode for Habitats D, B, and C, respectively (Figs. 4, 6 & 7, Table 2). Maximum daytime depths also differed between behavioral modes for most habitats; maximum daytime depths increased by ~30 to 50 m in Habitats B, C, and D with a shift from area-restricted search to transient behavioral mode (Fig. 8, Table 2).

Within behavioral modes, vertical habitat use varied between thermal habitats, especially when sharks engaged in area-restricted search behavior. Sharks in the warmest habitat (Habitat D) spent approximately half as much time at < 5 m than sharks in the

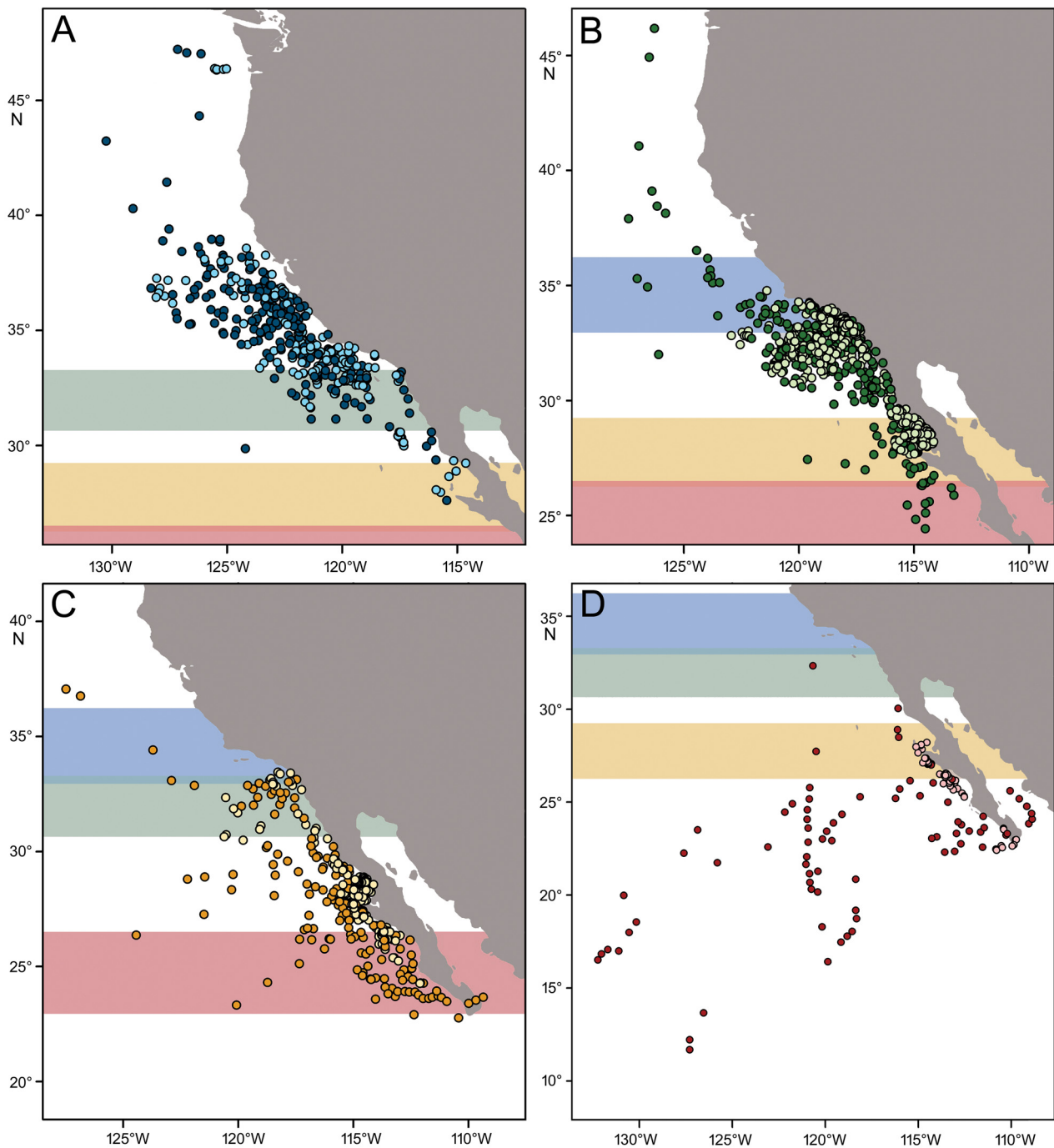


Fig. 3. Modeled daily locations of 30 mako sharks tagged in the Southern California Bight broken down by thermal habitats (A to D) denoted in Fig. 2. The shade of the points (light or dark) indicates whether the sharks were engaged in area-restricted movements or transiting behaviors, respectively. Shaded regions represent the latitudinal interquartile ranges of each of the 4 thermal habitats (A: blue; B: green; C: orange; D: red). Note: spatial scale differs between panels

other habitats (Fig. 4). The proportion of time spent at  $< 10$  m followed a similar overall pattern to that for time spent at  $< 5$  m, except that the only observed difference was between Habitats B and D (Fig. 5, Table 2). For deeper depths, sharks in Habitat B

tended to spend less time deeper than 50 m than sharks in the other habitats (Fig. 6, Table 2); time spent below 100 m was similar across habitats, although less time was spent at depth in Habitat C than A. While in the area-restricted search mode,

Table 1. Number of days (with percentage of locations in parentheses) spent within and number of sharks experiencing each habitat for area-restricted search and transient behavioral modes

	Area-restricted search		Transient	
	Days	Sharks	Days	Sharks
Habitat A	194 (12.8%)	21	209 (13.8%)	22
Habitat B	390 (25.8%)	25	256 (17.0%)	27
Habitat C	159 (10.5%)	15	158 (10.5%)	22
Habitat D	64 (4.2%)	7	80 (5.3%)	13

sharks had similar maximum daytime depths for all but the coldest water columns (Habitat A), which were approximately 25 to 40 m deeper than Habitats B and C, respectively (Fig. 8, Table 2). For sharks in the transient mode, habitat differences in vertical habitat use were only found for time spent at <5 and >50 m; sharks spent more time at <5 m in Habitat A than C (Fig. 4, Table 2) and more time at >50 m in Habitat D than A and B (Fig. 6, Table 2). Maximum daytime depths also differed between habitats when sharks were in the transient mode; maximum depths in Habitat A were shallower than those in Habitats B and D (Fig. 8, Table 2).

#### 4. DISCUSSION

Access to a large data set of double-tagged sharks provided the opportunity to model vertical habitat use when location estimates were accurate enough to model behavioral modes. Sharks, however, displayed high levels of inter- and intra-individual variability, suggesting that the relationship between horizontal and vertical behaviors in mako sharks is likely complex and will require better information on environmental factors and prey distribution, and finer-scale depth information to investigate dive patterns rather than overall depth distributions. Despite this high individual variability and the limitations of the depth data obtained from the PAT tags, our results suggest that mako shark depth distribution is related to size, water column characteristics, and behavioral state.

There was some evidence of differing patterns of mako shark vertical habitat use across thermal habitats when comparing transient and area-restricted search behaviors. Area-restricted search behaviors were generally associated with shallower daytime depth distributions. Maximum daytime depths were shallower, and, in some instances, less time was spent at depth during area-restricted search com-

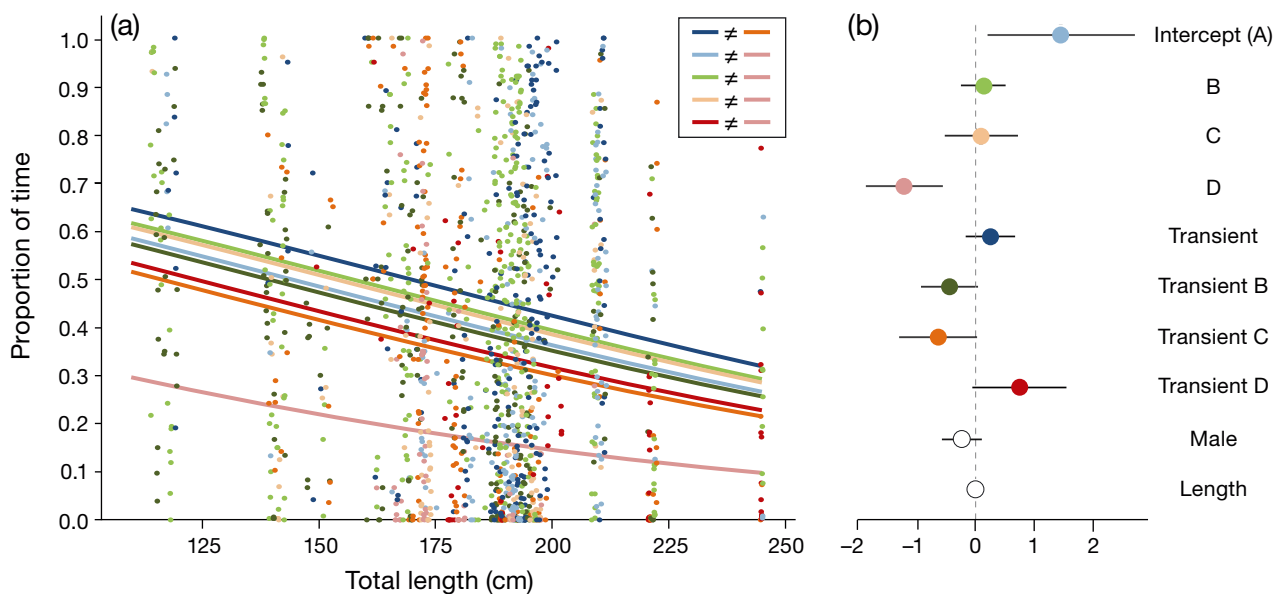


Fig. 4. (a) Model predictions of fixed effects for the proportion of time mako sharks tagged in the Southern California Bight spent at <5 m depth. Line colors (blue, green, orange, and red) indicate the thermal habitats denoted in Fig. 2. The shade of the line (light or dark) indicates whether the sharks were engaged in area-restricted movements or transiting behaviors, respectively. The inset indicates which lines differ. (b) Parameter estimates ( $\pm 95\%$  CI) on the logit scale of the fixed factors in the model. The model took the form  $y = \text{Sex} + \text{Habitat} + \text{Behavioral mode} + \text{Habitat} \times \text{Behavioral Mode} + \text{Length} + (\text{Habitat} | \text{Shark}) + (\text{Behavioral Mode} | \text{Shark}) + (\text{Habitat} \times \text{Behavioral Mode} | \text{Shark})$ . Random effects are in parentheses where A | B denotes effect A is conditional on effect B. Habitat A and area-restricted search mode are the baselines for Habitat and Behavioral Mode, respectively. Note: the length parameter is significant



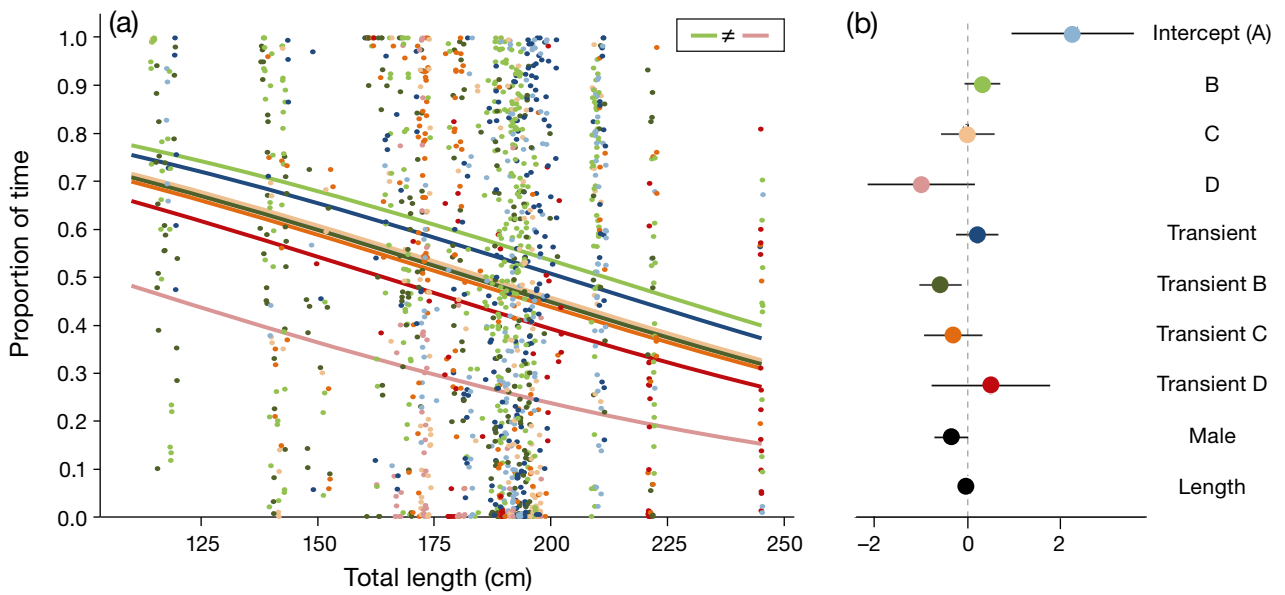


Fig. 5. (a) Model predictions of fixed effects for the proportion of time mako sharks tagged in the Southern California Bight spent at <10 m depth. Line colors (blue, green, orange, and red) indicate the thermal habitats denoted in Fig. 2. The shade of the line (light or dark) indicates whether the sharks were engaged in area-restricted movements or transiting behaviors, respectively. The inset indicates which lines differ. (b) Parameter estimates ( $\pm 95\%$  CI) on the logit scale of the fixed factors in the model. The model took the form  $y = \text{Sex} + \text{Habitat} + \text{Behavioral mode} + \text{Habitat} \times \text{Behavioral Mode} + \text{Length} + (\text{Habitat} | \text{Shark}) + (\text{Behavioral Mode} | \text{Shark}) + (\text{Habitat} \times \text{Behavioral Mode} | \text{Shark})$ . Random effects are in parentheses where  $A | B$  denotes effect A is conditional on effect B. Habitat A and area-restricted search mode are the baselines for Habitat and Behavioral Mode, respectively. Note: the length parameter is significant

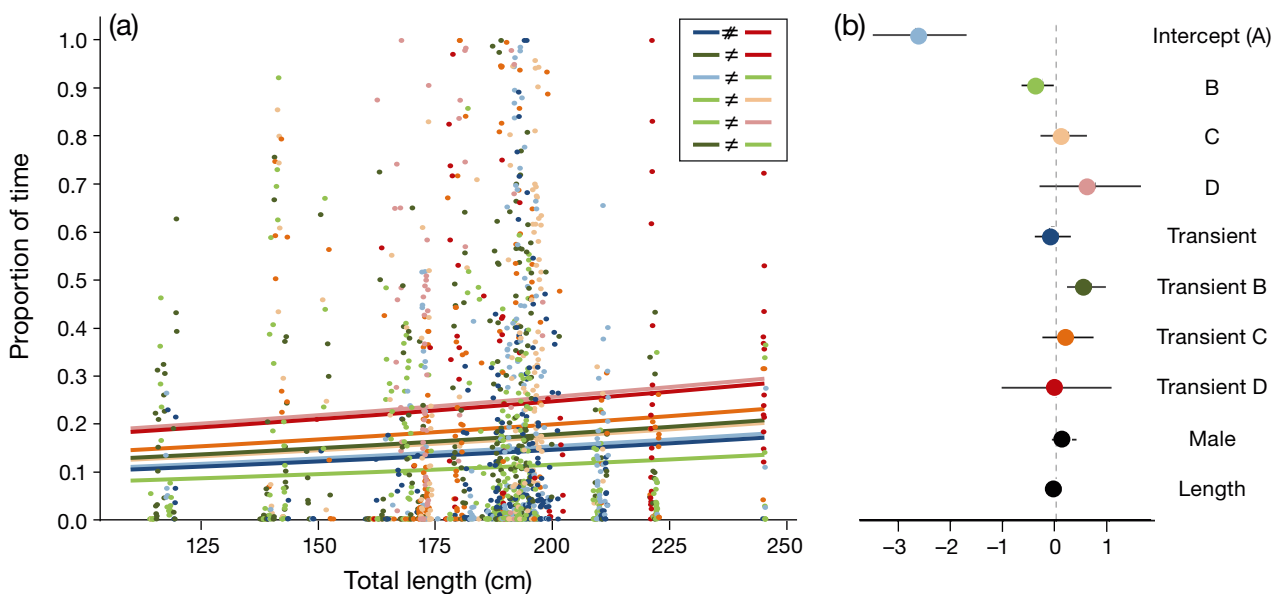


Fig. 6. (a) Model predictions of fixed effects for the proportion of time mako sharks tagged in the Southern California Bight spent at >50 m depth. Line colors (blue, green, orange, and red) indicate the thermal habitats denoted in Fig. 2. The shade of the line (light or dark) indicates whether the sharks were engaged in area-restricted movements or transiting behaviors, respectively. The inset indicates which lines differ. (b) Parameter estimates ( $\pm 95\%$  CI) on the logit scale of the fixed factors in the model. The model took the form  $y = \text{Sex} + \text{Habitat} + \text{Behavioral mode} + \text{Habitat} \times \text{Behavioral Mode} + \text{Length} + (\text{Habitat} | \text{Shark}) + (\text{Behavioral Mode} | \text{Shark}) + (\text{Habitat} \times \text{Behavioral Mode} | \text{Shark})$ . Random effects are in parentheses where  $A | B$  denotes effect A is conditional on effect B. Habitat A and area-restricted search mode are the baselines for Habitat and Behavioral Mode, respectively.

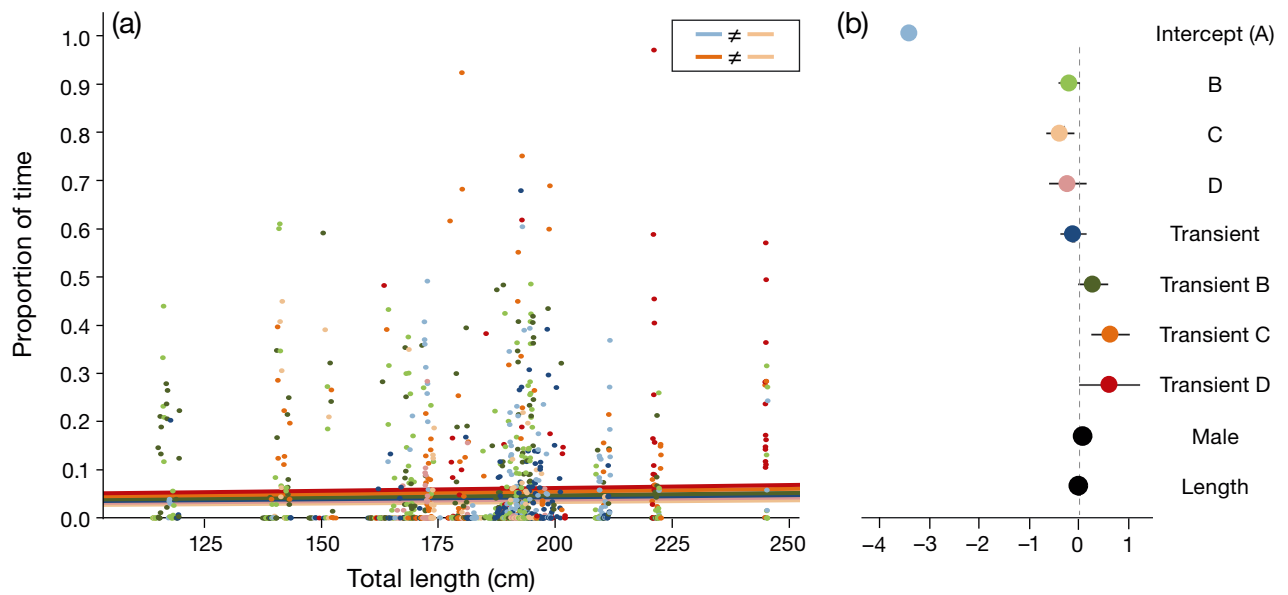


Fig. 7. (a) Model predictions of fixed effects for the proportion of time mako sharks tagged in the Southern California Bight spent at > 100 m depth. Line colors (blue, green, orange, and red) indicate the thermal habitats denoted in Fig. 2. The shade of the line (light or dark) indicates whether the sharks were engaged in area-restricted movements or transiting behaviors, respectively. The inset indicates which lines differ. (b) Parameter estimates ( $\pm 95\%$  CI) on the logit scale of the fixed factors in the model. The model took the form  $y = \text{Sex} + \text{Habitat} + \text{Behavioral mode} + \text{Habitat} \times \text{Behavioral Mode} + \text{Length} + (\text{Habitat} | \text{Shark}) + (\text{Behavioral Mode} | \text{Shark}) + (\text{Habitat} \times \text{Behavioral Mode} | \text{Shark})$ . Random effects are in parentheses where A | B denotes effect A is conditional on effect B. Habitat A and area-restricted search mode are the baselines for Habitat and Behavioral Mode, respectively

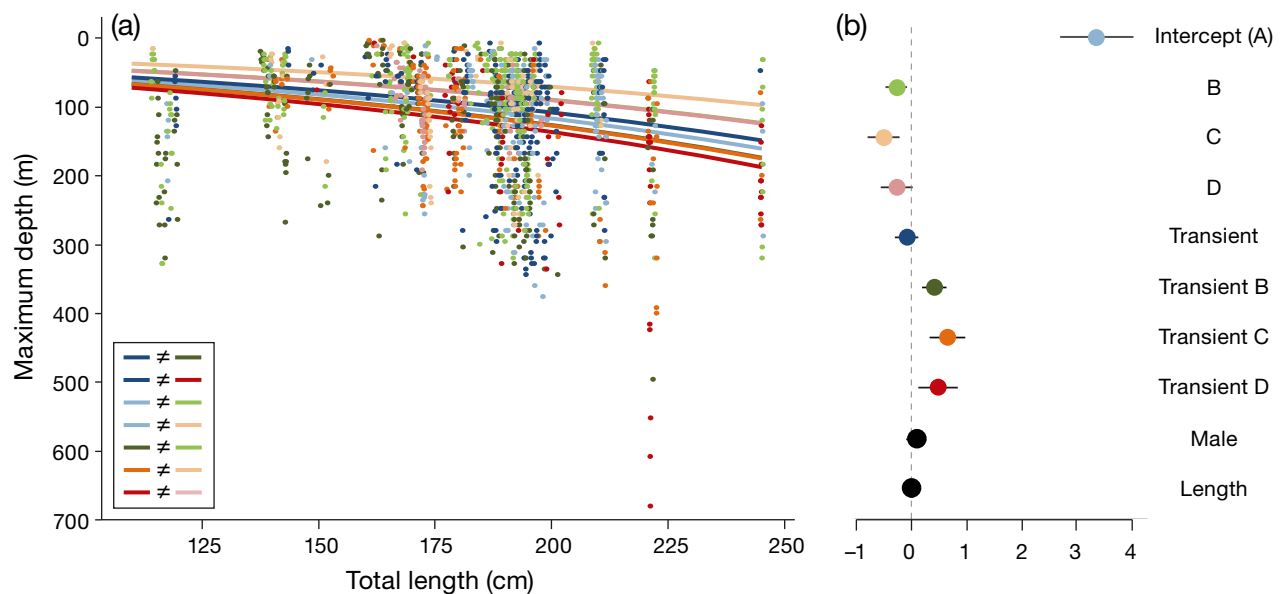


Fig. 8. (a) Model predictions of fixed effects for daytime maximum depth of mako sharks tagged in the Southern California Bight. Line colors (blue, green, orange, and red) indicate the thermal habitats denoted in Fig. 2. The shade of the line (light or dark) indicates whether the sharks were engaged in area-restricted movements or transiting behaviors, respectively. The inset indicates which lines differ. (b) Parameter estimates ( $\pm 95\%$  CI) on the log scale of the fixed factors in the model. The model took the form  $y = \text{Sex} + \text{Habitat} + \text{Behavioral mode} + \text{Habitat} \times \text{Behavioral Mode} + \text{Length} + (\text{Habitat} | \text{Shark}) + (\text{Behavioral Mode} | \text{Shark}) + (\text{Habitat} \times \text{Behavioral Mode} | \text{Shark})$ . Random effects are in parentheses where A | B denotes effect A is conditional on effect B. Habitat A and area-restricted search mode are the baselines for Habitat and Behavioral Mode, respectively. Note: the length parameter is significant

Table 2. p-values for pairwise comparisons between behavioral modes and within habitats for each behavioral mode for proportion of time spent at < 5, < 10, > 50, > 100 m, and maximum depth. Significant values ( $p < 0.05$ ) are in **bold**

Depth (m)	Area-restricted search vs. transient		Area-restricted search vs. area-restricted search				Transient vs. transient		
	Habitat A	Habitat B	Habitat A	Habitat B	Habitat C	Habitat A	Habitat B	Habitat C	
< 5	Habitat A	0.229	Habitat A	Habitat B	Habitat C	Habitat A	Habitat B	Habitat C	
	Habitat B	0.398	Habitat B	0.502		Habitat B	0.129		
	Habitat C	0.221	Habitat C	0.765	0.902	Habitat C	<b>0.015</b>	0.271	
	Habitat D	<b>0.008</b>	Habitat D	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	Habitat D	0.135	0.605
< 10	Habitat A	0.353	Habitat A	Habitat B	Habitat C	Habitat A	Habitat B	Habitat C	
	Habitat B	0.086	Habitat B	0.093		Habitat B	0.128		
	Habitat C	0.786	Habitat C	0.955	0.225	Habitat C	0.151	0.796	
	Habitat D	0.243	Habitat D	0.092	<b>0.021</b>	0.096	Habitat D	0.148	0.456
> 50	Habitat A	0.742	Habitat A	Habitat B	Habitat C	Habitat A	Habitat B	Habitat C	
	Habitat B	<b>&lt;0.001</b>	Habitat B	<b>0.029</b>		Habitat B	0.091		
	Habitat C	0.386	Habitat C	0.541	<b>0.012</b>	Habitat C	0.056	0.437	
	Habitat D	0.923	Habitat D	0.183	<b>0.038</b>	0.315	Habitat D	<b>0.003</b>	<b>0.041</b>
> 100	Habitat A	0.401	Habitat A	Habitat B	Habitat C	Habitat A	Habitat B	Habitat C	
	Habitat B	0.102	Habitat B	0.083		Habitat B	0.415		
	Habitat C	<b>&lt;0.001</b>	Habitat C	<b>0.008</b>	0.115	Habitat C	0.078	0.207	
	Habitat D	0.075	Habitat D	0.235	0.849	0.427	Habitat D	0.118	0.223
Max.	Habitat A	0.482	Habitat A	Habitat B	Habitat C	Habitat A	Habitat B	Habitat C	
	Habitat B	<b>0.001</b>	Habitat B	<b>0.008</b>		Habitat B	<b>0.038</b>		
	Habitat C	<b>&lt;0.001</b>	Habitat C	<b>&lt;0.001</b>	0.010	Habitat C	0.093	0.944	
	Habitat D	<b>0.014</b>	Habitat D	0.080	0.965	0.158	Habitat D	<b>0.040</b>	0.480

pared to transient behavior. This reduction in vertical space use associated with area-restricted search behavior is consistent with predictions for optimizing search behavior in a 3-dimensional habitat with a patchy resource distribution; similar to searching in 2 dimensions, predators should maximize time within the 3-dimensional prey patch by restricting themselves to the vertical distribution of the patch. Such vertical behaviors (i.e. repeated short displacements suggestive of foraging in a prey patch punctuated by longer re-orientation displacements) have been observed in bigeye tuna *Thunnus obesus*, Atlantic cod *Gadus morhua*, leatherback turtles *Dermochelys coriacea*, Magellanic penguins *Spheniscus magellanicus*, and basking sharks *Cetorhinus maximus* (Sims et al. 2008). When examined in conjunction with horizontal movements, although not at a fine-scale, variations in vertical search behaviors across geographic regions matched predictions based on the suspected prey distributions of those regions for pelagic species including sharks, tunas, and billfish (Humphries et al. 2010, Sims et al. 2012). For example, in basking sharks and blue sharks *Prionace glauca*, dive depth and variation in targeted depth decreased with higher levels of primary productivity, suggesting that the sharks were limiting their search behaviors when prey were more likely to be encountered (Queiroz et al. 2017).

The expanded vertical habitat use by sharks during transient periods is consistent with fine-scale patterns reported in other studies. Mako sharks often make repeated yo-yo dives as they travel (Sepulveda et al. 2004, Vaudo et al. 2016, Nasby-Lucas et al. 2019), a behavior also observed in a variety of predatory marine fishes (Klimley et al. 2002, Schaefer & Fuller 2007, Hoolihan et al. 2011). This yo-yo diving, in addition to possibly being energetically efficient (Iosilevskii et al. 2012), may be related to several behaviors, such as obtaining navigational cues (Klimley et al. 2002) or searching for prey throughout the water column (Nakamura et al. 2011). Successful mako shark feeding events have in fact been recorded during yo-yo dives (Sepulveda et al. 2004). Our data suggest that, during transient behavior, mako sharks likely perform deep yo-yo dives while searching the water column for prey patches, and switch to area-restricted search behavior when encountering prey patches. Once in area-restricted search behavior, sharks remain at or yo-yo dive to the depth where prey are found, with vertical movements becoming compressed because deeper depths are no longer searched. Similarly, juvenile loggerhead sea turtles *Caretta caretta* have been observed to be more likely to engage in deep diving behavior while transiting than when they were in areas thought to have high prey availability (Freitas et al. 2018).

As mako sharks consume a wide variety of prey occurring over a wide range of depths within the California Current large marine ecosystem (Preti et al. 2012), such adaptive behavior contributes to the variability observed in maximum depths and time spent at depth accompanying area-restricted search behavior within and between thermal habitats. For example, increased use of deep waters during area-restricted search behavior within Habitat A may be related to a shift to a more northerly biogeographic province (Briggs & Bowen 2012). This biogeographical shift is concomitant with an increase in the importance of jumbo squid *Dosidicus gigas* to the mako shark diet in the areas to the west and north of the Southern California Bight (i.e. the cold-temperate province; Preti et al. 2012). Further, jumbo squid, which increased in occurrence in the California Current in the early 2000s (Zeidberg & Robison 2007), are diurnal vertical migrators, typically spending most of the daytime at depths of 200 to 400 m off central California (Stewart et al. 2012). The increased importance of jumbo squid, a deep-water species, to the mako shark diet in this region could result in deeper dives and increased time at depth while presumably foraging in Habitat A.

As regionally endothermic fish, mako sharks have high metabolic rates and an estimated daily ration of 4.6% of their body weight (Wood et al. 2009). Given their high metabolic demand, it is surprising that mako sharks spent similar amounts of time engaged in area-restricted search and transient behaviors, and that transient periods sometimes lasted multiple months. Fasting or limited foraging during directed movements is not unprecedented for lamnid sharks. When migrating to offshore waters, white sharks in the eastern Pacific Ocean experience a decrease in buoyancy, indicating a loss of their lipid (energy storage) reserves (Del Raye et al. 2013). However, it seems that these extended periods of transient behavior, which are energetically costly, would be particularly detrimental to sharks if foraging was mostly limited to area-restricted search behaviors. Indeed, mako sharks are likely also foraging during transient behavior, as continuous and opportunistic foraging during directed movements may be more common in highly migratory pelagic fishes than believed. For example, southern bluefin tuna *T. maccoyii* were found to have high foraging success during the periods of continuous travel along their migration (Bestley et al. 2010). And although these tuna experienced fasts over multiple days, these typically occurred during periods of residency rather than travel (Bestley et al. 2008). Similarly, Pacific bluefin tuna *T. orientalis* along the Kuroshio-Oyashio transition region fed more frequently than tuna in the East

China Sea despite reduced diving activity and traveling great horizontal distances. Frequent foraging while on the move indicates that the front altered prey distributions and, therefore, optimal search behaviors (Kitagawa et al. 2004), and highlights that foraging is not limited to periods of area-restricted search.

This study represents an examination of the relationship between horizontal and vertical behaviors in mako sharks over a range of vertical water column thermal profiles. Despite limitations in the data including coarse-resolution depth data that varied in availability across and within tracks, the results support the hypothesis that vertical movements are more constrained during periods assumed to be related to foraging (area-restricted search behavior), and that mako sharks use more of the water column and spend more time at depth when engaged in directed horizontal movements (transient behavior). Results also show that water column characteristics influence behaviors during both area-restricted search and transient behaviors. This investigation builds on previous work on the movements of mako sharks in the eastern North Pacific (Nasby-Lucas et al. 2019) with more insight into factors influencing vertical distributions, while confirming scaling effects and the high levels of variability seen in vertical movements.

Given the range of factors that can influence predator behavior and prey distributions, additional work is needed to link predator vertical distributions to both oceanography and prey. For example, distributions differ among prey species and with factors including temperature, oxygen concentration, and primary productivity. Oxygen concentration also impacts the vertical range of pelagic predators (Prince & Goodyear 2006, Logan et al. 2023) and shoals in the study area (Bograd et al. 2008, McClatchie et al. 2010). Fine-resolution dive data could also improve analyses. As technologies and analytical methods advance, the ability to examine the relationship between horizontal and vertical movements will improve. PAT tags are now able to transmit fine-scale vertical movement data, enabling examination of individual dives (e.g. Merten et al. 2014, Thorrold et al. 2014), which had previously been limited to recovered PAT tags (e.g. Hoolihan et al. 2011, Queiroz et al. 2017). Additionally, new technologies, such as data loggers that measure 3-dimensional acceleration and swim speed, and record video make it possible to examine the fine details of shark movements and their encounters with prey, providing key insights into shark behaviors, although these technologies are currently limited to short-term movements on the order of days and require recovery of the data logger (Whit-

ney et al. 2019). These technologies are now being used to study pelagic sharks (e.g. Papastamatiou et al. 2018), including mako sharks (Saraiva et al. 2023, Waller et al. 2023), and are providing new insights into the movements, foraging, and energetics of free-swimming sharks, advancing efforts to understand foraging ecology and habitat use in 3 dimensions.

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