Temporal and oceanographic factors differentially affect two size classes of white shark at a Southern California aggregation site

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ABSTRACT: Ontogenetic habitat shifts are a common feature of many marine species, including sharks, which face conservation threats when their distributions overlap with human resource extraction and habitat modification. White sharks *Carcharodon carcharias*, for example, exhibit a distinctly coastal phase as juveniles, with a limited distribution compared to the basin-scale range of adults. Using an unoccupied aerial vehicle (UAV), we studied a coastal aggregation site within a Southern California Bight nursery area to determine how fine-scale temporal and oceanographic factors affect white sharks at different developmental stages. White shark density, as measured via UAV, was highly variable across time of day and day of year, with modest variation across years. Typically, more sharks were observed in the late afternoon hours. Sharks, especially those <3 m total length, were observed more often during periods of colder seafloor temperatures, potentially reflecting avoidance of these colder, deeper waters by more cold-intolerant smaller white sharks. Alternate models incorporating sea surface temperature showed a very small but significant association between surface temperatures and <3 m total length white sharks for the months we surveyed, but no such association for larger sharks. There were no or only modest effects of visibility, swell height, chl *a* levels, sea state, and tidal height on UAV-observed shark density. Understanding how temporal patterns and oceanographic predictors of density change over time as well as how shark ontogeny interacts with these factors can help us to better understand how this species uses coastal habitats and predict when they may be more likely to share marine space with humans.

KEY WORDS: White shark · *Carcharodon carcharias* · UAV · Aggregation · Density · Ontogeny

1. INTRODUCTION

Many marine species demonstrate ontogenetic shifts in habitat use, driven by changes in physiology, predation pressure, and diet (Pittman & McAlpine 2003, Snover 2008, Munsch et al. 2016). As they age and grow, demersal fish, for example, change depth and sediment preference (Macpherson & Duarte 1991, Laurel et al. 2007), reef fish migrate from mangrove or seagrass habitat to coral reefs (Shibuno et al. 2008), and crabs shift their distribution due to forage availability, predation, and host preference (Richards

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1992, Baeza & Stotz 2010, Pirtle & Stoner 2010). Ontogeny also affects the distributional response of many fish species to changes in climate (Barbeaux & Hollowed 2018). Various clades of marine mammals also exhibit ontogeny-specific habitat choice (Page et al. 2006, Fowler et al. 2007, Mendes et al. 2007, Campagna et al. 2021). Uncovering the connection between life stage and distribution is fundamental to our understanding of behavior, population demography, and critical habitat (Hazen et al. 2012).

Conservation threats to sharks, namely fishing and habitat loss, are dependent in part on patterns of space use (Cortés et al. 2010, Lucifora et al. 2011, Dulvy et al. 2021). Therefore, properly managing and conserving shark populations requires a better understanding of the changing threat landscape from the start to the end of sharks' lives (Cortés et al. 2011, Afonso & Hazin 2015, Carlisle et al. 2015, Stoffers et al. 2021). With 31% of all species threatened with extinction, sharks are among the most threatened groups of vertebrates on Earth (Dulvy et al. 2021) and exemplify a larger trend of global marine defaunation (McCauley et al. 2015). Large-bodied sharks, which can be ecologically important due to their high trophic position (Myers et al. 2007, Heithaus et al. 2008, Estes et al. 2016), are especially suffering from anthropogenic population declines (Ferretti et al. 2010, Dulvy et al. 2014). A preference for nearshore habitat during the juvenile stage can bring some species of large sharks into increased contact with fisheries and recreation (Heupel et al. 2015, Ajemian et al. 2020, Anderson et al. 2021b).

The white shark *Carcharodon carcharias* is a prime example of a large-bodied shark that exhibits ontogenetic shifts in its distribution and which faces conservation threats (Rigby et al. 2022). Specifically, juvenile white sharks use coastal habitats more frequently than adults (Kerr et al. 2006, Carlisle et al. 2012, Skomal et al. 2017). These coastal areas are considered to be white shark 'nurseries' if they meet all of these criteria: exhibit a high density of young-of-year (YOY) individuals relative to other areas, relatively high site fidelity of those YOY individuals, and persistence of use across years (Heupel et al. 2007). Areas meeting some or all of these criteria for white sharks have been identified in the Southern California Bight (SCB) (Weng et al. 2007, White et al. 2019, Anderson et al. 2021b), Baja California, Mexico (Santana-Morales et al. 2012), southeastern Australia (Bruce et al. 2019), the New York Bight (Curtis et al. 2018), and eastern South Africa (Dicken & Booth 2013).

A variety of biotic and abiotic factors have been used to explain the abundance and distribution of juvenile and adult white sharks, with temperature often believed to be among the most important (White et al. 2019, Spurgeon et al. 2022). White sharks exhibit regional endothermy (Carey et al. 1982, McCosker 1987, Goldman 1997), allowing them to tolerate a wide temperature range, cross vast swaths of open ocean, and traverse coastlines along large latitudinal and longitudinal gradients (Bonfil et al. 2005, 2010, Bruce & Bradford 2012, Curtis et al. 2014). Nevertheless, smaller, younger white sharks appear to prefer a narrower range of temperatures than larger conspecifics (Boustany et al. 2002, Weng et al. 2007, Curtis et al. 2014), potentially because of a limited ability to thermoregulate (White et al. 2019). This temperature-mediated habitat selection could be the result of behavioral thermoregulation by juvenile white sharks, or it may be driven by the thermal optima of their prey (Weng et al. 2007, Bruce et al. 2019, Anderson et al. 2022).

Prey availability is considered to be a defining characteristic of both nursery areas and other essential habitat for sharks (Heithaus 2007, Heupel et al. 2007). Prey availability is related to ontogenetic habitat shifts, because juvenile and adult white sharks, like many other species of shark (Wetherbee & Cortés 2004), have dissimilar diets (French et al. 2018). As evidenced by their less-serrated, narrower teeth (Hubbell 1996), juvenile white sharks tend to have a diet composed predominantly of teleosts and rays and then expand their diet as adults to include marine mammals; this transition generally occurs at around 300 cm total length (TL) (Tricas & McCosker 1984, Estrada et al. 2006, Hussey et al. 2012, Kim et al. 2012).

Aggregation sites provide a useful context for studying if and how environmental factors shape the local abundance of different white shark life stages, as multiple life stages have been observed using these sites. Uncovering the mechanisms that drive the formation of, and abundance at, these critical habitats is a key directive for white shark research (Huveneers et al. 2018). In addition to creating nursery areas, age-specific habitat requirements cause white sharks to form aggregations with high densities of immature individuals within nursery areas (Anderson et al. 2021b, Rex et al. 2023, E. Spurgeon et al. unpubl. data). Most research of white shark aggregations, however, has focused on larger individuals at foraging grounds outside of nursery areas (Robbins 2007, Domeier & Nasby-Lucas 2007, Domeier et al. 2012, Duffy et al. 2012, Jorgensen et al. 2012, Schilds et al. 2019, Kanive et al. 2021), so environmental and temporal drivers of density at aggregation sites within

nursery areas are poorly understood. Previous work on juvenile white sharks has largely relied on various telemetry methods to examine patterns of shark behavior over larger spatial scales (e.g. White et al. 2019, Spurgeon et al. 2022, Rex et al. 2023). In the present study, insight is more focused on very fine-scale spatial and temporal variation. We also consider such patterns over a range of white shark size classes within this finer-scale spatial domain.

Despite demonstrated relations between the aforementioned factors (e.g. diet, temperature, ontogeny) and broad-scale white shark distribution, the impact of these factors on fine-scale habitat choice within the nursery area, and across life history stages, is yet to be fully understood. For example, month, time of day, water temperature, tidal height, swell height, and lunar phase collectively explained only 1.8% of the deviance in a model of white shark acoustic detections in eastern Australia (Spaet et al. 2020). Temperature, while well-supported as a driver of basin-scale movement (Spurgeon et. al 2022), may not be useful for predicting occupancy at individual locations; temperature was associated with juvenile density at aggregation sites within the SCB nursery in only 4 of 9 years of one study, and other variables such as chlorophyll a (chl a) and season were also inconsistent in their effects (Anderson et al. 2021a). Therefore, additional research using novel technology at fine spatial scales is needed to better understand why white sharks form aggregations within nursery areas and what factors determine abundance at aggregation sites (Anderson et al. 2021b, Jorgensen et al. 2022, Rex et al. 2023).

Unoccupied aerial vehicles (UAVs) can provide valuable insights complementary to traditional methods (e.g. telemetry) for studying the factors that shape white shark abundance in these high-density aggregation habitats. Advantages conferred by UAVs include the ability to provide a snapshot view of the surface waters of an entire aggregation site (e.g. Ayres et al. 2021b); they are non-invasive (Christiansen et al. 2016, Butcher et al. 2021); and their low cost-per-use provides the opportunity to repeatedly survey aggregation sites at high temporal frequency. However, there are also many disadvantages of UAVs for these applications. They do not permit observation of sharks at depths below the detection limit for UAVs or outside of daytime hours; they cannot track individuals or populations for prolonged periods and over significant distances; detectability can be impacted by environmental factors; and they often cannot aid with identification of specific individuals. In study sites, such as the focal site for this research, where many of the sharks have already been found to spend the majority of their time in surface waters (within 2 m of the surface regardless of depth), concern about some of these shortcomings can be lessened. Taken in sum, however, UAVs are well-suited for creating new insight into the factors that shape abundance patterns in white shark aggregation sites.

As UAVs become more common in the study of shark biology and as a tool for public safety and coastal management (Butcher et al. 2021), more information is needed about the efficacy of UAV surveys compared to other methods, as well as the oceanographic factors that may introduce bias or otherwise affect UAV-derived shark counts (Elphick 2008, Williams et al. 2017, Butcher et al. 2021, Rex et al. 2023). For example, sea state and water visibility can affect the ability to distinguish objects in the water but do not always have an effect on UAV surveys (Koski et al. 2009, Hodgson et al. 2013, 2017, Hensel et al. 2018, Butcher et al. 2019, Colefax et al. 2020a).

In this study, we analyzed a 2 yr (2020−2021) data set of UAV surveys of white sharks at an inshore aggregation site in the SCB (hereafter referred to as the Carpinteria aggregation site). We used generalized additive models to determine the effects of temporal (day of year, time of day) and oceanographic (water temperature, chl a, tide, swell height, visibility, sea state) factors on shark density estimates. We conducted equivalent modeling procedures on juvenile (<3 m TL) and sub-adult or adult sharks (⩾3 m TL, sensu Bruce & Bradford 2012) independently, to explore whether the relationship between temporal and oceanographic factors and observed shark density was mediated by ontogeny.

2. MATERIALS AND METHODS

2.1. Survey methods

White shark UAV surveys were conducted off the coast of Carpinteria, California, at the northwest extent of the SCB off Santa Claus Beach (34° 24′ 33′′ N, 119° 33′ 10′′ W) a known aggregation area for white sharks (Fig. 1) (Anderson et al. 2021a, Rex et al. 2023). The benthic habitat in the study area (from surf zone to a maximum of 600 m from shoreline) is fairly homogeneous, consisting largely of shallow, sandy-bottom habitat of <10 m depth, with little observable rocky reef substrate or kelp forest habitat. Surveys took place over the immediate inshore area, covering around 2 km of coastline and extending up to 600 m from shore (~1.2 km²; Fig. S1 in the Supplement at
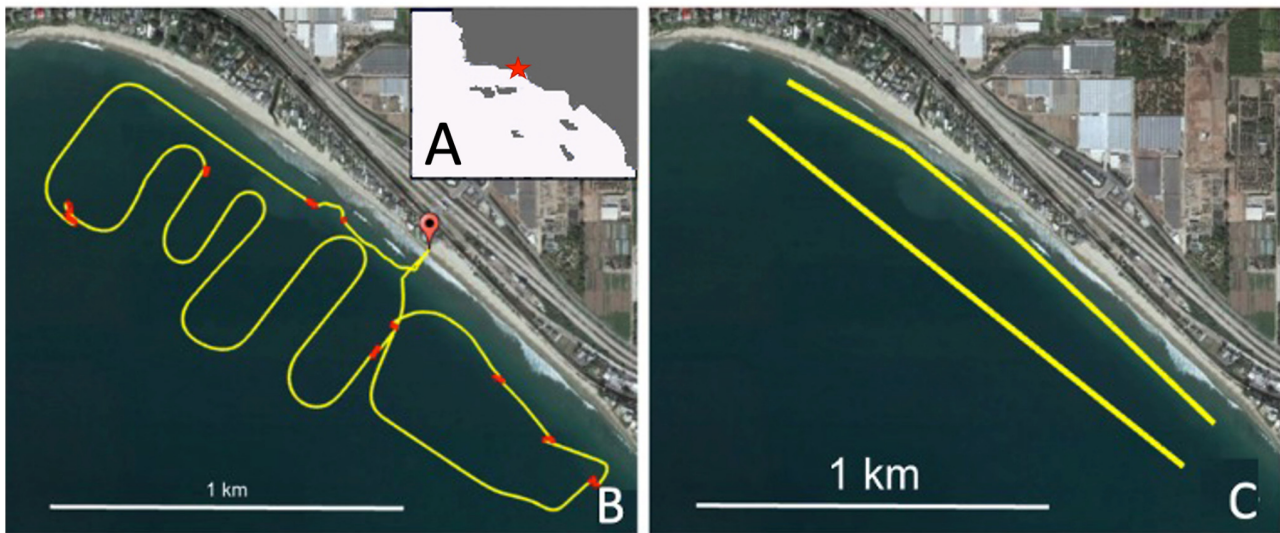
Fig. 1. (A) All unoccupied aerial vehicle (UAV) surveys were conducted in a known aggregation site in the Southern California Bight off Santa Claus Beach. Daily shark densities used in this study were calculated as the total number of all presumed unique individuals from 2 survey types conducted back-to-back and standardized by total survey area. The first survey type was a (B) roaming survey, where the flight path shown for the roaming survey is representative of a typical survey and varied depending on the presence and location of sharks. The 9 red portions of the example roaming survey flight path shown in red indicate where the UAV pilot observed a shark and lowered the altitude of the UAV. The second type of survey was a (C) belt transect survey that included both an 'inshore' and an 'offshore' transect. Maps produced in Google Earth, satellite image© 2022 TerraMetrics

www.int-res.com/articles/suppl/m744p101_supp.pdf). Despite the shallow nature of this particular study location, surface heating and localized wind and current patterns do lead to considerable microscale variation in temperature and temperature stratification (Spurgeon et al. 2024).

UAV surveys at the Carpinteria aggregation site were conducted between 24 June and 11 December 2020 and 20 April and 18 December 2021. Surveys were conducted all weekdays during these 2020 and 2021 survey periods during daylight hours when the weather was safe and suitable for UAV flights. Surveys were performed with a Mavic 2 Pro quadcopter (SZ DJI Technology) with a 4K resolution camera that films at 30 frames s^{-1}; focal length of 35 mm, format equivalent: 28 mm; and aperture of f/2.8–f/11. Save for a polarizing filter over the camera lens, the UAV was otherwise unmodified. The Mavic Pro 2 uses a barometric sensor to determine relative altitude (height above a consistently located takeoff location). Empirical field tests were conducted with the DJI Mavic 2 Pro resulting in a field of view (FOV) measurement of 73°. Specifically, FOV was measured in overwater tests at the study beach with the drone at a range of different altitudes imaging 2 objects (i.e. a PVC rod and surfboard; Text S1) of known size and via overland flights at the same altitude flown over a transect tape laid on flat ground. During data collec-

tion flights, the camera was always positioned at the nadir (i.e. at an angle of 90° to the sea surface).

We utilized 2 UAV survey methods, performed back-to-back each day that surveys were conducted. One was an automated 'belt transect' survey, similar to Rex et al. (2023), with inshore and offshore flight paths, and one was a survey flight, manually operated by the UAV pilot conducted in a 'roaming' manner (Fig. 1, Fig. S1). The order of these belt transect and roaming surveys was alternated randomly between survey days.

For the belt transect survey, the UAV flew automatically along 2 belt-shaped transects that were pre-programmed using Litchi autonomous flight software (VC Technology): one 1560 m long transect positioned just seaward of the surf zone ('inshore transect') and one of the same length, ~200 m farther offshore ('offshore transect') (Fig. 1). While there are modest differences in depths of water between inshore and offshore transects, both transect types are generally deeper than 3 m, the approximate maximum depth at which sharks can usually be detected through UAVs. There are also some differences in visibility across transects due to higher turbulence in inshore waters near breaking waves. We binned data from both transects in our analyses; however, in Text S2 we discuss differences in sitings between these 2 transects.

For the roaming surveys, the UAV was launched from the same starting point as the belt transects. A search boundary for the roaming surveys was pre-centered over the study site, enclosing an area within which roaming flights were contained (and these boundaries were then delineated on the UAV video monitor overlay). The pilot manually piloted the drone in a sinusoidal search pattern back and forth within these boundaries, attempting to cover as much area as possible while moving generally parallel to the coastline and transiting freely across the areas defined as inshore and offshore in the belt transect method (Fig. 1). The duration of these roaming survey flights was dictated by the battery life of the UAV. Most flights lasted approximately 20 min, with a resultant mean ($\pm$SD) search area of roaming surveys of 0.304 ± 0.134 km^2 (n = 238). For both transect methods, the UAV was flown at an altitude of 40 m above sea level and a speed of 5.6 m s^{-1}. However, during roaming surveys only, when a shark was detected, the pilot descended to ~20 m to observe markings, acoustic and/or satellite tags from other research projects, and to obtain a clearer image of the shark for photogrammetric estimation of body length.

The specific areas of both the belt transect and the roaming surveys were calculated based on the total length of the flight, altitude (i.e. in the case of roaming surveys when the drone dropped to size sharks), and the width of the FOV of the camera, which fluctuates with altitude (Kiszka et al. 2016). Given that roaming flight paths were non-linear, we generated 'FOV rectangles' for every GPS point (taken every 0.1 s) along the flight path during the active search portion of each survey flight (i.e. when the UAV was at the 40 m search altitude). The rectangles were converted to spatial polygons with GPS coordinates attached, allowing each rectangle generated during the survey to be stitched into a single total survey geospatial polygon. The total area of this polygon was then calculated, corresponding to the total area surveyed. Interestingly, despite the different characteristics of the belt and roaming surveys, supplemental analyses indicated that when standardized by area, they yield quite similar shark density estimates (Text S3, Fig. S2).

A single integrative measure was manually derived from a review of data collected in the back-to-back belt transect and manual flights to avoid overcounting sharks. To obtain this single measure, we compared the video record from each of the 2 surveys immediately after the flight to determine the total number of unique observable sharks present in the study site during the survey day. Infor-mation such as body length, distinguishing features such as scarring or the presence of tracking tags, and the spatial position in the survey area were all used to reduce, as much as possible, incidences of double counting (both within and between surveys) in this integrative measure. For example, a large shark marked with a tracking tag to the left of its dorsal fin traveling in the western area of the survey region that was observed in both the belt transect and roaming surveys would be counted only once. This count of total number of unique sharks observed on a daily basis was then standard-ized by dividing the total number of unique sharks observed in a day by each survey's total area cov-ered in both survey types, and is hereafter referred to as 'daily unique shark density' and was the re-sponse measure inputted into our analytical models. Notably, unique shark density was very closely cor-related with belt survey density (Fig. S3). All shark data were included in the modeling; i.e. inclusive of days where count data were estimated to be zero.

2.2. Environmental variables

Environmental variables used in our models in-cluded sea surface temperature (SST) averaged across 2 sensor locations at the Carpinteria aggrega-tion site in 2020 and 7 locations in 2021, along with seafloor temperature (SFT) averaged across 7 loca-tions (Spurgeon et al. 2022); satellite-derived chl a levels, averaged across the 3 most proximal 0.0125° grid cells (https://coastwatch.noaa.gov); tidal height from the nearest NOAA tide station ~12 km to the west (https://tidesandcurrents.noaa.gov Station 9411 340); and swell height from the nearest offshore NOAA swell buoy ~31 km to the southwest (https://ndbc.noaa.gov Station 46053). We used hourly aver-ages for these variables to match the temporal scale of the surveys. We also assessed Beaufort sea state and assigned a daily visibility score (1−5) based on the video collected by the UAV. Given that few survey days occurred at the extremes of each scale, we binned sea state into 2 levels (0−1 and 2+) and visibil-ity into 3 levels: 1−2 ('low'), 3 ('medium'), and 4−5 ('high').

2.3. Sizing of sharks

As described previously, overland and overwater calibration flights were used to estimate the FOV of the UAV. Timestamps in the GPS log were used to

determine the altitude of the UAV at the moment when the length of each shark was measured. We also conducted in-water field tests with target objects of known length to quantify and correct for measurement error (see Text S1). Analysis of length estimations from these field tests revealed that for a UAV altitude of 20 m, the same altitude that was used for most length estimations of sharks, a combination of accounting for takeoff elevation and shark depth produced accurate length estimations, while also allowing for the collection of details on individual sharks that were helpful for avoiding the double counting of individuals (Fig. S4). Further details are shared in Text S4 but overall, correcting for these 2 factors at 20 m altitude resulted in a mean error in these controlled trials of 1.7%. The mean error for uncorrected length estimates, meanwhile, was 12.8%.

We used this method, taking into account elevation and depth, for all shark length estimations reported herein. Takeoff elevation above sea level was taken from the UAV flight log. Shark depth was visually categorized by analysts from video data into 3 depth bins: 'surface' (< 0.75 m), 'shallow' (between 0.75 and 1.5 m), and 'deep' (between 1.5 and 3 m). Depth categories were estimated based on easily observable reference indicators of depth (e.g. dorsal or caudal fin creating ripples on the surface of the water for the surface category). The midpoints of the shallow and deep categories (1.125 and 2.25 m, respectively) were used as the depth correction factors for those categories. We did not make and do not report measurements of sharks estimated to be deeper than 3 m due to a general inability to accurately identify the tail and snout positions beyond this depth.

Using these inputs and following a similar process as Colefax et al. (2020b), we calculated shark length by (1) determining the width of ocean surface, in meters, captured in the frame of interest (i.e. when the shark was centered in the frame with a linear body position) based on a trigonometric calculation using the FOV, UAV altitude, and takeoff elevation above sea level; (2) dividing this frame width in meters by the frame pixel width (2704 pixels for video taken at 2.7K resolution) to obtain the size in meters of each pixel; (3) measuring the total length of the shark in pixels using a digital image processing application; (4) converting shark length in pixels to total length in meters using the size of each pixel calculated in step 2; (5) estimating a correction factor for shark depth calculated by adding estimated shark depth to total UAV altitude and dividing this sum by the original measured UAV altitude; and (6) multiplying the total shark length estimate by this aforementioned correc-

tion factor. This final step treats shark depth as an increase in the distance between the UAV and the shark.

2.4. Modeling shark density

We constructed generalized additive models (GAMs) to determine the association between temporal and oceanographic variables (Table S1) and the density of observed white sharks. GAMs were implemented in the R software environment (R Core Team 2022) using RStudio (RStudio Team 2022) and the 'mgcv' package (Wood 2017). We fit GAMs to the daily unique shark density (hereafter 'overall model'), the subset of sharks included in the daily unique shark density metric that were <3 m TL (hereafter 'small shark' model), and the subset of unique sharks included in the daily unique shark density metric that were 3 m TL or longer (hereafter 'large shark' model). Data were drawn only from days where both types of UAV surveys were conducted to generate daily unique shark densities and included all data for which the estimated abundance was zero. The overall model was included to determine if a larger sample size would significantly change the patterns of density compared to the small shark and large shark models and to understand overall patterns of behavior across size classes. While we present here data from the 3 models that use SFT data as our focal model, in Text S5 and Table S2, we also present data from parallel GAMs using SST data. In Tables S3 & S4 we also rerun GAM models, separating them between the 2 types of UAV surveys. In all models, year was included as a parametric term. The day of the year was also stratified by year to account for between-year variability.

We used restricted maximum likelihood (REML) smoothing parameter estimation, with a negative binomial family distribution due to overdispersion. Rather than performing backward term selection, which has the potential to exclude important terms, we used the double penalty approach to automatically remove non-contributing smooth functions from the model (Marra & Wood 2011). For each smooth function, k was set at 10 to avoid overfitting (Anderson et al. 2021b).

Smooth functions were used for oceanographic variables. We accounted for intra-annual variation using a continuous 'day of year' smoothing spline, rather than a categorical 'season' (e.g. Anderson et al. 2021b) or 'month' (e.g. Spaet et al. 2020) term, to test for temporal non-linearity in shark density. Day of year was included as a smoothed term strati-

fied by year, to account for variance in the intra-annual temporal pattern of environmental factors. The other temporal factors in the GAMs were the time of day (binned hourly) at which the surveys were conducted and year (categorial). The model structure was thus:

Shark density ~ year + s(hour) + s(day of year, by = year) + wave height + visibility + s(tidal height) + s(temperature*) + s(sea state) + s(chl a)

where s() denotes that a smoothing function was used and * denotes that either SST or SFT was used (varies across the 2 models).

For each GAM, we determined the deviance explained (DE) of each term by dropping it from the full model and calculating the difference in DE between the full model and the model without the term in question (Spaet et al. 2020). This procedure also enabled us to test the model for sensitivity to the terms included. Model diagnostics were performed with the 'gam.check' function.

We recognize that the use of DE remains a developing strategy (Gislason et al. 2020, Spaet et al. 2020, Chen et al. 2024) and that for some in the ecological community, making inferences based on DE can be viewed as a speculative and a non-preferred method for interpretation. Thus, in addition to the GAM modeling approach described above, we also analyzed the data using a more traditional Akaike Information Criterion (AIC)-based approach. In Table S5, we provide results from this secondary analysis. The results of this complimentary AIC approach align very closely with the DE results reported below.

3. RESULTS

A total of 232 survey days (104 in 2020; 128 in 2021) were conducted that included both belt and roaming surveys and generated a daily unique shark density data point for inclusion in the modeling. We were unable to obtain length estimates for observations where the depth of the shark was indeterminate, its snout and/or tail position were obscured, or the altitude of the UAV was unavailable from the flight metadata. These unsized individuals were mostly observed in autonomous surveys which did not allow for a descent from altitude to view and more accurately measure detected sharks. After removing these unsized individuals, the small and large shark models included survey data with 481 and 304 shark observations, respectively; the size distribution of sharks followed a unimodal distribution, with a median size of ~2.44 m (Fig. S5).

While we ran separate models for environmental prediction of shark abundance for small sharks, large sharks, and overall sharks (i.e. daily unique shark density), the factors associated with observed shark density were broadly consistent across each of these models (Table 1). Our central model that included SFT performed best for overall sharks (44.1% of DE) and large sharks (29.6% of DE) compared to small sharks, for which only 21% of deviance is explained. For better visualization of these data, in Fig. S6 we have also plotted the models directly, creating plots of the model terms against their smoothed function response.

The effects of each term in the model were largely consistent between the models using SFT and those for which SST was used (Table S2). However, the SST models explained a slightly lower proportion of the deviance (36.3, 20.7, and 29% of DE for overall shark, juvenile, and large shark models, respectively, for SST vs. 44.1, 21.2, and 29.6% of DE for SFT). SFT itself also explained more deviance within the SFT model than did SST in the SST model. Therefore, from here forward we focus on results for the SFT models unless mentioned otherwise (see Table S2 and Fig. S7 for full SST results).

Similarly, results from integrated models (using both transect and roaming survey methods) were qualitatively similar to the models that separately

Table 1. Total deviance explained (DE) and DE of each temporal and oceanographic term in generalized additive models (GAMs) of observed density of overall sharks and density of observed small (<3 m total length [TL]) and large (>3 m TL) white sharks using seafloor temperature (SFT) data. DE in **bold** indicates that a term was significantly associated with density (p < 0.05 in the respective GAM output). DE is not reported when total DE was higher in the reduced models than in the global model. See Table S5 for complementary analyses reporting Akaike's information criterion values

| | — Deviance explained (%) — | | |
	Overall sharks	Small sharks	Large sharks
Year	**1.5**	6.3	**1.9**
Day of year	**20.9**	13.5	4.8[a]
Time of day	**8.7**	2.6	**8.5**
Seafloor temperature	**8.2**	**2.1**	0.7
Chl a	–	1.3	0.1
Tidal height	**0.1**	1	**4.7**
Swell height	0.4	3.7	0.1
Sea state	**2.9**	0	0.3
Visibility	**2.3**	0.6	6.7
Total DE	44.1	21.2	29.6

[a]Day of year was significantly associated with large shark density in 2021 only
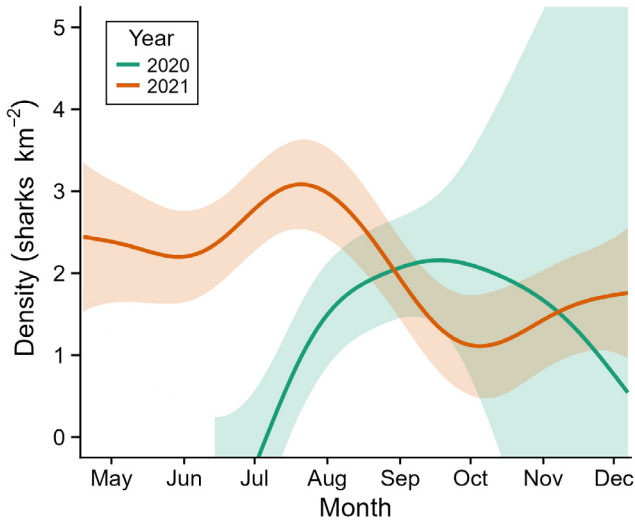
Fig. 2. Variation in observed white shark density by year, pooled for all shark size classes (i.e. overall model), as determined by the smooth function for 'day of year' in the generalized additive model. Results shown are on the response scale, with all other parameters held constant. Shaded regions: 95% confidence interval for each year
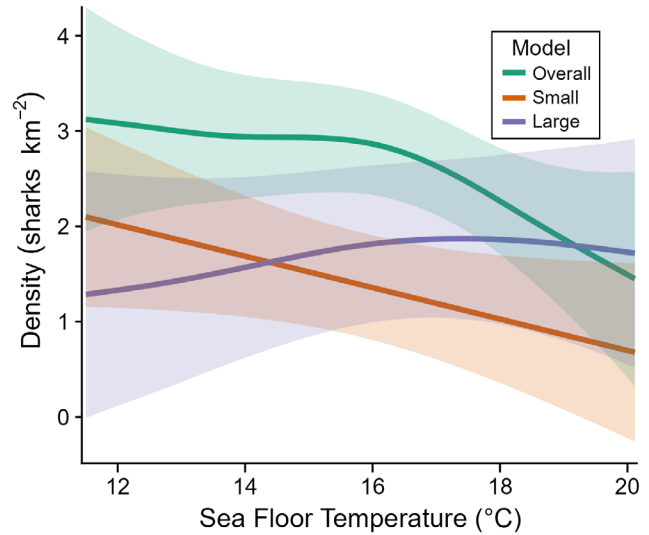

Fig. 3. Relationship between seafloor temperature and modeled daily unique shark density in the overall (all observed sharks), small shark (<3 m total length [TL]), and large shark (>3 m TL) generalized additive models. Shaded regions: 95% confidence interval for each model

treated only one of the 2 survey methods. Thus, we hereafter discuss only results from integrated models but include discussion and data from the separate models in Tables S3 & S4.

Day of year was the variable most highly associated with density in all overall and small shark models (see Fig. 2, Fig. S8). Although the effects of day of year varied between the 2 years, within each year, the intra-annual trend in density (represented by day of year) was similar across the overall, small shark, and large shark models. However, day of year explained over twice as much deviance in the overall and small shark models (20.9%, p < 0.001 and 13.5%, p < 0.01, respectively) as in the large shark model (4.8%), where day of year was only significantly associated with density in 2021 (p < 0.01). While year itself was a significant factor in adult shark models, it was not significant in juvenile or overall shark models and explained <2% of deviance in the adult shark model.

Time of day was also moderately important in overall shark models, explaining 8.7% of the deviance in overall shark density (p < 0.001), but this was driven almost entirely by large shark density. The association between time of day and density was not significant for small sharks, which our data modeled least well. For large sharks, density increased throughout the day, peaking from 16:00 to 18:00 h (the latest hour at which surveys were conducted) (Fig. S9).

SFT (Fig. 3) was associated with overall density (8.2% of DE, p < 0.01) and small shark density (2.1% of

DE, p = 0.04), but not large shark density (0.7% of DE, p = 0.2). Small shark density exhibited a negative relationship with SFT, with the model predicting maximum small shark density observed at the lowest temperatures (<12°C) and minimum density at the highest temperatures (>22°C). Overall density was driven by small shark numbers and was thus higher at lower SFTs, particularly below 16°C.

Sea state and visibility had only modest explanatory power. Visibility had a weak significant relationship with density only in the overall shark SFT model, explaining just 2.3% (p = 0.047). Sea state similarly only explained 2.9% of the variance (p = 0.037) in the overall shark model.

Tidal height explained just 0.1% of deviance in the overall model (p = 0.012), and 4.7% of deviance in the large shark model (p = 0.015); it was not significant in small shark models. Higher tides corresponded to lower observed density in the overall and large shark model.

Chl *a* and swell height were not associated with density in any of the 3 models.

4. DISCUSSION

Our study conferred the opportunity to observe and attempt to explain the factors potentially shaping white shark relative abundance at this aggregation site from a unique vantage point. Surveys conducted

by UAV can offer an opportunity to observe a wider range of size classes, and potentially a higher number of unique individuals, compared to other methods. For example, UAV surveys may be well positioned to observe transient sub-adult and adult sharks in addition to high-residency YOY and juvenile white sharks (White et al. 2019, Spaet et al. 2020, Anderson et al. 2021a,b). UAV surveys are, however, disadvantaged by imperfect detection probability (Koski et al. 2009, Hodgson et al. 2017, Butcher et al. 2019, Ayres et al. 2021b, Rex et al 2023), an inability to detect sharks outside of surface waters, and the difficulty in determining whether each sighting is of a unique individual. These limitations may cause biases towards overestimating or underestimating density compared to other methods (Hodgson et al. 2016, Williams et al. 2017). There may also be some biases towards sighting large individuals and missing smaller individuals. We discuss these and other limitations further below.

We included a visibility score in our models to attempt to disentangle detection availability from actual patterns of shark density, a key limitation to UAV surveys, and found that low visibility was largely not strongly associated with shark density, especially in our 'large shark' and 'small shark' models, although there was a very small effect on overall sharks (Table 1). While visibility is a subjective measurement, this is similar to results from other UAV studies of large predatory sharks (Colefax et al. 2020a) and mock-shark targets (Hensel et al. 2018), where little to no effect of visibility on detections was found. We found a similarly very minor association between sea state and shark density (Table 1). The lack of strong association in this particular study may in part derive from the fact that many of the sharks at this site are found in waters very near to the surface, reducing some of the potentially confounding effects of visibility on detectability; i.e. juvenile white sharks at this site spend approximately 71% of their time in waters <2 m from the sea surface, regardless of site depth.

Time of year was the most consistent predictor of YOY white shark density across a multitude of aggregation sites in Southern California (Anderson et al. 2021b, Rex et al. 2023). Day of year also played a primary role in explaining shark density at the Carpinteria aggregation using these UAV methods in our data (Table 1). White shark density in our overall model (all shark classes pooled) peaked around September and October in 2020 and around July and August in 2021, a pattern broadly consistent with other observations across Southern California showing decreased observations during the boreal winter and summertime peaks. Interestingly, day of year ex-

hibited a more than 2 times stronger association with the density of small sharks compared to large sharks, suggesting more sensitivity by these smaller sharks to day of year at this site. Year, as a factor in our model, showed only a very weak effect on shark density, and then only significantly so for large sharks (Table 1). Additional longer-term monitoring may be required to better understand the role and importance of across-year variation in shark density and to better consider how climate oscillations, such as those that typify these years (e.g. this study period occurred during an extended multi-year La Niña period), may affect white shark density (Fig. S10 shows within-year variation in SFT and SST by month for the duration of this study).

We also observed a relatively strong diel pattern in overall density, where surveys conducted later in the day were largely associated with higher density estimates. Such patterns were much more evident for the 'overall shark' model and for the 'large shark' model. This general diel pattern of UAV-observed density is consistent with acoustic tracking studies of depth use by white sharks at the Carpinteria aggregation, where sharks utilized deeper waters around dawn and dusk, with a transition to shallow near-surface waters in the late afternoon (Spurgeon et al. 2024). However, these results largely pertained to smaller white sharks. Our observations would indicate that UAV surveys conducted in the late afternoon might result in a more accurate assay of the true shark abundance at this site. It should be noted, however, that juvenile white shark distribution in coastal waters off eastern Australia showed little response to time of day (Spaet et al. 2020), suggesting the potential for regional variation in these patterns. Diel patterns of the kind detected for the white sharks in this study here have been observed in UAV surveys of blacktip *Carcharhinus limbatus*, lemon *Negaprion brevirostris*, bull *Carcharhinus leucas*, and Pacific nurse shark *Ginglymostoma unami* aggregations in coastal habitats (Ayres et al. 2021a,b).

Of the environmental factors that we investigated, the effects of temperature had amongst the strongest effects on shark density. In particular, in our primary model, which included SFT, the density of observed small sharks and overall sharks had a negative relationship to SFT (Table 1, Fig. 3). The best explanation for this pattern likely stems from avoidance of these colder SFTs and preferential use of these typically warmer SSTs by these smaller white sharks, which have been shown to be less tolerant of colder temperatures (Weng et al. 2007, Curtis et al. 2018, Spurgeon et al. 2024). The lack of such a strong relation-

ship observed between SFT and larger sharks would seem likely to arise from the higher surface area to body size ratios of these larger sharks. Alternate models that explored the role of SST on shark density found much weaker relationships with SST (Table S2). Generally, higher shark densities were associated with higher SSTs (Fig. S7). As with SFT, larger sharks showed much less association with SST than their smaller-sized counterparts. It should be recalled that UAV field sampling in this study did not include some of the traditionally coldest-water months of the year (e.g. January, February, March); thus, these models only examine associations across a portion of the year. Taken collectively, results from the SFT and SST models appear to indicate that (1) smaller white sharks exhibit greater temperature sensitivity than larger white sharks and (2) the general trend in overall shark density patterns was such that sharks at this site were avoiding colder SFTs and showing a weak positive association with warmer SSTs until those temperatures became too warm. Our findings are thus broadly consistent with other works describing the preferred thermal niche for white sharks in this region, as well as in Australia and the Atlantic (Curtis et al. 2014, White et al. 2019, Lee et al. 2021). Whether these relationships mechanistically arise from effects of temperature on shark physiology or behavior — or whether they reflect sharks tracking the effects of these same temperatures on their prey, or both — remains to be directly tested.

The environmental variables tested in our primary SFT model, namely chl a, tidal height, swell height, and sea state, showed generally less strong or variable associations with white shark density (Table 1). There was one modest significant association between tidal height and density of large sharks — with a higher density of large sharks observed at lower tides. It is difficult to assign a definitive causal link between this potential relationship with lower tides. It is plausible that periods of lower tides are associated with less wave energy in the inshore area of this particular study beach, as it has a flat low tide terrace and steeper upper beach face, and that such lower energy conditions are preferred by these sharks. Some of the environmental variables that we tested in this study have been found to influence the behavior of sharks in other studies (Fallows et al. 2016, Skubel et al. 2018). It must also be considered that the abiotic variables we examined do affect white sharks, but that the spatial resolution of these data (especially for chl a, which was derived from satellite data) precluded us from detecting these relationships. If there were to have been an observed influence of chl a in these models, this

would most likely have affected sharks indirectly by affecting prey abundance. While numerous candidate prey items were observed in these UAV surveys (e.g. stingrays, bat rays, baitfish schools), future research will be required to properly incorporate contemporaneous, local data on prey abundance with observed shark density.

Based on the data we collected in the field and the explanatory variables that we modeled, it seems clear that there is not a simplistic answer that determines precisely why sharks were using the Carpinteria aggregation site and thus what was driving these observed fluctuations in their density. Despite conducting hundreds of UAV surveys, we observed none of the hunting behaviors described in Colefax et al. (2020b), who studied white sharks with a UAV along coastal beaches in eastern Australia. However, we do note that observations of white shark predation events are rare, even at pinniped colonies (Brown et al. 2010). Other observations of prey species, along with telemetry data on swim speeds and long periods of residency of white sharks at the Carpinteria aggregation site (Anderson et al. 2021b, 2022), suggest that sharks are indeed foraging in the area. Other potential drivers that shape density at the aggregation site and deserve future consideration include intraspecific interactions (Schilds et al. 2019, Anderson et al. 2021a), such as competitive exclusion of smaller sharks from other areas used by larger sharks (Goldman & Anderson 1999, Martin et al. 2009), and as a refuge from predation (Pyle et al. 1999, Benson et al. 2018, Jorgensen et al. 2019, Towner et al. 2022). Future research using UAVs could perform targeted behavioral observations, rather than density surveys as performed in this study, to better understand such drivers and the variable influence of these factors on different shark size classes. Part of the challenge of explaining shark density using these modeling approaches derives almost certainly from the fact that white sharks exhibit complex interannual patterns with inshore–offshore dynamics that vary ontogenically (Kerr et al. 2006, Carlisle et al. 2012, Jorgensen et al. 2012, Skomal et al. 2017). A more extended time series of UAV observations might better document these types of patterns and lead to more holistic explanations of variation in local shark density. Also, we note that these data were collected from a fairly homogenous area of sandy beach habitat. Additional research that surveys white shark patterns in Southern California across a more diverse range of representative coastal habitats (e.g. rocky reef, kelp forest, areas with increased bathymetric complexity) will shed more light on how microhabitat shapes some of the patterns reported herein (Heithaus et al. 2006).

5. CONCLUSIONS

We demonstrated that a number of factors, especially time of year, time of day, and water temperature, are associated with white shark density, as estimated via UAV survey. Ontogeny appears to influence how white sharks respond to these factors, as the observed density of larger sharks was less temporally variable, and smaller individuals exhibited more of a response to colder SFTs and slightly more of a response to intermediately warm SSTs. Researchers and safety officials alike should take diel variability in shark density into account when planning the time of day during which surveys are to be conducted so as to most accurately monitor changes in shark abundance. Our observed intra-annual variability in shark density estimates also suggests that long-term data may be needed to accurately capture patterns of shark abundance and properly describe the factors shaping their abundance.

UAV surveys have many disadvantages and limitations relative to other shark research methodologies, including the short-duration, snapshot nature of density estimates, the inability to simultaneously collect ancillary oceanographic data at the same fine spatial scale at which sharks choose habitat, and the inability to collect data at night or during inclement weather; which, in some contexts, are conditions that are known to shape shark behavior (Hammerschlag et al. 2006). UAV approaches can also only detect sharks in surface waters, so we are unable to detect sharks below observable depths. These limitations, however, do not prevent UAV surveys from establishing useful benchmarks of shark density and behavior at local scales — especially when blindspots from UAV research are filled by complimentary insight from other research methods.

The capability of conducting relatively lower cost, higher temporal frequency surveys of white sharks (as well as other megafaunal species) may become even more advantageous as climate change and other human uses alter these coastal marine ecosystems. Early evidence already suggests, for example, that increasing water temperatures in the SCB (Rasmussen et al. 2020) may be causing new aggregation sites to form (Tanaka et al. 2021) and potentially altering spatiotemporal patterns of shark abundance and residency at these sites. Tracking such changes in near-time via UAV monitoring and, to the degree possible, anticipating such shifts using these data, can potentially help manage any potential conflicts between white sharks specifically (and other sharks more broadly) and beach users, fisheries, and other human uses of coastal environments. Such information will also improve our ability to track the efficacy of management efforts for such species and generate useful new information about their basic ecology.

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